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RESEARCH ARTICLE

Inferring inter-colony movement within metapopulations of yellow-footed rock-wallabies using estimates of kinship

Deane A. Smith[1,2,3] · **Mark R. Lethbridge**[4] · **Benjamin L. Allen**[1,5] · **Rose L. Andrew**[3]

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Abstract

Understanding the exchange of individuals between wildlife populations, particularly those with naturally fragmented habitats, is important for the effective management of these species. This is of particular consequence when the species is of conservation concern, and isolated populations may be lost due to pressures from predation or competition, or catastrophic events such as wildfire. Here we demonstrate the use kinship and population structure analysis to show potential recent movement between colonies in metapopulations of yellow-footed rock-wallaby (*Petrogale xanthopus* Gray 1854) at two sites in the Grey Range of Queensland, and at four sites in the Gawler Ranges of South Australia. These colonies are also compared to a single colony from the Flinders Ranges, a connected landscape of rock-wallaby habitat. Using reduced representation next-generation sequencing, we acquired and filtered a set of ~ 17,000 single-nucleotide polymorphisms to examine population genetic variation, structure and relationships within populations, and also identify putative migrants. Initial STRUCTURE analysis re-confirmed each population should be considered separately. Tests of population genetic variation identify several colonies appearing to be experiencing genetic erosion, also with low calculated effective population sizes ($N_e = 4.5–36.6$). Pairwise comparisons of individual relatedness (relatedness coeffiecients; *r*) implied several contemporary movement events between colonies within both the Gawler and Grey Ranges ($r > 0.125$), which was then affirmed with tests for putative first generation migrants. These results are of particular note in South Australia, where threat abatement (management of key predators and competitors) may facilitate dispersion. Additionally, in Queensland, colonies are separated by anthropogenic barriers: predator exclusion fencing designed to exclude dingoes (*Canis familiaris*) from grazing land, which may hinder dispersal. This work highlights the usefulness of population genetics to inform management outcomes in wildlife, in this case, highlighting the need for threatened species management at the landscape level.

Keywords Cluster fence · Conservation · Exclusion fencing · Reduced representation sequencing · Rock-wallaby · Threatened species

Introduction

A metapopulation is the group of spatially distinct populations of the same species connected by movement of individuals (Wells and Richmond 1995). For species in such systems, movement behaviours are essential, as they insure against risk of extinction from negative pressures (such as predation, competition and catastrophic events; Holyoak and Lawler 1996), and protect against the negative genetic effects of inbreeding (Olivieri et al. 1995; Perrin and Mazalov 1999). Movement behaviour also gives rise to potential recolonization of "empty" sites or the formation of new populations at suitable sites (Hanski 1998). Understanding such movement is therefore critical for effective species management.

✉ Deane A. Smith
deane_smith@me.com

1 Institute for Life Sciences and the Environment, University of Southern Queensland, Toowoomba, QLD 4350, Australia

2 New South Wales Department of Primary Industries, Armidale, NSW 2351, Australia

3 School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia

4 College of Science and Engineering, Flinders University, Adelaide, SA 5001, Australia

5 Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth 6034, South Africa

For timid and reclusive species, it can be hard to determine whether individuals are moving between isolated colonies. In these species, the use of genetic techniques to identify the relationships between individuals of a population could be used to infer recent movement events, and be extremely useful to understanding barriers to dispersal (Escoda et al. 2019).

The yellow-footed rock-wallaby (*Petrogale xanthopus* Gray, 1854) is a threatened macropod found in the semi-arid zone of Australia. There are two subspecies of *P. xanthopus*: *P. x. xanthopus* is found in several remote mountain ranges of South Australia (SA; Threatened Species Scientific Committee 2016a), and also a single population in New South Wales (NSW; Lim and Giles 1987), and *P. x. celeris* is found in the Grey Range in Queensland (QLD; Threatened Species Scientific Committee 2016b). The distribution of both subspecies is assumed to have significantly decreased since European settlement (Copley 1983). Rock-wallabies (*Petrogale* spp.) have high habitat specificity, only occupying complex rocky habitats (see Gordon et al. 1993; Lim and Giles 1987; Smith and Allen 2021; Telfer et al. 2008). As a result of this habitat specificity, suitable rock-wallaby habitat is naturally fragmented, forming metapopulations (Lethbridge et al. 2019; Lethbridge and Strauss 2015; Murray et al. 2008; Ruykys and Lancaster 2015). Primary evidence of movement between colonies of *P. xanthopus* is surprisingly scarce given the quantity of literature describing the species, particularly in South Australia, though it is not completely absent. A study using tracking collars and ear-marked rock-wallabies in Queensland found evidence of a single movement event over 36 months (Sharp 2002), and another (also with collars) revealed several long distance transient movements of released captive-bred rock-wallabies (Lapidge 2001). The latter also inferred several dispersal events from wild rock-wallabies that were trapped at the previously empty reintroduction sites.

The limitations of radio tracking and capture-mark-recapture to detect all movement behaviours is evident—both rely on the captured individual moving *during* the study period. In addition to this, the ability to detect or recapture individuals that have moved is further limited by the distance of the movement. Detecting long distance movements, such as natal dispersal, with such techniques is understandably infrequent for *P. xanthopus*. The use of genetic data would mitigate both these shortcomings, as it would detect any contemporary movement event between colonies at any distance, as long as two related individuals are sampled. To this end, a recent study assessing the genetic variation of *P. x. xanthopus* identified 13 putative first generation migrations of between 2 and 60 km over connected habitat in the Flinders ranges using population assignment methods based on the individuals' genetic structure gained through microsatellite analysis (n = 194, Potter et al. 2020). Potter et al. (2020) built on earlier genetic analysis of dispersal (also using microsatellite analysis), that had concluded that yellow-footed rock-wallabies rarely move between colonies, even within connected habitat (Pope et al. 1996), although the methods employed were reliable, this earlier study was limited by sample size. Advancements in genetic technologies such as next-generation sequencing (NGS), and the development of more robust methods of determining kinship values also provides greater confidence in the results of kinship analysis. This confidence can allow for more reliable inferences to be drawn between kinship values and the probability of a contemporary movement between colonies (Escoda et al. 2017). These early *P. xanthopus* studies were also performed without or with limited threat abatement practices (effective management of key predators and feral competitors) in place, which may be critical to allow rock-wallaby movement behaviours (Pope et al. 1996, 1998).

While the recent publications on the same species are highly informative, a greater understanding of *P. xanthopus* inter-colony movement is needed to understand potential metapopulation dynamics for the purpose of informing management of the species. The distribution of *P. x. celeris* has recently (2016) been heavily subdivided by agricultural exclusion fences (Smith et al. 2020c). While the fences may ultimately be of a benefit to the species' long term persistence (Smith et al. 2020c), exclusion fencing has the potential to isolate colonies, which may lead to genetic consequences (Smith et al. 2020a, b, c). The conservation of *P. x. xanthopus* may also be reliant on an understanding of inter-colony relations and connectivity. Predation from red foxes (*Vulpes vulpes*), competition with feral goats (*Capra hircus*) and catastrophes can all contribute to extinction risk of the entire metapopulation by restricting dispersal behaviours between colonies. Understanding the interchange of the individuals between sites would give insight into the effect of pest species control on metapopulation dynamics and the utility of broad scale pest management in the effective conservation of *P. xanthopus*.

Given the cryptic nature of the species, its disjunct distribution, and threats facing both subspecies, here we use *P. xanthopus* to demonstrate the usefulness of reduced representation next-generation sequencing to study metapopulation movement, population structure and how outcomes from such studies can help inform threatened species management. Our objective is to assess if there has been recent movement of *P. xanthopus* between geographically distinct colonies, using population structure analysis, pairwise relatedness coefficients and identification of first-generation migrants. We then discuss the value of kinship analysis to infer species movement within potential metapopulations, and how this analysis affects the management of *P. xanthopus*, both in South Australia and Queensland.

