

# Disproportionate admixture improves reintroduction outcomes despite the use of low-diversity source populations: population viability analysis for a translocation of the greater stick-nest rat

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## Keywords

conservation genetics; population viability analysis; reintroduction biology; admixture; translocation; *Leporillus conditor*; reintroduction; genetic diversity.

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Editor: Jeff Johnson

Associate Editor: Lisanne Petracca

Received 21 July 2021; accepted 20 July 2022

doi:10.1111/acv.12812

## Abstract

Translocation is becoming an increasingly important approach to threatened species conservation. Coupled with the knowledge that maximizing genetic diversity aids population establishment, the growing use of translocations can place unsustainable harvesting pressure on critical and vulnerable source populations. However, adaptive, genetically informed modelling tools such as Population Viability Analysis (PVA) can be used to predict translocation outcomes and optimize harvesting strategies. In this study, we use PVAs for the frequently translocated greater stick-nest rat (*Leporillus conditor*) to demonstrate the value of admixing founder populations for translocation, even when one source population is deemed genetically depauperate. This approach not only maximizes genetic diversity in the translocated population but reduces harvesting pressure on critical populations. Further, we show that admixed harvesting ratios can be skewed significantly towards the genetically depauperate population in order to further protect the critical population while still producing favourable outcomes, providing adequate founder numbers are used. As many threatened species are limited to fragmented and bottlenecked populations, these results are broadly applicable to the science of reintroduction biology, and demonstrate the value of PVAs for preliminary translocation planning and species management.

## Introduction

Australia's biodiversity faces a growing number of threats associated with land use changes, habitat loss and climate change, and many conservation managers have employed the practice of translocation, the facilitated movement of a species from one area to another, to combat extinctions and secure populations (Seddon, 2010; IUCN, 2013). Translocation programs face a number of practical challenges both pre- and post-release, including funding shortages, monitoring difficulties, predation, poor habitat quality and lack of baseline knowledge (Clayton *et al.*, 2014; Short *et al.*, 2019; Berger-Tal, Blumstein, & Swaisgood, 2020). Translocation success may often rely on sufficient numbers of genetically diverse individuals. Low founder numbers are associated with high failure rates due to the increased likelihood of

inbreeding and founder effects (Weeks *et al.*, 2011; McCoy *et al.*, 2014; Pacioni, Wayne, & Page, 2019). Similarly, low genetic diversity (either from founders or due to founder effect/post-release bottlenecks) also places translocations at risk of inbreeding depression or a lack of adaptive potential (Jamieson, 2011; Biebach & Keller, 2012; Ramstad *et al.*, 2013; Murphy *et al.*, 2019).

One of the guiding principles of translocations is to ensure that the source population is not negatively impacted by harvesting (IUCN, 2013). The increasing use of translocation programs combined with the importance of maximizing genetic diversity for population establishment and persistence means that source populations are under more pressure for conservation reintroductions (Armstrong & Seddon, 2008; Jamieson & Lacy, 2012; IUCN, 2013; Schäfer *et al.*, 2020). As many threatened species have already suffered genetic

bottlenecks (Jamieson *et al.*, 2008), it is paramount that harvesting for translocations does not jeopardize the persistence of small and/or genetically depauperate source populations. In some cases, harvesting for translocations can have negative effects on the source population, such as population declines, disruption of social networks, loss of allelic richness and reduced genetic diversity (Goldenberg *et al.*, 2019; Pacioni *et al.*, 2019; Furlan *et al.*, 2020; Morrison *et al.*, 2020). For example the sole remaining wild population of redfin blue eye, a small endangered fish endemic to Australia, lost a significant amount of genetic diversity when it was used as a source for eight translocations between 2009 and 2012, which the authors predicted would reduce adaptive potential in the long term (Furlan *et al.*, 2020). Harvesting of remnant populations of the banded hare-wallaby (*Lagostrophus fasciatus*) in Western Australia has been predicted to result in slower drought recovery within the remnant populations (White *et al.*, 2020a). Further, population models of threatened *Leiopelma* frog species in New Zealand revealed that harvesting more than 150 individuals from source populations would result in declines in allelic retention (Easton, Bishop, & Whigham, 2020).

One method which has proved helpful in mitigating the unsustainable harvesting of source populations and maximizing translocation success is adaptive and genetically informed population modelling (Dimond & Armstrong, 2007; Pacioni *et al.*, 2019). These approaches often employ a population viability analysis (PVA), that incorporate population-specific survival parameters, genetic data and environmental variability in order to model demographic stochasticity over time and, ultimately, predict loss of genetic diversity and extinction risk (Morris & Doak, 2002). PVAs can be used to predict the impact of harvesting on a source population, while simultaneously determining the likelihood of successful establishment of the translocated population. Well-designed PVAs can be useful in assisting conservation decision-making (Brook *et al.*, 2000; Chaudhary & Oli, 2020) and are considered to be of most value when comparing multiple scenarios to determine the most effective management strategy, rather than delivering an absolute result (Akçakaya & Sjögren-Gulve, 2000).