Materials and methods

Study sites

Petrogale xanthopus were trapped and ear biopsies were obtained at four sites in the Gawler Ranges, and one site in the Flinders Ranges (South Australia) by Lethbridge and Andrews (2014) and later Lethbridge (*unpublished report*), under a S.A. Wildlife Ethics approval: S23997-19, and at two sites in the Grey Range, near Quilpie in central-western Queensland, under a University of Southern Queensland Animal Ethics approval: USQ-17REA011 (Fig. 1). The Gawler Ranges (GWL), the Flinders Ranges (FLD) and the Grey Range (GRY) will hereafter be referred to as 'populations'. Trapping sites within populations will be referred to as 'colonies'. Trapping in the Flinders and Gawler Ranges (South Australia) took place from August 2012 to September 2016, and in the Grey Range (Queensland) in 2018 and 2019. The two colonies in Queensland are separated by 8 km, including approximately 5 km of unsuitable habitat. Historically this gap between the two colonies was thought to be traversable by *P. xanthopus*, but an exclusion fence was erected 2 years prior to sampling to alleviate the pressures of wild dog predation on sheep grazing properties. The colonies in the Gawler Ranges are not disrupted by fencing but vary in distance from Yandinga, a theorised source/refuge population (Fig. 1). The Gawler Ranges populations were also historically disrupted by exclusion fencing (circa 1920s), but spatial and temporal information on this fencing is minimal/non-existent.

Trapping, sampling, extraction and sequencing

Rock-wallabies were trapped using established methods in soft-walled treadle cage. A tissue biopsy was removed from each rock-wallaby's ear using a 3 mm punch. The sample is taken from the opposite ear to an ear-tag employed for potential future visual identification in the field. Morphometric data was also collected before each rock-wallaby was microchipped for identification on recapture. Tissue samples were placed in Longmire's buffer solution (Queensland samples—Longmire et al. 1997) or 100% ethanol (South

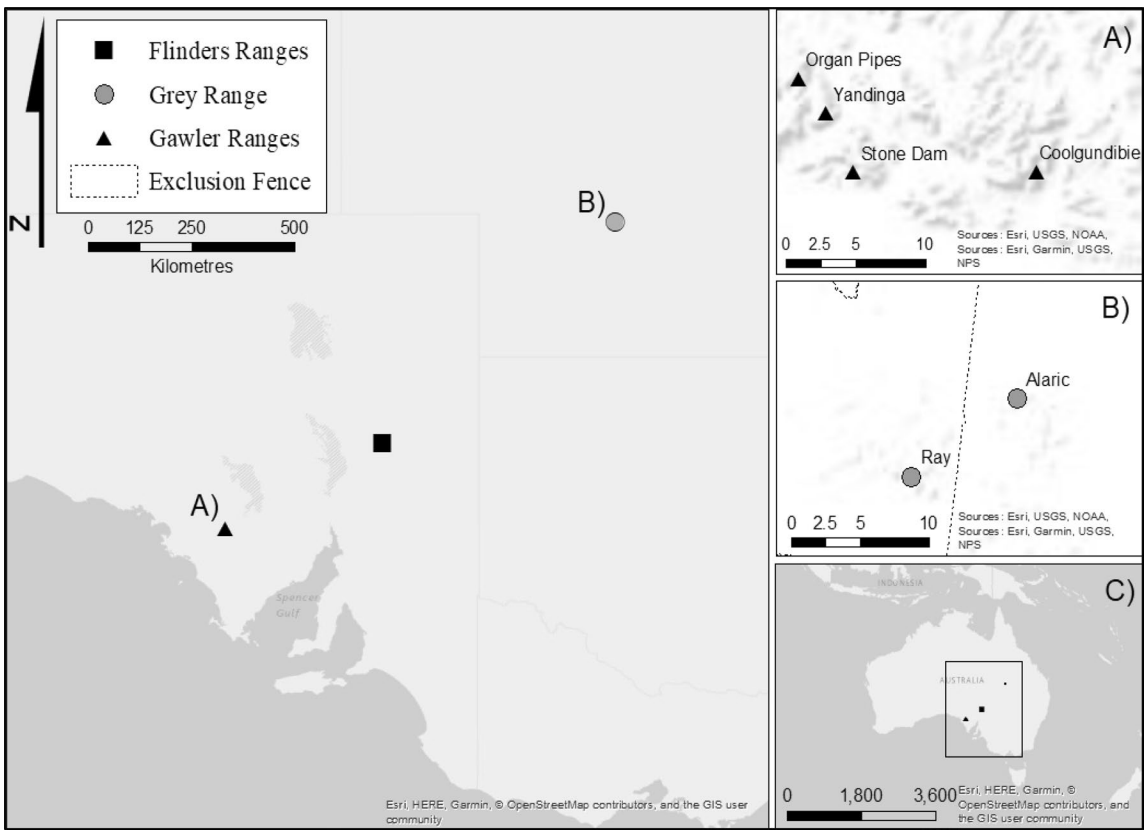

Fig. 1 Yellow-footed rock-wallaby trapping sites. The main map displays the locations of the Gawler Ranges, Flinders Ranges and Grey Range. Inset **A** shows the locations of the 4 colonies trapped in the Gawler Ranges (SA). Inset **B** shows the location of 2 colonies trapped in the Grey Range (QLD). Inset **C** shows the context of the main map within the broader global region. Waukawoodna Gap (SA; the only trap site within the Flinders Ranges) is marked by a solid square (■) on the main map

Australian samples) and stored in a cool place until extraction. DNA was extracted from 95 samples (Table 1) using a salt-based ethanol extraction (Ebert and Andrew 2014) and quantified on a Qubit™ Flurometer and quality controlled using a NanoDrop™ 3000. One sample from the Flinders Ranges site was not of high enough quality for accurate sequencing (based on quality control steps) and therefore was removed from the samples sent for sequencing. Samples were then sent to Diversity Arrays Technology (DArT P/L) in Canberra, ACT for sequencing via their DArTseq service (Kilian et al. 2012). The protocol involves technical replicates, which provides an empirical measure of the repeatability of the resulting loci. DArT conducted filtering and reference-free clustering of reads, followed by genotyping using their proprietary analysis pipeline (see https://www.diversityarrays.com). Three samples did not meet DArT's internal quality control thresholds, and therefore data was not returned for these samples.

Data filtering

The single-nucleotide polymorphism (SNP) data returned by DArT was first explored in `R` (version 3.6.2) using the `dartR` v1.1.11 package and following the workflow suggested in the package documentation (Gruber et al. 2019a, b). The reports generated by this initial analysis were used to inform filtering thresholds (Tables S1–S5, Figs. S1, S2). The primary dataset was later subdividedbased on population structure results. This was completed to look for hierarchical structuring (see Results) and for further analysis of kinship (see *(v) Coefficients of relationship, relatedness networks*). As these subsets reflect the source populations, these datasets were named after the population. The filtered, total dataset will be referred to as the primary dataset (Table 1). Monomorphic loci are automatically removed during this sub-setting. Data were first filtered for the average repeatability of each locus (loci with repeatability > 0.95 were kept), and the call rate by locus (> 0.95) and by individual (> 0.90). The data was then filtered to remove over-split loci (< 0.2 Hamming distance), and for observed heterozygosity greater than 0.6. Finally, loci with minor allele frequencies lower than 0.05 were removed before all metrics were recalculated. Filtering thresholds were chosen based on the recommendations of Gruber et al. (2019b) and O'Leary et al. (2018).

Relatedness estimates range from 0 (totally unrelated individuals) to 1 (clones). Preliminary data exploration identified four samples with high pairwise relatedness to other samples, which is not consistent with outbreeding and random mating. These values may have arisen in a number of ways: monozygotic twinning, duplicate sampling or pipetting error prior to sequencing. Twins are known to occur in *Petrogale assimilis* (Spencer and Marsh 1997), and the twinning rate in *Macropus* is low, but non-zero (Inns 1980; Norbury 1986; van Oorschot and Cooper 1989). Additionally, pouch young have DNA samples taken, but are not ear tagged/microchipped and may have been sampled again as adults. Nevertheless, as pipetting error cannot be excluded, we removed samples with high pairwise kinship estimates prior to all analyses. The sample of higher quality was kept and the sample of lower quality was removed prior to filtering and final analysis.

Population structure, statistics, genetic distances, and PCoA

Population structure analysis was performed using `STRUCTURE` (v2.3.4; Pritchard et al. 2000). Parameter settings varied by dataset. The primary dataset was first analysed from for all clusters (K) from 1 to 10, with 10 independent repeats of 100,000 MCMC (Markov Chain Monte Carlo) iterations after a 10,000 iteration burn-in. Based on these results, Datasets 2–4 (subsets of the primary dataset) were analysed, using more robust methods. Each dataset was analysed from $K = 1$–10, after 50,000 burn-in and 500,000 MCMC iterations with sampling populations as priori. K values were estimated through an assessment of both

Table 1 Table of datasets

	Dataset/population	Colonies	*n*	Loci pre-filtering	Loci post-filtering
1	Primary/all	–	88	17,863	9037
2	Gawler Ranges	Coolgundibie (10) Organ Pipes (11) Stone Dam (6) Yandinga (19)	46	6354	3578
3	Flinders Ranges	Waukawoodna Gap (17)	17	12,358	7979
4	Grey Range	Alaric (18) Ray (7)	25	8538	5481

Summary of each numbered *P. xanthopus* DArTseq dataset. Sample sizes, the subdivision of populations into colonies, and the number of samples for each colony are shown. The Loci pre-filtering column shows the total number of loci (17,864) minus monomorphic loci removed automatically in subsetting

Pritchard's model likelihood method (Pritchard et al. 2000) and Evanno's ΔK method (Evanno et al. 2005) implemented in `Structure Harvester` (Earl and vonHoldt 2012), and scrutinised following recommendations detailed in Cullingham et al. (2020) for $K = 2$ results. The production of population structure bar plots was performed in `CLUMPAK` (v1.1; Kopelman et al. 2015). Also, Principle Coordinate Analysis (PCoA) was performed using Euclidean distance in `R` with `dartR`. Each dataset was analysed and informative dimensions examined. Plots of the two most informative axes of each population were generated with `ggplot2` v3.3.2 (Wickham 2006).

Mean observed heterozygosity (H_O), expected heterozygosity (H_E), population Allelic Richness (rarefied allelic counts, per locus and population; A_R), and inbreeding coefficients (F_{IS}) were reported using `hierfstat` v0.04–22 in `R` (*basic.stats* function) with 98% confidence intervals (1000 bootstraps). Population divergence was explored using several approaches; pairwise private and fixed alleles, Euclidean and Nei's (Nei 1972) genetic distance matrices as well as pairwise F_{ST}. Pairwise F_{ST} values were also estimated using `StAMPP` (1000 bootstraps, 95% CI), which follows Weir and Cockerham's (Weir and Cockerham 1984) methods. An unrooted neighbour joining tree was constructed from a Euclidian distance matrix before effective population sizes (N_e) were estimated for each colony using `NeEstimator` (v2.1; Do et al. 2014) using the Linkage Disequilibrium (random mating) methods for a minimum allele frequency at 0.05, 0.02 and 0.01 with jack-knife confidence intervals (Jones et al. 2016).

Coefficients of relationship, relatedness networks

The `R` package `SNPRelate` v1.16.0 (Zheng 2013) was first used to calculate Identity-By-State (IBS) fractions for each pair of rock-wallabies in each of the Datasets 1–4. Hierarchical cluster analysis using the average link (UPGMA) method was then performed on each of the IBS matrices to produce a genetic distance trees. Kinship was estimated independently in Datasets 2–4, to ensure that later filtering was not biased by sample size, and that appropriate population-specific allele frequencies were used. The primary dataset contains SNPs that are monomorphic in individual populations and kinship values can be inflated by these fixed alleles. Identity-By-Descent coefficients (calculated by Maximum Likelihood Estimation) were estimated in `R` using the `SNPRelate` package (Zheng 2013). Pairwise kinship values were estimated based on these IBD coefficients, also using `SNPRelate`. Kinship values vary from 0 to 0.5 so, for ease of comprehension, coefficients of relationship (r), which vary from 0 to 1, were calculated by doubling kinship values (Wright 1922). Full siblings and parent–offspring pairs are expected to have r values of approximately 0.5, half siblings 0.25, and first cousins 0.125, and so on. To visualise close r values geographically, the program `GEPHI` (v0.9.2; Bastian, Heymann and Jacomy, 2009) was used to produce relatedness networks with the plugin `GeoLayout`. Individuals were treated as nodes and relatedness estimates as edge values, weighted by increasing r. These visualisations were limited to coefficients of relationship greater than 0.0625 (i.e. 1/16th, e.g. first-cousin once removed, half-first-cousin).

First-generation migration

`GeneClass2` (Piry et al. 2004) was used to identify presumed first generation (f_0) migrants. This was performed using the Rannala and Mountain (1997) methods with Monte-Carlo resampling at both the 0.01 and 0.05 probability threshold and all loci. This approach follows the same methods as Potter et al. (2020). The distance between the trapping (source) colony and the putative origin colony (as well as the site map, Fig. 1) was also then generated in `ArcMap` (v10.5.1; Environmental Systems Research Institute 2019).

Results

Population structure, statistics, genetic distances, and PCoA

The Gawler sites (Coolgundibie, Organ Pipes, Stone Dam and Yandinga) consistently had the lowest observed and expected heterozygosity (H_O and H_E, respectively), followed by the Gray Range population and Flinders Ranges sites (Table 2; Fig. S3).. F_{IS} (inbreeding coefficient; calculated as $F = 1 - H_O/H_E$) showed several colonies to have heterozygote excess (negative values) and several to be deficient in heterozygotes. FIS values were indicative of heterozygote deficiency in the Yandinga and Organ Pipes colonies of the Gawler Ranges and Waukawoodna Gap (Table 2). All other colonies excepting the Alaric Colony, where FIS was not significantly different from 0, showed evidence of heterozygote excess (Table 2). These results were also reflected in the results of allelic richness, which was highest within the Flinders Ranges colony, followed by the Grey Range and finally Gawler Ranges (Table 2). Pairwise F_{ST} was greatest between the Coolgundibie and Ray colonies, and the lowest value was between the geographically nearby Yandinga and Organ Pipes colonies (Table 3). Average F_{ST} by population was 0.03 within Grey Range colonies, and 0.04 within Gawler Ranges. Average pairwise F_{ST} was greatest between the Grey and Gawler Ranges ($\overline{F_{ST}} = 0.63$). Flinders Ranges to Grey Range comparisons resulted in slightly higher F_{ST} values ($\overline{F_{ST}} = 0.47$)

Table 2 Table of effective population sizes (N_e), H_O, H_E, A_R, and F_{IS}, for each colony

Colony	*n*	N_e	CI (lower)	CI (upper)	H_O (*SD*)	H_E (*SD*)	A_R (*SD*)	F_{IS}
Coolgundibie	10	8.4	5.5	35.9	0.161 (0.24)	0.144 (0.20)	1.336 (0.44)	− 0.098*
Organ Pipes	11	31.1	28.6	∞	0.143 (0.21)	0.156 (0.21)	1.359 (0.44)	0.065*
Stone Dam	6	4.5	2.0	8.8	0.154 (0.24)	0.147 (0.21)	1.344 (0.45)	− 0.035*
Yandinga	19	36.6	27.2	108.6	0.154 (0.21)	0.161 (0.20)	1.371 (0.44)	0.038*
Waukawoodna Gap	17	21.4	13.7	39.5	0.254 (0.22)	0.258 (0.20)	1.596 (0.42)	0.017*
Alaric	18	21.3	18.5	395.2	0.193 (0.23)	0.194 (0.21)	1.448 (0.45)	0.008
Ray	7	5.1	1.9	12.8	0.201 (0.26)	0.184 (0.22)	1.427 (0.47)	− 0.086*