Here, we aim to incorporate genetically informed population models into planning the translocation of an endemic Australian rodent, the greater stick-nest rat (*Leporillus conditor*) (hereafter GSNR). Once widespread across the southern half of the continent, the combined pressures of land use changes and introduced predators and herbivores reduced the species to a single location (on the East and West Franklin Islands, near Ceduna, South Australia) by the 1930s (Copley, 1999a). GSNRs were listed as 'Endangered' under the IUCN assessment criteria in 1996 but have since been downlisted to 'Vulnerable' due to successful translocations to a captive colony at Monarto Safari Park in the late 1980s and several conservation areas since 1990 (Short *et al.*, 2019). All five of the surviving translocated populations have lower genetic diversity than the Franklin Islands individuals (White *et al.*, 2020b), possibly due to founder effects in the Monarto captive population, over- and under-representation of founders in translocated populations, and/or genetic drift after release. As the last remaining wild (and most genetically diverse)

population, the Franklin Islands GSNRs represent both an important source for translocation harvesting and a critical population that must be conserved for the ongoing viability of the species. Indeed, White *et al.* (2020b) identified the Franklin Islands as the most appropriate source population for future GSNR translocations but suggested that other populations with lower diversity were good candidates for cross-translocations. We therefore aimed to use PVAs to determine an optimized harvesting strategy for a new reintroduction of GSNRs on Dirk Hartog Island, Western Australia, whereby natural Franklin Island stock is supplemented with individuals from an additional established translocated population in order to improve the translocation outcome while minimizing negative effects on source populations. A former pastoral lease, the majority of Dirk Hartog Island was gazetted as a National Park in 2009. The Dirk Hartog Island National Park Ecological Restoration Project (or 'Return to 1616') aims to return the island to a similar ecological state to how it was when the first Europeans landed there in 1616 (Morris *et al.*, 2017). To achieve this, eradication programs were successfully enacted for sheep (*Ovis aries*; completed in 2010), goats (*Capra hircus*; 2017) (Heriot *et al.*, 2019) and feral cats (*Felis catus*; 2018) (Algar, Johnston, & Pink, 2019). With these key threats removed, the restoration project is now focused on the reintroduction of 13 locally extinct fauna species, including the GSNR (Algar *et al.*, 2020). Of highest importance for the GSNR translocation is establishing a viable, genetically diverse population via translocation, while minimizing harvesting impact on the critical population of the Franklin Islands.

## Materials and methods

### Study species & source populations

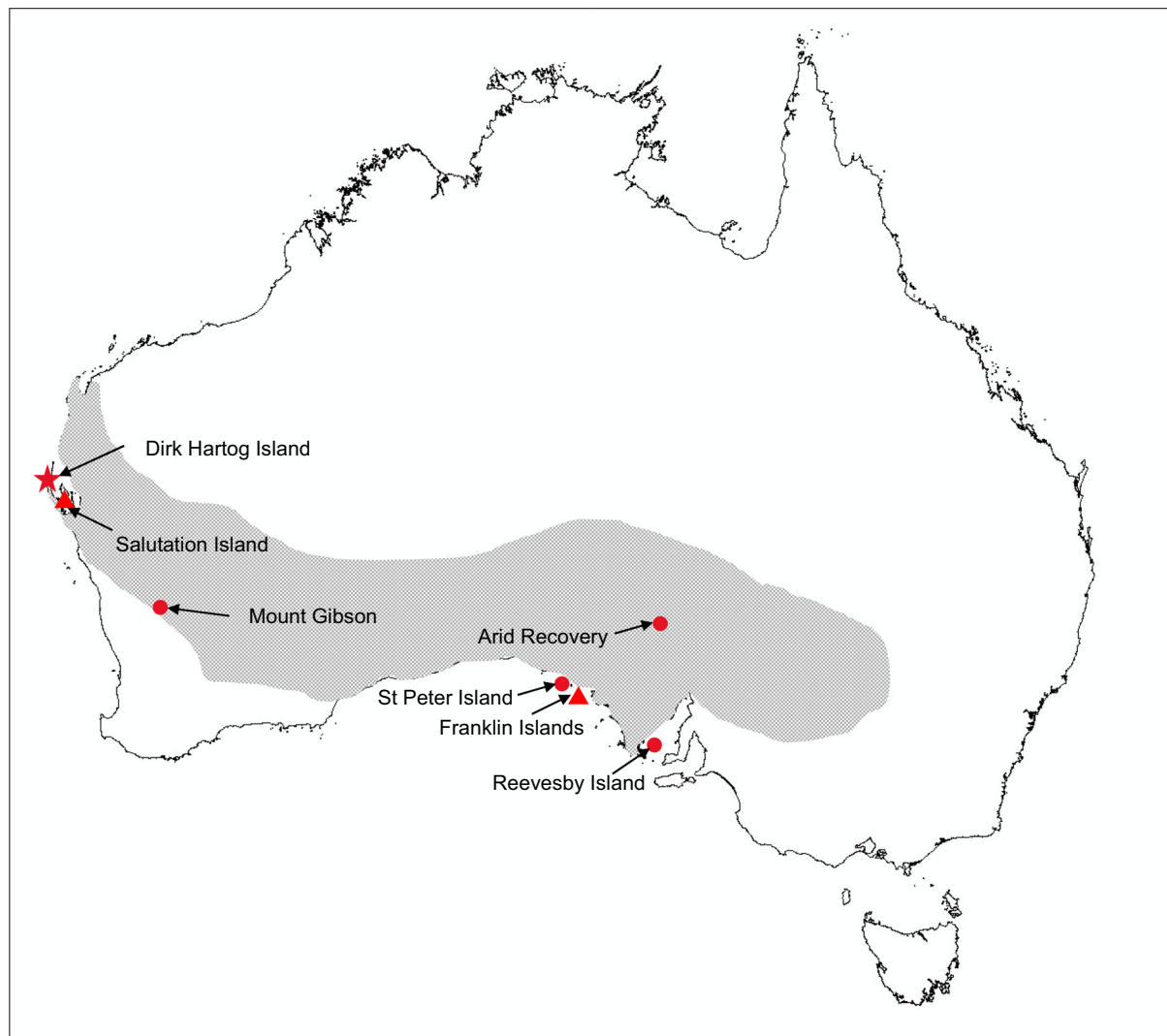
GSNRs are herbivorous, medium-sized rodents (180–450 g), feeding predominantly on perennial succulent plants and grasses (Robinson, 1975; Copley, 1988; Ryan, Moseby, & Paton, 2003; Procter, 2007). They build and inhabit communal stick nests, with females remaining in or nearby their natal nest while males disperse (Onley, *et al.* in review). Offspring are produced throughout the year, and once born remain attached to the mothers' teats until weaned (Le Souef, 1922; Copley, 1988). While the species has suffered a rapid decline due partly to predation by cats (*Felis catus*) and foxes (*Vulpes vulpes*), native predators include various species of owls, kites, snakes and other reptiles such as monitors (Pedler & Copley, 1993; Copley, 1999a; Moseby & Bice, 2004). Since the 1980s, the species has been the subject of multiple translocation attempts from the single remaining extant population on the Franklin Islands (harvested periodically from 1985 to 1998, and again in 2011 and 2019 (Page *et al.*, 2011; Short *et al.*, 2019; AWC, 2020)) and resulting captive breeding colonies with varying levels of success (see Short *et al.*, 2019). Successful translocations have occurred to Salutation Island (first release 1990) (Copley, 1999b), Reevesby Island (first release 1990) (Pedler & Copley, 1993), St Peter Island (first release 1993) (Copley, 1999b), Arid Recovery (fenced reserve) (first release 1998) (Moseby *et al.*, 2011) and Mt. Gibson (fenced reserve) (first release 2011) (Short *et al.*, 2019).