Table shows the number of individuals in the population (*n*), effective population sizes (N_e) for each colony and the lower and upper jack-knife confidence intervals of that estimate, observed heterozygosity (H_O), expected heterozygosity (H_E), allelic richness (A_R) and the inbreeding coefficient (F_{IS}), significant F_{IS} values (98% confidence, 1000 bootstraps) are denoted by an asterisk (*)

Table 3 Pairwise F_{ST} and significance (from p values)

Range		Grey		Gawler				Flinders
	Colony	**R**	**A**	**OP**	**Y**	**SD**	**C**	**WG**
Grey	**Ray**		*	*	*	*	*	*
	Alaric	0.0286		*	*	*	*	*
Gawler	**Organ Pipes**	0.6365	0.6152		*	*	*	*
	Yandinga	0.6334	0.6164	0.0083		*	*	*
	Stone Dam	0.6401	0.6142	0.0310	0.0268		*	*
	Coolgundibie	0.6514	0.6247	0.0401	0.0361	0.0769		*
Flinders	**Waukawoodna**	0.4643	0.4745	0.3502	0.3587	0.3405	0.3635	

Pairwise F_{ST} values calculated significance tested based on 1000 bootstrap repeats and 95% CI. Cell colour is scaled (green to red) by increasing F_{ST} below the diagonal. An asterisk (*) above the diagonal indicates that the corresponding value is significantly greater than zero after Bonferroni corrections

than Flinders Ranges to Gawler Ranges ($\overline{F_{ST}} = 0.35$). All F_{ST} values with the exception of Organ pipes-Yandinga were significant ($p < 0.001$; Table 3).

The neighbour-joining tree clearly separates colonies by population (Fig. 2). This was also evident using several other different genetic distance measures (Supplementary Information), as well as through Principal Coordinates Analysis (Fig. 3). The first two eigenvalues in the PCoA of the primary dataset corresponded to 47.1% and 12.0% (Fig. S5) of the variation between samples.

Effective population size (N_e) estimates ranged from 4.5 for the Stone Dam colony, to 36.6 for the Yandinga colony in the Gawler Ranges. In the Flinders Ranges, the Waukawoodna Gap colony had an N_e of 21.4, and in the Grey Range, the Ray and Alaric colonies had N_e estimates of 5.1 and 21.3, respectively (Table 2).

After `STRUCTURE` analysis, Evanno's ΔK method from `STRUCTURE HARVESTER` indicated that $K = 2$ was the best supported K value for the primary dataset 1; however, the maximum $L(K)$, pairwise F_{ST} values (Table 3), neighbour-joining trees (Fig. 2), genetic distances (Table S7-10), PCoA results (Fig. 3) and other analyses all gave $K = 3$ greater support. Therefore, delimitations of $K = 3$ (Fig. 4) were used to subset the primary dataset into populations for further investigation of hierachical population structure and kinship analysis.

PCoA analysis of the Gawler ranges showed some potential structure (Fig. 3) though the percentage contributions of each axis to differentiation were relatively low (Supplementary Information). Genetic distance trees showed little structure. Bayesian cluster analysis with `STRUCTURE` showed the greatest support for $K = 2$ in the Gawler Ranges, but again $K = 3$ (Fig. 4), which also had a high ΔK value, appeared to be better supported by other analysis. The colonies from the Grey Range also showed some limited genetic differentiation from PCoA, distance trees and `STRUCTURE` analysis ($K = 2$ and $K = 6$, supported from ΔK and $L(K)$).

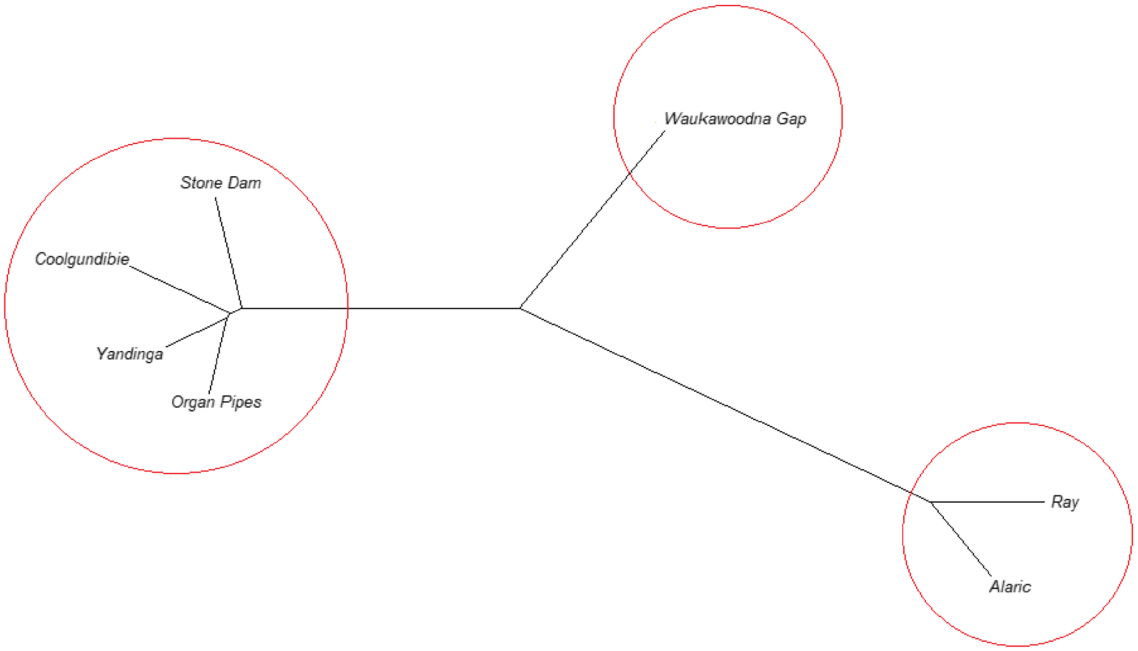

Fig. 2 Unrooted neighbour-joining tree of all YFRW populations. Neighbour joining tree generated from Euclidean genetic distance matrix of YFRW. Circles indicate population groups based on mountain ranges, Gawler ranges—left, Flinders Ranges—centre, Grey Range—right

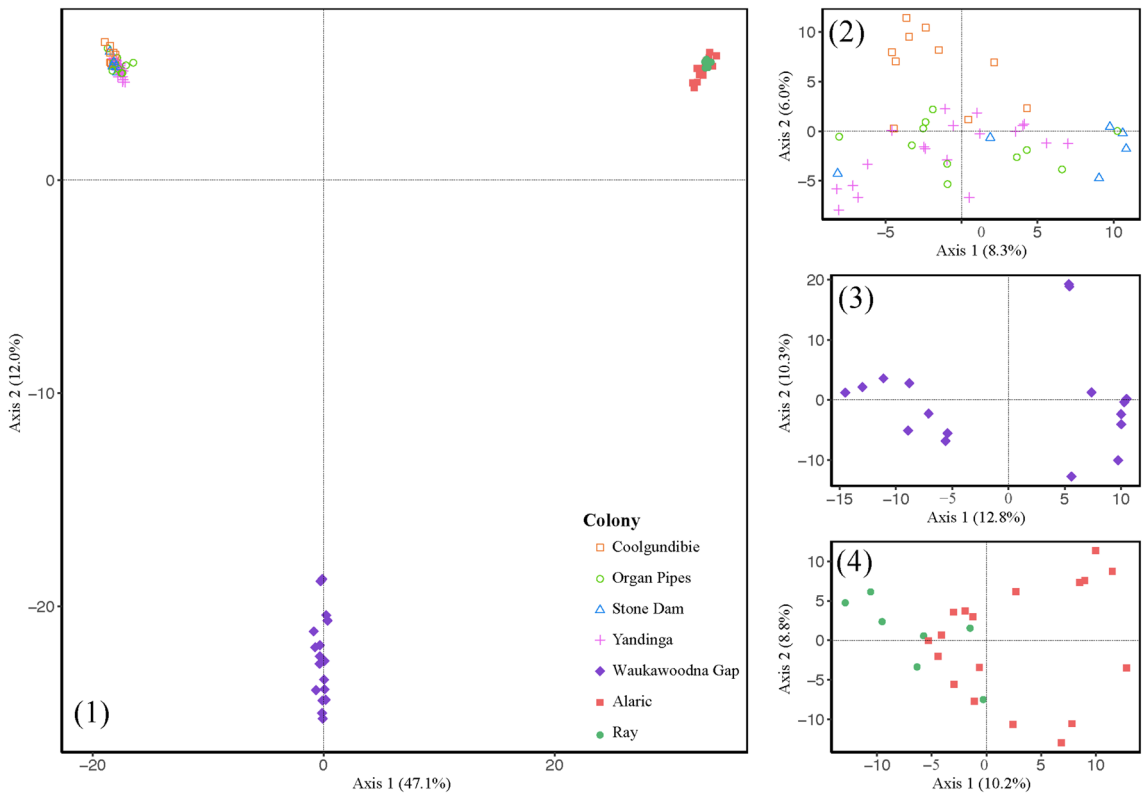

Fig. 3 PCoA by Dataset. Principal Coordinate analysis of each Dataset, respectively, coloured by colony. X- and Y-axes show the first and second most informative eigenvalues, correspondingly, and their percentage contributions (in parentheses) to total variance

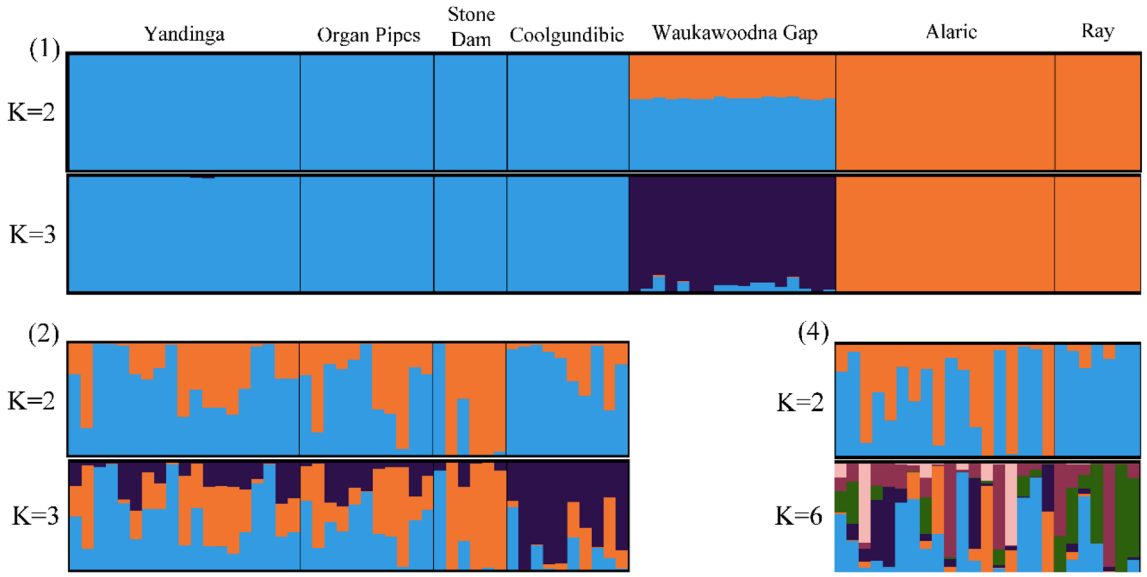

Fig. 4 STRUCTURE bar plots for the Primary Dataset, Galwer Range Dataset, and Grey Range Dataset. (1) Bar plots showing the major clusters for $K=2$ and $K=3$ (all 10/10 iterations, i.e. no minor clustering). $K=2$ was most supported by Evanno's ΔK method, though $K=3$ was better supported by other methods of examining population structure. (2) Bar plots showing $K=2$ and $K=3$ for the Gawler Dataset and (4) $K=2$ and $K=6$ for the Grey Range Dataset-from structure analysis are also shown. Graphs of ΔK and L(K) over each value of K and bar plots of all clusters ($K=1$–10) can be found in the Supplementary material

These results were also supported by pairwise F_{ST} values, which were low, but still significant ($p<0.001$; Table 3).

Coefficients of relationship, relatedness networks

Average intra-population relatedness ($\bar{r}$) was greatest in the Gawler Ranges (0.031). The Gawler Ranges populations had 419 relationships greater than $r=0$ (out of a potential 1035 pairwise relationships, 40.5%), and 161 relationships greater than the $r=0.0625$ threshold (15.5%; Fig. 5). This was followed by the Grey Range where average $\bar{r}$=0.027, with 67 of the 300 possible relationships greater than $r=0$ (22.3%), and 30 greater than the r-threshold (10.0%). Finally, in the Flinders Ranges, 25 out of a possible 136 relationships were greater than 0 (18.4%), with 15 relationships greater than the threshold (11.0%; $\bar{r}$=0.027), (see Figs. S10, S15, S17 and S22).

First-generation putative migration

Putative migration here is defined as shared sequence similarities (based on genetic distance, allele frequency and Bayesian criterion; Piry et al. 2004) exhibited geographically, thus suggesting a permanent movement event from one site to another, rather than the more general definition of ecological migration, which relates to season and resource. Out of 71 individuals (46 in the Gawler Ranges and 25 in the Grey Range) 17 were identified as putative f_0 putative migrants (Table 4). Of the 15 potential migrations within the Gawler Ranges, seven (41.1%) were between Organ Pipes and Yandinga. Two rock-wallabies caught at Stone Dam appeared to be immigrants, one from Yandinga and one from Organ Pipes, and three emigrants of Stone Dam were caught at other colonies (two at Yandinga, one at Organ Pipes). Lastly, there were three occurrences of putative migration to Coolgundibie, from the Yandinga (two) and Organ Pipes (one) colonies. These putative migrations were of ~ 13.32 and ~ 15.70 km, respectively. There were no occurrences of putative migrants from Coolgundibie caught at any other trapped site in the Gawler Ranges. Within the Grey Range population two rock-wallabies were identified as potential f_0 putative migrants; both suggest emigration from Alaric to the Ray colony.

Figures from reports used for filtering, distance matrices, scree plots of Eigen values of PCoA, output figures of `Structure Harvester`, bar plots of all values of K from `CLUMPAK`, histograms of relationship coefficients, outputs of `GeneClass2` and other additional results for all datasets can be found in the Supplementary Information. The data underlying this analysis is also available online (Smith et al. 2020a, b, c).