The source populations considered in our models were the Franklin Islands (East and West) and Salutation Island (Fig. 1). The Franklin Islands – East and West, 225 ha and 247 ha, respectively, and joined at low tide by a tombolo – populations were chosen because of their relatively high genetic diversity (White *et al.*, 2020b) and relatively large population size (1000–1200) (Robinson, 1975; Copley, 1988, 1999a). Genetic comparisons between West and East Franklin GSNRs indicate that the two island populations are weakly genetically distinct, with historical, but little contemporary, gene flow (White *et al.*, 2020b). We, therefore, estimated allele frequencies for West and East Franklins separately, with an equal harvesting ratio from both islands. Salutation Island (169 ha) was chosen because it has one of the largest populations of GSNRs (500–1000) (Copley, 1999b; Short *et al.*, 2019) and is closest to the release site, thereby minimizing travel time for animals. However, it has lower genetic diversity in comparison to other potential source sites (White *et al.*, 2020). Other extant GSNR populations were

not considered in this PVA due to either low population sizes (Arid Recovery) or difficult logistics for an overland translocation combined with reduced genetic diversity (Mt Gibson, St Peter Island, Reevesby Island) (White *et al.*, 2020).

### Translocation site

Dirk Hartog Island (DHI) lies at the western boundary of the Shark Bay World Heritage Area in Western Australia and at 63,300 ha in size it is the state's largest island. Avian predators of GSNRs, such as eastern barn owl (*Tyto javanica*) and Australian boobook (*Ninox boobook*), are infrequently encountered on DHI but known reptilian predators such as sand monitors (*Varanus gouldii*) are common and widespread (Moseby & Bice, 2004; Cowen *et al.*, 2018, 2020). The western quoll (*Dasyrurus geoffroii*) is locally extinct on DHI and is planned for translocation, once prey species have established populations predicted to be sufficiently large to withstand predation



**Figure 1** Map of current extant GSNR populations (red circles/triangles), proposed harvesting sites (red triangles), proposed translocation site (red star) and historic GSNR distribution (grey stipple).

by quolls. A trial reintroduction of western quolls to Arid Recovery found GSNRs were not frequently found in quoll scats (West, Tilley, & Moseby, 2020) but the sample size was low and observations at rat nest sites suggest it is likely that quolls represent a significant predator of stick-nest rats (Arid Recovery unpublished data). Furthermore, the successful establishment of GSNRs on DHI may lead to the increased presence of avian predators. Given the relatively large size of the island and extensive areas of suitable habitat, it is anticipated that the carrying capacity of GSNRs is significantly higher than any extant populations – we, therefore, estimate the carrying capacity as 10000 in our models. Successful establishment of GSNRs on DHI would therefore represent an important outcome for the recovery of the species (Woinarski, Burbidge, & Harrison, 2014).

## Genetic data

To incorporate genetic information into our PVA, we used single nucleotide polymorphism (SNP) data generated and first published by White *et al.*, 2020b. These data were generated using ddRAD-seq (Poland *et al.*, 2012) from ear or tail clips sampled from GSNRs trapped on the Franklin Islands in 1994 and on Salutation Island in 2016. SNPs with minor allele frequencies of <0.05 and more than 25% of missing data were removed (White *et al.*, 2020b). Demultiplexed and adapter-trimmed sequencing data are available from NCBI's sequence read archive (accession number: PRJNA389954) and more detailed methodology regarding sampling, library preparation and bioinformatic processing can be found in White *et al.* (2020b). We chose to not identify and remove close-kin from this dataset as we have no evidence that sampling on the Salutation and Franklin Islands was non-random with respect to relatedness (Waples & Anderson, 2017; Wang, 2018). Thus, we assume relatives are present in the sample in proportion to their prevalence in the populations and that our sample is representative.