Discussion and summary

Key findings

This study aimed to examine contemporary movement between disjunct colonies of *P. xanthopus* with varying

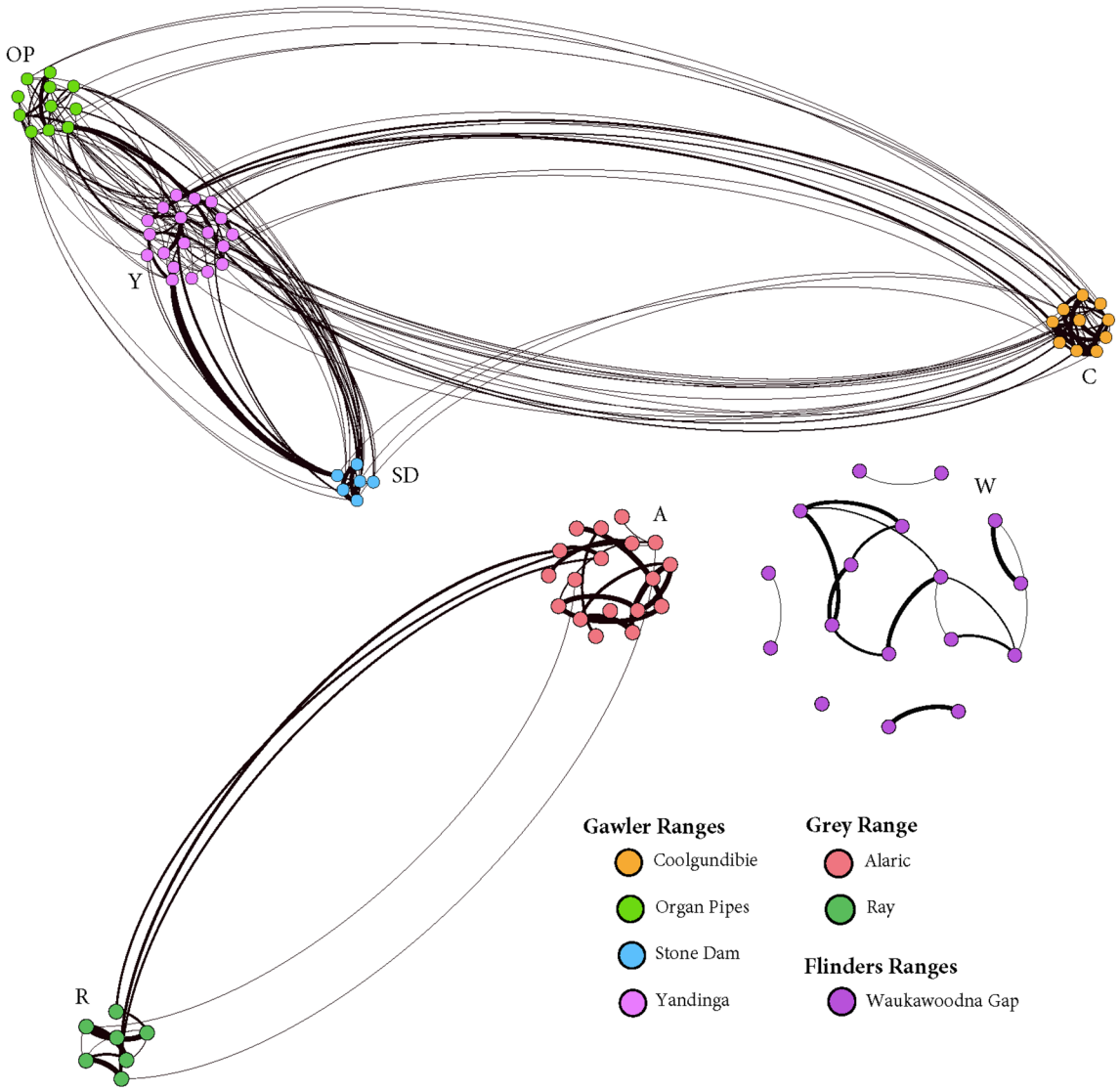

Fig. 5 YFRW relatedness networks generated from IBD estimates. Visual representation of relatedness estimates greater than 0.0625 generated though Identity by Descent (IBD) analysis. Coloured circles (nodes) show individuals of each population, relatedness lines (edges) are weighted by the strength of the relationship (not comparable between populations). Grouped node locations correspond to geographic locations (Fig. 1)

levels of connectedness in both South Australia and Queensland. We found though the examination of population structure, kinship analysis and maximum likelihood analysis of putative migration that there has likely been recent contemporary movement. Individuals with kinship values greater than 0.0625 were common between colonies within the Gawler Ranges with several movements greater than 13 km, and despite an approximately 5 km gap of unsuitable habitat, related individuals were present from the two sampled locations in the Grey Range. Further to this, multiple putative f_0 migrations were identified within both the Gawler and Grey Ranges. From these results it is clear that *P. xanthopus* are more mobile within mountain ranges than previously assumed. The results from the Gawler ranges colonies in particular add weight to recently published results also showing several potential long distance migration events of *P. xanthopus* in the Flinders Ranges (Potter et al. 2020). This previous study primarily focused the genetic variation of colonies, but provided insight into potential movements between colonies that was more thoroughly examined here. Greater mobility of rock-wallabies also fits closer with metapopulation theory, where movement between semi-isolated demes and back into locally extinct or new sites helps maintain the genetic and ecological viability of the broader population (Hanski 1998). This new understanding is likely to affect future management of the species.

Table 4 Putative first generation migrants identified with GeneClass2

Sampling colony	Pop	$-log\frac{L[home]}{L[max]}$	Distance (km)	Emigrated from
Coolgundibie	Gawler	1.113	13.32	*Yandinga*
Coolgundibie	Gawler	127.519	15.7	*Organ Pipes*
Coolgundibie	Gawler	59.84	13.32	*Yandinga*
Organ Pipes	Gawler	157.855	2.89	*Yandinga*
Organ Pipes	Gawler	62.546	2.89	*Yandinga*
Organ Pipes	Gawler	99.705	2.89	*Yandinga*
Organ Pipes	Gawler	56.835	2.89	*Yandinga*
Organ Pipes	Gawler	25.571	2.89	*Yandinga*
Organ Pipes	Gawler	84.131	7.23	*Stone Dam*
Stone Dam	Gawler	176.771	7.23	*Organ Pipes*
Stone Dam	Gawler	505.72	4.38	*Yandinga*
Yandinga	Gawler	27.72	4.38	*Stone Dam*
Yandinga	Gawler	29.924	2.89	*Organ Pipes*
Yandinga	Gawler	0.5	2.89	*Organ Pipes*
Yandinga	Gawler	72.667	4.38	*Stone Dam*
Ray	Grey	149.602	8.76	*Alaric*
Ray	Grey	192.074	8.76	*Alaric*

Individuals identified as potential first generation migrants in GeneClass2. Table shows the colony the individual was captured in (Sampling colony) and the likely colony the individual emigrated from. The distance between the source and original colony is listed in kilometres. The log value of the ratio of 'likelihood of home' over 'likelihood of all populations', the log value of the 'likelihood of home', and the log value of the greatest likelihood (corresponding to the Emigrated from colony) were also included. All probabilities of the log-likelihood ratio were equal to 0

Population structure

The initial analysis of population structure across all samples (Primary Dataset) showed that each mountain range should be considered independent of the others when considering genetic monitoring within the species. These results are in agreement with the literature on *P. xanthopus* genetics and phylogeny which splits the South Australian and Queensland species into subspecies, and shows that separate mountain ranges/populations are genetically distinct (Eldridge 1997; Pope et al. 1996, 1998; Potter et al. 2012, 2020). Populations of *P. xanthopus* were shown to have an order of magnitude greater pairwise F_{ST} values between mountain ranges than within mountain ranges (Table 3), and all other methods employed for determining genetic differentiation between populations and individuals supported this result (Figs. 2, 3, Fig. S4 and Tables S6–S10). Given the ΔK method has the propensity to lead to over identification of $K=2$ (Cullingham et al. 2020; Janes et al. 2017), `STRUCTURE` and other methods indicated that3 was best supported K value). From the initial structure analysis there was also evidence of some population substructuring, leading us to examine fine-scale structure in data subsets based on each of the populations. This showed that there was indeed some genetic structuring between colonies of each population, though not nearly as distinct as between mountain ranges (Figs. 3, 4). Fine scale structure is also supported by the recent analysis of microsatellite loci, which showed some structure within colonies within the Flinders Ranges (Potter et al. 2020).