The SNP dataset includes 8723 loci genotyped from 19 individuals from Salutation Island, and 15 individuals from the Franklin Islands (8 from East Franklin and 7 from West Franklin). From this total dataset, SNPs were randomly subset to 500 loci as a representative sample of the genetic diversity of each population, and an allele frequency table was created using the R package 'adegenet' (version 2.1.5) as per the requirements of the population modelling software.

Given that genetic samples from the Franklin Islands were collected in 1994, we first modelled a 25-year scenario of the Franklin Islands, including periodic harvesting for translocation, to ensure that no significant changes to allele frequency were likely to have occurred since sampling (Supplementary Information 1). Changes in genetic diversity were minimal (<0.005 expected heterozygosity) and were not considered significant enough to impact the outcome of PVAs.

## Population modelling

Population modelling software Vortex (version 10.3.6.0) was used to conduct the PVA (Lacy & Pollak, 2017). Vortex uses Monte Carlo simulations based on life history and population

parameters and incorporates uncertainty and stochastic events in order to predict demographic changes over time. Life-history parameters (Table 1) were developed using a combination of published literature and observations by conservation managers with decades of experience in GSNR husbandry. A full description of life-history parameters and rationale is detailed in Supplementary Information 2.

It should be noted that the GSNR is a relatively understudied species, and reported breeding and mortality rates vary between environments and conditions. Many reproductive rates and lifespan parameters available in the literature and used in this PVA are based on data from captive populations. While we may not expect wild populations to exhibit identical traits to captive animals, this information was still informative in developing realistic parameters, especially when releasing individuals into a new environment (such as DHI), where resources are not likely to be limiting in the medium term at least. Inevitably though, some uncertainty around the parameters used remains, and future PVAs for this species would benefit from further life-history studies, the chosen parameters were developed and validated in consultation with experienced practitioners specializing in the species in question. Furthermore, as the present study was a comparative analysis of harvesting techniques, absolute values are of less importance to our models than if they were to be used to predict the actual extinction risk of a real-life population, and more conservative estimates would cloud the central question of the influences of founder size and source population on translocation outcomes.

## Harvesting scenarios

Eleven different scenarios were modelled based on various harvesting numbers and source populations (Table 2). These scenarios were chosen to reflect the outcome of translocations using both single and multiple source populations with a range of founder numbers and ratios. Simulations (hereafter 'Sims') 1 and 2 and Sims 3 and 4 represent single source translocations with baseline ( $n = 120$ ) harvesting numbers and low ( $n = 64$ ) harvesting numbers respectively. Sims 5 to 7 represent multiple-sourced translocations with baseline, low and high ( $n = 240$ ) founder numbers. Sims 8 and 9 and Sims 10 and 11 are multiple-sourced translocations with skewed harvesting ratios, and baseline and high founder numbers respectively. The number of baseline founders was determined following Weeks *et al.* (2015), who advocated for sampling up to 50 unrelated individuals to capture 95% of genetic diversity. Accounting for related individuals and mortality following translocation, we chose 120 individuals (60 from each population) as our baseline harvest number. Survival during and after translocation was estimated at 70%, based on monitoring results from translocation of GSNRs to Mount Gibson (Short *et al.*, 2019). GSNRs have been observed to demonstrate some mortality during trapping and transportation, as well as post-release (Pedler & Copley, 1993; Short *et al.*, 2019). Each scenario was simulated 1000 times over a 50-year period. Carrying capacity (K) for DHI was estimated to be 10000 individuals, but this is likely to be conservative given the carrying capacity of Salutation Island (just 169 ha in size) appears to be 500–1000 individuals (Short *et al.*, 2019). Salutation Island's K and initial population size were set to 600 individuals (K. Branch, *pers. comm.* 2020).

**Table 1** Life-history parameters used in population modelling of GSNR translocation. EV denotes environmental variation. SD denotes standard deviation

Population Parameters		Male	Female	Sensitivity Testing Range (min-max)	Reference (see also Supplementary Information 2)
Species	Lethal equivalents	3.14		2–6.5	(Ralls, Ballou, & Templeton, 1988)
Description	Percent due to recessive lethal alleles	50			
	EV correlation between reproduction and survival	1			
	EV correlation among populations	0.8			
Reproductive System (monogamous)	Age of first offspring (years)	1	1		
	Maximum age of reproduction (years)	5	5		(Procter, 2007; K. Branch, <i>pers. comm.</i> 2021)
	Maximum lifespan (years)	5	5		
	Maximum number of broods per year	-	3		(Copley, 1988; K. Branch, <i>pers. comm.</i> 2020)
	Maximum number of progeny per brood	-	3		(Copley, 1988; Pedler & Copley, 1993; Copley, 1999a).
Reproductive Rates	Sex ratio at birth (%)	50	50		
	Adult females breeding (%)		$= (80 - ((80 - 50) * ((N/K)^2))) * (N / (1 + N))$		(Barclay <i>et al.</i> , unpublished data)
	SD in % breeding due to EV		8		
	Number of broods per year (% distribution)		0 broods – 0 1 broods – 10 2 broods – 60 3 broods – 30		(Copley, 1988; Pedler & Copley, 1993; Copley, 1999a).
	Number of offspring per brood (% distribution)		1 offspring – 52 2 offspring – 41 3 offspring – 7		(Copley, 1988)
Mortality Rates	Mortality from age 0 to 1 ( $\pm$ SD) (%)	36 $\pm$ 11	36 $\pm$ 11		(Barclay <i>et al.</i> , unpublished data)
	Annual mortality after age 1 ( $\pm$ SD) (%)	15 $\pm$ 4	16 $\pm$ 4	10–20	(Barclay <i>et al.</i> , unpublished data)
Catastrophes (drought)	Frequency (%)	16			(White <i>et al.</i> , 2020a)
	Reproduction (% of normal rate)	15			(Copley, 1999b; Barclay <i>et al.</i> , unpublished data)
	Survival (% of normal rate)	70			(Copley, 1999b; Barclay <i>et al.</i> , unpublished data)
Mate Monopolization	Males in breeding pool (%)	100		70–100	

Based on density estimates (Copley, 1988) and the fact that both East and West Franklin Islands are larger than Salutation Island, we estimated K of each of the Franklin Islands to be 800, but the current population size was set to 500 individuals on East and West respectively.

## Data analysis

All Vortex outputs were collated using the package ‘vortexR’ (Pacioni & Mayer, 2017) in R Studio (version 4.0.2). Post hoc analysis of translocated populations was conducted using the package ‘stats’ (version 4.0.2) (R Core Team, 2020). Since data were determined to be abnormally distributed, we conducted a

non-parametric analysis of variance (ANOVA; Kruskal–Wallis test) model followed by a pairwise Wilcoxon rank sum test of all 1000 iteration outputs for population size, expected heterozygosity, inbreeding and probability of extinction averaged over each year of the PVA in order to test for significant differences between translocation scenarios. Finally, to determine relative impact to founder populations, expected heterozygosity, inbreeding coefficient and size of each population were compared at years 1 and 5 under each scenario.

While a reasonable amount of data on breeding and survival rates was available for this species (strengthened by consultation with leading practitioners), it is possible that variation to breeding and survival rates may occur in the

**Table 2** Harvesting scenarios used in population modelling for GSNR translocation to Dirk Hartog Island. Symbols denote the following; \*single source, †multiple source, ‡low founder numbers, §baseline founder numbers, ¶high founder numbers, #skewed harvesting ratio

Scenario	Harvest strategy (50:50 sex ratio)	Total <i>n</i>
Sim 1*§	60 from Franklin Islands in Year 1; 60 from Franklin Islands in Year 2	120
Sim 2*§	60 from Salutation Island in Year 1; 60 from Salutation Island in Year 2	120
Sim 3*‡	32 from Franklin Islands in Year 1; 32 from Franklin Islands in Year 2	64
Sim 4*‡	32 from Salutation Island in Year 1; 32 from Salutation Island in Year 2	64
Sim 5†§	60 from Salutation Island in Year 1; 60 from Franklin Islands in Year 2	120
Sim 6†‡	32 from Salutation Island in Year 1; 32 from Franklin Islands in Year 2	64
Sim 7†¶	120 from Salutation Island in Year 1; 120 from Franklin Islands in Year 2	240
Sim 8†§#	40 from Salutation Island in Year 1; 80 from Franklin Islands in Year 2	120
Sim 9†§#	80 from Salutation Island in Year 1; 40 from Franklin Islands in Year 2	120
Sim 10†¶#	200 from Salutation Island in Year 1; 40 from Franklin Islands in Year 2	240
Sim 11†¶#	180 from Salutation Island in Year 1; 60 from Franklin Islands in Year 2	240

population following reintroduction. We, therefore, used sensitivity testing in Vortex to determine the impact of variation in three key parameters on population establishment, represented by probability of extinction, inbreeding, heterozygosity and population size. These parameters were lethal equivalents, % males in the breeding pool and % mortality after age 1 (Table 1). Sensitivity testing was performed on the source population of East Franklin Island, due to computing restraints encountered when attempting sensitivity testing on multiple populations with extremely large carrying capacity (e.g. 10000 individuals on DHI). The results of the sensitivity tests were analysed using a binomial logistic regression, with all parameters of the sensitivity test included as predictor variables (Rayner *et al.*, 2021).

## Results

### Population growth

All scenarios, regardless of founder source population, reached a stable population size just below the estimated carrying capacity within 35 years of translocation to DHI (Fig. 2a).

### Genetic diversity

Scenarios resulting in the lowest expected heterozygosity were those with single source populations and low founder numbers (Sim 3 Franklins only and Sim 4 Salutation only),

followed by single source populations with baseline founder numbers (Sim 1 Franklins only and Sim 2 Salutation only) (Fig. 2b). Multiple-sourced translocations with low numbers performed better (Sim 6), but not as well as multiple source populations with baseline and high numbers (Sims 5, 7, 8, 9, 10 and 11), even when the ratios were skewed. Whether the harvesting was skewed towards the critical population (Franklins) or not had little impact on the outcome.

### Inbreeding

Inbreeding coefficients for each scenario were relatively similar at the beginning of the translocation, with the exception of single-sourced translocations from the Franklin Islands (Sims 1 and 3), which had a higher inbreeding coefficient than all other scenarios initially. By year 50, however, single-sourced populations (Sims 1 to 4) and the population with two sources but low founder numbers (Sim 6) had the highest degree of inbreeding, while all others remained relatively constant (Fig. 2c).

### Probability of extinction

In 1000 iterations, all scenarios had a low probability of extinction ( $\leq 1.5\%$ ). Of these scenarios, single-sourced translocations with low founding numbers (Sims 3 and 4) had the highest probability of extinction (Table 3).