Genetic diversity

Greater genetic diversity in populations is closely linked to a population's ability to withstand genetic pressures associated with small population size and to adapt to changing environmental conditions (Frankham 2005). Our results in rock-wallabies showed that the smaller, less geographically connected, populations in the Gawler and Grey Ranges have lower genetic diversity (H_O and A_R) than those of the Flinders Ranges (Waukawoodna site—Table 2). This outcome is in concordance with assumptions that genetic diversity should be positively correlated with population size (Frankham 1996). Significance testing of F_{IS} also revealed all colonies (with the exception of Alaric in the Grey Range) significantly deviate from zero, the null value, indicating either heterozygote deficiency (Yandinga, Organ Pipes, Waukawoodna) or heterozygote excess (Ray, Coolgundibie and Stone Dam). While the theory behind inbreeding leading to heterozygote deficiency is well established (Buri 1956), the processes leading to heterozygote excess are less clear. Though there are several potential explanations (referenced and discussed in Stevens et al. 2007), this case is likely due to the small population sizes. Binomial sampling error can cause differences in allele frequencies of male and female breeders, leading to heterozygote excess in their progeny (Luikart and Cornuet 1999; Robertson 1965; Waples 2015). This explanation of heterozygote excess in these rock-wallaby colonies is supported by the estimates of effective population size (N_e), which are substantially smaller in the corresponding colonies (Table 2).

Inter-colony relationships and movement

The first step employed here to examine how *P. xanthopus* move between colonies was assessing pairwise relatedness (r) between all individuals of a population. The analysis revealed relationships greater than the 0.065 (i.e. a common ancestor within 4 generations) threshold between all colonies within each population (excluding the Flinders Ranges), and one relationship of ~ 0.5 (indicating a full-sibling or parent-progeny relationship) between two colonies in the Gawler Ranges.. These relationships also indicate that there may be greater mobility between populations than previously recognised based on early genetic assessments (Pope et al. 1996).

While these results indicate recent movement between the colonies, inter-colony r values that are further apart

than full-sibling or parent-offspring (less than ~ 0.5) may be a result of stepwise movement events through intermediate and unsampled colonies. To identify the likely colonies-of-origin, putative f_0 migrants were identified in `GeneClass2`. The program identified 15 potential first generation migrants in the Gawler Ranges, and two in the Grey Range (Table 4). As might have been postulated from the analysis of population structure, movement between Organ Pipes and Yandinga constituted a large percentage of putative migrants. These colonies are separated by only 2.9 km of suitable habitat (Fig. 1). As *P. xanthopus* are known to move up to 1.5 km to water points (Sharp 2011), this regular exchange of individuals was expected. Less predictable were the putative migrants into and from Stone Dam, and those from the Yandinga/Organ Pipes area, found at Coolgundibie. Interestingly, no f_0 migrants were identified as having dispersed in the reverse direction, i.e. Coolgundibie to any other colony in the Gawler Ranges. Despite this exception, within the Gawler Ranges rock-wallabies appear to move readily to areas of connected habitat, even over relatively large distances.

Within the Grey Range population, only two migrants were detected, with both indicating the individual moved from Alaric to Ray. These movements are of particular relevance, both to the understanding of species population dynamics, and to future management of the species in Queensland. The area of the Grey Range that these two colonies reside in is at the very Southern end of *P. x. celeris*' distribution. The Alaric colony is located on the Canaway Fault, a line of connected rock-wallaby habitat/cliffs that run the North–South. The Ray colony, however, is approximately 8 km distant on fragmented rocky outcrops known as The Matrix. As previously mentioned, the shortest distance between suitable rock-wallaby habitat between the Canaway Fault and The Matrix is ~ 5 km of open, flat, farmland. Moreover, this dispersal route is now impeded by an exclusion fence (Fig. 1).

Management implications

Early assessments of the Gawler ranges had not found colonies of *P. xanthopus* at Coolgundibie (Lethbridge 2004a) or Stone Dam (Lethbridge et al. 2012; Lethbridge et al. 2010). In part, samples were collected from these colonies to assess whether theylikely represent recolonisation events from the other established colonies under threat abatement. The high kinship values between samples from these colonies and those of Yandinga and Organ Pipes suggest that movement reported here likely reflect recolonisation as a result of 25 years of goat and fox control (and some kangaroo management) and a major drought in the Gawler Ranges (Lethbridge et al. 2019). Integrated pest management (of feral rabbits *Oryctolagus cuniculus*, foxes, goats, cats *Felis catus* and weeds) may have driven this pulse of movement as a reduced number of predators, and also a shortage of resources in core *P. xanthopus* colonies, induced density-dependant dispersal behaviours. Continued recovery of rock-wallabies under these conditions likely depends on the threat abatement being widespread enough to facilitate further recolonisation events at sites that, without abatement, would be unsuitable.

For *P. x. celeris*, the rapid expansion of pest-exclusion fencing in the area (Smith et al. 2020c) potentially divides colonies that have previously relied on movement to maintain greater levels of genetic diversity, such as that of the Flinders Ranges (Table 2). In all cases, identified f_0 migrants (Table 4) were also those with higher inter-colony kinship values in the relatedness network (Fig. 5). The fence between the two colonies was completed in 2016, so either the rock-wallabies were able to pass across the exclusion fence, or the rock-wallabies relocated colonies prior to the exclusion fences construction. The fences have proved highly effective at preventing the movement of other species (RAPAD and QFPI 2018), and aging the potential migrants based on tail-length data (Lethbridge 2004b) showed that dispersal pre-2016 was possible. It would be reasonable to assume that the migrants moved colonies pre-fence, and that the population in Queensland is now fragmented by exclusion fencing (Smith et al. 2020c). Indications that the rapid reduction in *P. xanthopus* distribution over the past century has already had negative genetic impacts on population viability which makes this assessment all-the-more troubling (Potter et al. 2020). This is particularly true of colonies, such as the Ray colony, that were already not part of connected and continuous rock-wallaby habitat. To allay the potential negative impacts, the genetic variation of isolated populations would have to be monitored into the future and mitigation strategies such as meta-population management be employed if/when the populations appear to be experiencing genetic erosion. Meta-population management has been successfully employed for the maintenance of genetic variation issues caused by fencing in the past (Boast et al. 2018; Miller et al. 2015; Schroeder 2019).

Limitations

While most F_{IS} values deviated significantly, they may not reflect the true value in the populations. Estimation of both F_{IS} and N_e assumes random mating and random sampling in the population; both assumptions may have been violated here. For *P. xanthopus* there is evidence of social structure, dominance behaviours and philopatry (Lapidge 2001; Potter et al. 2020; Sharp 2002) and territorial defence (or more specifically, trap bait defence) which may result in non-random sampling. Additionally, clear delimitations between sampling populations is needed to avoid Wahlund effects (De

Meeûs, 2018; Wahlund 1928; Waples 2015). As it appears colonies have an exchange of individuals (Fig. 5), colonies likely represent demes of a metapopulation, and this may have altered F_{IS} estimates of colonies.

This study also lacked a proper 'control' site, which demonstrably functions as a healthy metapopulation, and replication within the separate populations. Understandably, even with sufficient time and resources, finding and sampling populations and colonies to remove this limitation is difficult in threatened species.

Future research

It is clear from the results above that for the effective conservation and recovery of *P. xanthopus*, the management of the species needs to be considered at a broader scale. The long term conservation of the species relies on the ability of individuals to immigrate into neighbouring colonies for the maintenance of genetic variation (Potter et al. 2020). Further to this, the recovery of the species relies on an increase in the species distribution as potentially suitable habitats become available as a result of broad scale management of threatening processes (Lethbridge et al. 2012; Lethbridge et al. 2019). Future research should seek to elucidate whether recolonised sites continue to be genetically supplemented from other colonies in the metapopulation. Additionally, as new sites arise, genetic assignment of colonising rock-wallabies should be made a priority to establish source populations. More specifically for *P. x. celeris*, continuing genetic monitoring should be implemented alongside long term studies of behaviour (and simulations of metapopulation movement and genetics) both to ensure genetic viability of the population is maintained and as a study of the long term effects of anthropogenic barriers on species genetics and behaviour (Smith et al. 2020a, b, c).