### Statistical differences

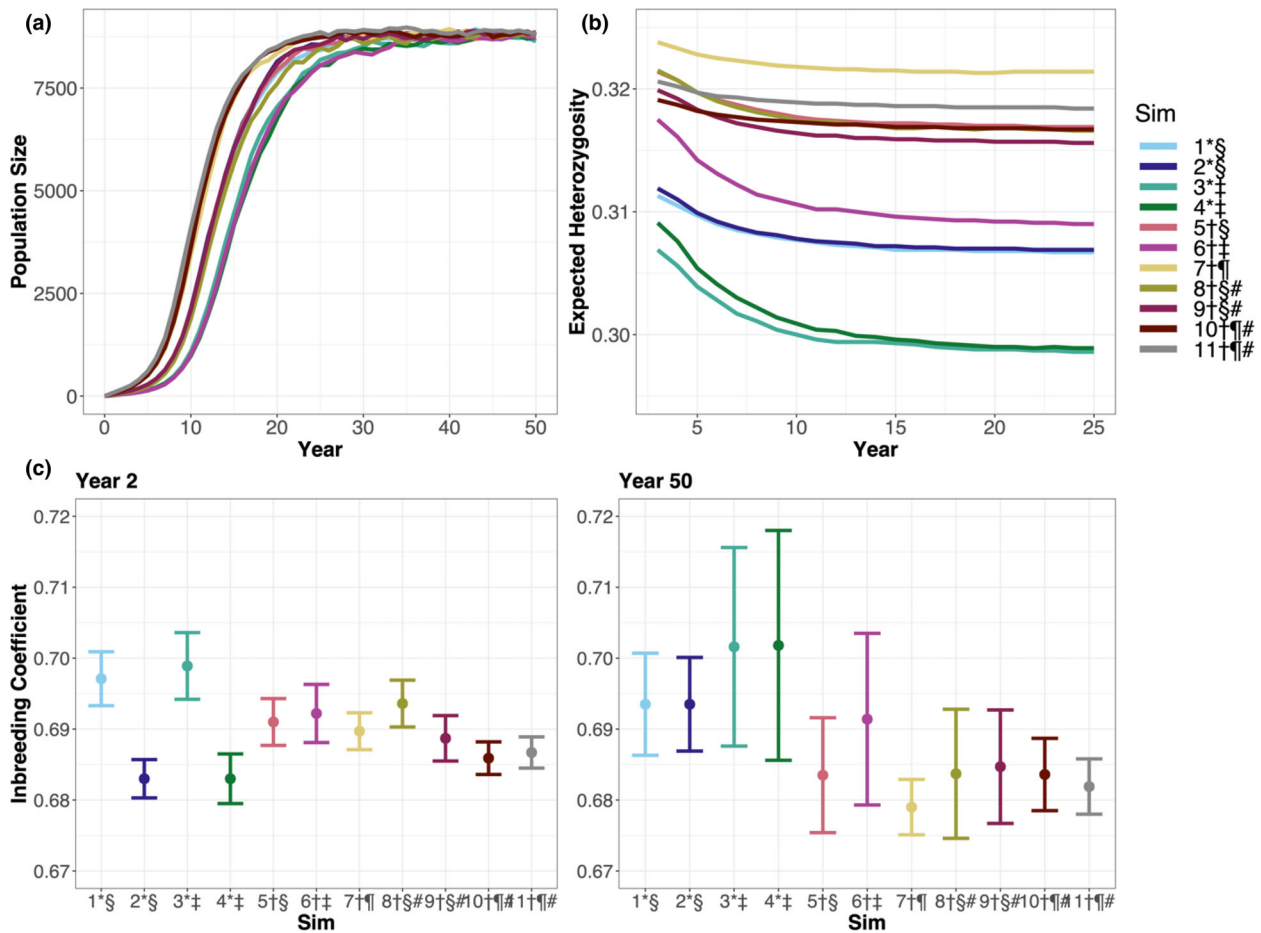
Non-parametric ANOVA models of four key outputs – population size, expected heterozygosity, inbreeding coefficient and probability of extinction – averaged across 1000 iterations for each year of the 50-year PVA per scenario revealed a significant difference between scenarios in outcome for all parameters (Table 4).

Pairwise testing revealed that differences in inbreeding coefficients and expected heterozygosity were statistically significant between all models except Sims 1 and 2, Sims 3 and 4 and Sims 8 and 10 (Supplementary Information 3). Sims 5 and 10 were not significantly different in terms of inbreeding coefficient, but were significantly different in expected heterozygosity. Single source populations with low and baseline founder numbers had therefore higher inbreeding values and lower expected heterozygosity than all multiple-sourced translocations, even when low founder numbers were used.

Sensitivity testing did not reveal significant impacts of variation of lethal equivalents, % males in the breeding pool or % adult mortality rates on GSNR populations (Supplementary Information 4). Of the life-history parameters we examined, % mortality after age 1 appeared to have the strongest effect on heterozygosity and extinction probability, however, these effects were not statistically significant.

### Impact of harvesting on source populations

Harvesting did not appear to have any impact on the source populations long term, regardless of numbers removed from



**Figure 2** (a) Population size, (b) expected heterozygosity as a measure of genetic diversity, and (c) comparison of inbreeding coefficients (mean and SD) of greater stick-nest rats at Dirk Hartog Island under each scenario over 50 years. Symbols denote the following; \*single source, †multiple source, ‡low founder numbers, §baseline founder numbers, ¶high founder numbers, #skewed harvesting ratio.

the population; 10 years after harvest, expected heterozygosity for all founding populations and harvesting scenarios decreased  $<0.003$ , inbreeding values increased by  $<0.002$ , and population size remained constant. Values for these outputs for each founder population at years 1, 5 and 10 of each harvesting strategy are detailed in Supplementary Information 5.

## Discussion

PVAs are a valuable tool in conservation planning, management and decision-making (Chaudhary & Oli, 2020). Population modelling of 11 different scenarios for the translocation of GSNRs to DHI revealed that sourcing founders from multiple populations improved the outcome of reintroductions in comparison to single-sourced translocations. In translocated populations with multiple sources, inbreeding coefficients were, on average, lower, while expected heterozygosity was higher than single-sourced populations. Inbreeding values for single-sourced translocations were higher initially, but this is likely due to a Wahlund Effect resulting from the slight genetic divergence between the East and West

Franklins (Hartl, 1988; Frantz *et al.*, 2006). Founder numbers also contributed to the outcome of translocations; where multiple sources were used, those scenarios with higher harvesting rates produced higher genetic diversity and lower inbreeding in the long term. Skewing the harvesting strategy towards either source did not appear to change the outcome of the translocation, particularly when overall founder numbers were high. Interestingly, impact on source populations did not appear to vary between harvesting strategies, regardless of number of individuals taken in the scenarios we tested. Sensitivity testing on variable values of mate monopolization, lethal equivalents, and % mortality after age 1 did not reveal a significant impact on population parameters of interest. This may be due to the large population sizes and carrying capacities of the populations considered within this study.

## Value of skewed admixture for translocations

The results of our PVA support previous studies indicating that sourcing founder individuals for translocation programs from multiple populations not only reduces the risk of

**Table 3** Year and probability of extinction of Dirk Hartog Island stick-nest rat population for each PVA scenario over 50 years and 1000 iterations. Symbols denote the following; \*single source, †multiple source, ‡low founder numbers, §baseline founder numbers, ¶high founder numbers, #skewed harvesting ratio

Scenario	Years population went extinct	Probability of extinction
Sim 1*§	11, 12, 18, 27	0.4%
Sim 2*§	9	0.1%
Sim 3*‡	6, 8, 10, 12, 13, 14, 18, 20, 26, 27	1.5%
Sim 4*‡	5, 7, 8, 10, 11, 12, 16, 23	0.9%
Sim 5†§	6, 7, 9, 15	0.4%
Sim 6†‡	9, 10, 12	0.5%
Sim 7†¶	21	0.1%
Sim 8†§#	11, 12, 17, 20	0.5%
Sim 9†§#	7, 12	0.2%
Sim 10†¶#	-	0%
Sim 11†¶#	-	0%

**Table 4** P-values of output parameters for all PVA scenarios determined by non-parametric ANOVA models

	Population size	Expected heterozygosity	Inbreeding Coefficient	Extinction Probability
P-value	<0.001	<0.001	<0.001	<0.001

placing harvesting pressure on critical source populations but can also improve the outcome of the reintroduction as a whole (Biebach & Keller, 2012; Wirtz *et al.*, 2018; McLennan *et al.*, 2020). Both genetic diversity and levels of inbreeding were significantly improved in the DHI GSNR population when founders were sourced from both Salutation Island and the Franklin Islands, in comparison to single-sourced translocations from either location. This pattern has been observed in real-world translocations of other taxa, such as sea otter (*Enhydra lutris*) (Bodkin *et al.*, 1999; Albrecht & McCue, 2010; Robinson *et al.*, 2021), Tasmanian devils (*Sarcophilus harrisii*) (McLennan *et al.*, 2020) and bighorn sheep (*Ovis canadensis*) (Olson, Whittaker, & Rhodes, 2013; Jahner *et al.*, 2019; Poirier *et al.*, 2019). The improved genetic diversity outcomes in the admixture scenarios are particularly interesting given that Salutation Island is considered a genetically depauperate population (White *et al.*, 2020b), demonstrating that even populations of low diversity can act as valuable sources for reintroductions when combined with other populations. Further, skewing the proportion of animals harvested towards either the Franklin Islands or Salutation Island did not appear to significantly alter the outcome of the translocation. Skewing towards Salutation Island when founder numbers were high (Sim 10) had similar outcomes to Sim 8, where there was a skew towards the Franklin Islands. This key finding indicates that the critical population of GSNRs can be protected in future translocations by admixing with a high proportion of animals from the genetically depauperate population of Salutation Island.

Although we found little difference in the likelihood of population persistence/extinction or population growth across the simulated scenarios, admixture may still improve population sustainability for the DHI GSNRs through positive fitness effects. Our simulations modelled inbreeding depression through the inclusion of a number of lethal equivalents equal to the average for diploid organisms. It is possible that the true number of lethal equivalents in the GSNR populations is higher than this average – for example GSNRs have been observed to suffer from cataract formation in both captivity and the wild, though it remains unknown whether this is associated with genetics or diet (Robertson, 2007). If this is the case, the probability of positive fitness effects in admixed individuals through the reversal of inbreeding depression (i.e. genetic rescue, (Frankham, Ballou, & Briscoe, 2010; Frankham, 2015; Whiteley *et al.*, 2015)), may also increase. This result has been demonstrated in practice for several taxa, including genetic rescues of the South Island robin (*Petroica australis*) and the mountain pygmy possum (*Burramys parvus*) (Heber *et al.*, 2013; Weeks *et al.*, 2017). Future investigation on the potential fitness benefits associated with translocation would be valuable for the management of GSNRs and other threatened species.

### Role of founder numbers in translocation success and source population impacts

Our models support previous findings that founder numbers play a role in conservation outcomes (Weeks *et al.*, 2011; McCoy *et al.*, 2014; Pacioni *et al.*, 2019). While scenarios with multiple source populations performed better overall, of these scenarios, those with higher founder numbers appeared to be the most successful in terms of retaining genetic diversity and minimizing inbreeding over time. The positive impact of increased founder numbers has been reported on many times in recent years (Griffith *et al.*, 1989; Lee *et al.*, 2020; Furlan *et al.*, 2020; White *et al.*, 2020a), while low founder numbers have been attributed to a number of failed reintroductions, including several translocations of woylies (brush-tailed bettong) (*Bettongia penicillata*) where the genetic effects of small founder numbers were further compounded by predation and drought (Fischer & Lindenmayer, 2000; Mawson, 2004; Germano & Bishop, 2009; Short, 2009). However, given the importance of conserving critical source populations, a trade-off must be reached between optimizing translocation outcomes and minimizing impacts to existing populations. Although we found no noticeable impact of higher harvesting numbers on source populations, detrimental effects of overharvesting have been observed (Goldenberg *et al.*, 2019; Furlan *et al.*, 2020), and the possibility of this occurring should be avoided where possible. Our PVAs showed similar genetic outcomes between Sims 5 and Sims 8 and 9, wherein 120 total founders were used in both, but the harvesting ratios from Salutation Island and the Franklin Islands were 50:50 and ~70:30/30:70 respectively. Further, increasing the founder numbers to 240 individuals but heavily skewing the



harvesting towards the genetically depauperate population (Salutation Island) as in Sims 10 (~85:15) and 11 (75:25) also produced favourable results. Our results indicate that managers may consider alleviating harvesting pressure on critical source populations by heavily supplementing translocations with individuals from other, less diverse, populations, as long as a high number of founders are used.

### Limitations and considerations

While PVAs are a valuable, and often highly accurate, method of predicting translocation outcomes (Brook *et al.*, 2000), they are not infallible. The single-species focus and inability to account for all survival factors mean that there will always be some uncertainty associated with the results. Here, all scenarios produced a very low risk of extinction ( $\leq 1.5\%$ ). In reality, the likelihood of translocation failure is far higher; a study of Australian macropod translocations found between 51% and 61% of translocations to be successful, depending on the criteria (Clayton *et al.*, 2014). Similarly, Short (2009) collated 380 translocations of 102 Australian species and identified 54% as successful. For GSNR translocations specifically, the success rate is 40% (Short *et al.*, 2019). It is therefore unlikely that the extinction probability for the DHI translocation of GSNRs is as low as our models predict due to the inability to include all potential risk factors, and the values should be considered as relative, rather than absolute (Akçakaya & Sjögren-Gulve, 2000). Furthermore, understudied species often have limited demographic data available; for example in our analysis, we assume that all males have equal breeding success. While no data currently exist for GSNRs that suggest otherwise, it should be acknowledged that the potential for unequal reproductive success rates may have genetic impacts on translocated populations. However, in this comparative analysis of translocation scenarios, we feel it is unlikely that greater certainty around variation in male breeding success would result in any changes to our conclusions. The results of the sensitivity testing support this.

### Conclusions and recommendations

Our models show that skewed harvesting ratios towards genetically depauperate source populations can produce favourable outcomes following translocation, highlighting a promising approach to protect critical populations without jeopardizing reintroduction programs. These results are broadly applicable, as many native species have suffered range contractions and genetic bottlenecks similar to those of greater stick-nest rats. Disproportionate admixed harvesting, rather than a single-source approach, has the potential to lessen harvesting impacts on the genetic diversity of critical naturally occurring populations, even if one source population is genetically suboptimal. These findings are a timely contribution to the growing science of reintroduction biology. Managers working with other species should take a case-by-case approach and consider species-specific life-history parameters such as reproduction rates, brood size and

breeding age to determine appropriate founder numbers. Tailored, species-specific PVAs are a valuable tool for incorporating this information into conservation planning, and should be used to assist with decision-making for future reintroductions.

### Acknowledgements

The authors acknowledge and thank Shaun Barclay, William Sherwin and Kim Branch for providing data incorporated into this analysis. We also thank Jeremy Austin and two anonymous reviewers for constructive feedback on the paper, Aline Gibson Vega for assistance with the sensitivity analysis and Kym Ottewell for assistance in preparing genetic data for input into Vortex. Open access publishing facilitated by The University of Adelaide, as part of the Wiley - The University of Adelaide agreement via the Council of Australian University Librarians.

### Author contributions

IO and SC conceived the ideas and designed the methodology. PC and KM contributed to the methodology and data. LW provided genetic data and contributed to the methodology. IO led the writing of the paper. All authors contributed to developing the paper, editing drafts and provided final approval for publication.

### Funding

This research was supported by the University of Adelaide and funded by the following organizations and awards: Arid Recovery, Australian Government Research Training Program Scholarship, Nature Foundation South Australia Grand Start Grant (Grant No. 2019-07), Biological Society South Australia/Nature Conservation Society of South Australia Conservation Biology Grant and Field Naturalists Society of South Australia Lirabenda Endowment Fund Research Grant. The Dirk Hartog Island National Park Ecological Restoration Project (Return to 1616) is being undertaken by the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA) and is funded by the Gorgon-Barrow Island Net Conservation Benefits Fund.

### Conflicts of interest

The authors declare no conflicts of interest.

### Ethics approval

All samples were collected and sequenced as part of a previous study (White *et al.*, 2020).

### Availability of data and material

All de-multiplexed raw sequencing data are available from NCBI's sequence read archive (accession number: PRJNA389954).

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## Supporting information

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

**Appendix S1.** Supplementary Information for population viability analyses of translocated greater stick-nest rat populations.