Molecular ecology tools can often be overlooked in favour of more traditional methods of assessing species. The above study clearly demonstrates the application of genetic ecology methods, specifically kinship analysis, to help inform management of a threatened species. By applying these more appropriate methods for a cryptic and disjunct species we were able to infer regular movement between colonies where previous studies failed to find movements or significantly underestimated their regularity. Studies of species that have had similar short comings should consider how genetic analysis could overcome these obstacles and better inform the species management.

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Author contributions DS and MRL collected tissues samples from Queensland and South Australia, respectively. The methods and study design was decided on by DS and RLA as part of a broader project conceptualised by DS and BLA. DS performed all analysis. The main body of the writing was completed by DS. All authors contributed to the editing and review of the manuscript pre-submission.

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Data availability Data accessibility: Metadata (Sampling locations), and genotypes are available at GitHub: https://github.com/D-A-Smith/YFRWgenetics. https://doi.org/10.5281/zenodo.7412787.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

References

Bastian M, Heymann S, Jacomy M (2009). Gephi: an open source software for exploring and manipulating networks. In: Proceedings of the Third international AAAI conference on weblogs and social media. (San Jose, California).

Boast L, Chelysheva E, van der Merwe V, Schmidt-Küntzel A, Walker E, Cilliers D et al (2018) Cheetah translocation and reintroduction programs: past, present, and future. In: Marker L, Boast L, Schmidt-Kuentzel A (eds) Cheetahs: biology and conservation. Academic Press, London, pp 275–289

Buri P (1956) Gene frequency in small populations of mutant *Drosophila*. Evolution 10(4):367–402

Copley P (1983) Studies on the yellow-footed rock-wallaby, *Petrogale xanthopus* Gray (Marsupialia: Macropodidae) I. Distribution in South Australia. Wildl Res 10(1):47–61

Cullingham C, Miller J, Peery R, Dupuis J, Malenfant R, Gorrell J, Janes J (2020) Confidently identifying the correct K value using

the ΔK method: when does K = 2? Mol Ecol 29(5):862–869. https://doi.org/10.1111/mec.15374
De Meeûs T (2018) Revisiting FIS, FST, Wahlund effects, and null alleles. J Hered 109(4):446–456
Do C, Waples R, Peel D, Macbeth G, Tillett B, Ovenden J (2014) NeEstimator v2: re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. Mol Ecol Resour 14(1):209–214
Earl D, vonHoldt B (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4(2):359–361
Ebert D, Andrew R (2014) DNA extraction from tissue preserved in ethanol or *Longmires lysis* buffer. School of environmental and rural science. University of New England, Australia
Eldridge M (1997) Restriction analysis of mitochondrial DNA from the yellow-footed rock-wallaby, *Petrogale xanthopus*: implications for management. Wildl Res 24(3):289–294
Environmental Systems Research Institute (2019) ArcMap (Version 10.5.1). USA: ESRI. Retrieved from https://desktop.arcgis.com/en/arcmap/
Escoda L, González-Esteban J, Gómez A, Castresana J (2017) Using relatedness networks to infer contemporary dispersal: application to the endangered mammal *Galemys pyrenaicus*. Mol Ecol 26(13):3343–3357. https://doi.org/10.1111/mec.14133
Escoda L, Fernández-González Á, Castresana J (2019) Quantitative analysis of connectivity in populations of a semi-aquatic mammal using kinship categories and network assortativity. Mol Ecol Resour 19(2):310–326. https://doi.org/10.1111/1755-0998.12967
Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. Mol Ecol 14(8):2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x
Frankham R (1996) Relationship of genetic variation to population size in wildlife. Conserv Biol 10(6):1500–1508
Frankham R (2005) Stress and adaptation in conservation genetics. J Evol Biol 18(4):750–755
Gordon G, McRae P, Lim L, Reimer D, Porter G (1993) The conservation status of the yellow-footed rock-wallaby in Queensland. Oryx 27(3):159–168
Gruber B, Georges A, Unmack P, Clark L, Berry O (2019a) dartR: importing and analysing SNP and silicodart data generated by genome-wide restriction fragment analysis. Retrieved from https://CRAN.R-project.org/package=dartR
Gruber B, Georges A, Unmack P, Clark L, Berry O (2019b) Introduction to dartR. Retrieved from https://CRAN.R-project.org/package=dartR (Unpublished)
Hanski I (1998) Metapopulation dynamics. Nature 396:41–49
Holyoak M, Lawler S (1996) Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. Ecology 77(6):1867–1879
Inns R (1980) Occurrence of twins in macropod marsupials. Search 11:118–119
Janes J, Miller J, Dupuis J, Malenfant R, Gorrell J, Cullingham C, Andrew R (2017) The K= 2 conundrum. Mol Ecol 26(14):3594–3602
Jones A, Ovenden J, Wang Y (2016) Improved confidence intervals for the linkage disequilibrium method for estimating effective population size. Heredity 117(4):217–223
Kilian A, Wenzl P, Huttner E, Carling J, Xia L, Blois H et al (2012) Diversity arrays technology: a generic genome profiling technology on open platforms. In: Pompanon F, Bonin A (eds) Data production and analysis in population genomics. Humana Press, USA, pp 67–89
Kopelman N, Mayzel J, Jakobsson M, Rosenberg N, Mayrose I (2015) Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. Mol Ecol Resour 15(5):1179–1191
Lapidge S (2001) Reintroduction biology of yellow-footed rock wallabies (*Petrogale xanthopus celeris* and *P. x. xanthopus*). (Doctoral Thesis), University of Sydney, Australia
Lethbridge M (2004a) A survey of the yellow-footed rock-wallaby in the Gawler Ranges and recommendations for further monitoring. A report to Flinders University, Australia
Lethbridge M (2004b) Tail length to age *P. xanthopus* (software). Ecoknowlegde, Australia
Lethbridge M, Andrews L (2014). Yandinga gorge yellow-footed rock-wallaby (*Petrogale xanthopus xanthopus*) trapping, Gawler Ranges National Park July 2014. EcoKnowledge report to Department of Environment, Water and Natural Resources: Australia
Lethbridge M, Strauss J (2015) A novel dispersal algorithm in individual-based, spatially-explicit population viability analysis: a new role for genetic measures in model testing? Environ Model Softw 68:83–97
Lethbridge M, Harper M, Strauss J (2010). An analysis of the population viability of the yellow-footed rock-wallaby at selected sites in South Australia report to Flinders University & DEH Bounceback Program: Adelaide, Australia
Lethbridge M, Andrews L, Harper M (2012). An analysis of mark-resighting of the yellow-footed rock-wallaby (*Petrogale xanthopus xanthopus*) in the Gawler Ranges, South Australia EcoKnowledge report to Department of Environment, Water and Natural Resources: Australia
Lethbridge M, Shute E, Wells C, Stead M (2019) Population trends of the yellow-footed rock-wallaby (*Petrogale xanthopus xanthopus*) and feral goats (*Capra hircus*) from aerial survey data in the Flinders and Olary Ranges, South Australia. EcoKnowledge report to Department for Environment and Water: Australia
Lim L, Giles J (1987) Studies on the yellow-footed rock-wallaby, *Petrogale xanthopus* Gray (Marsupialia: Macropodidae). 3. Distribution and management in western New South Wales. Wildl Res 14(2):147–161
Longmire J, Maltbie M, Baker R (1997) Use of "lysis buffer" in DNA isolation and its implication for museum collections. Occasional Pap Museum 163:1–3
Luikart G, Cornuet J (1999) Estimating the effective number of breeders from heterozygote excess in progeny. Genetics 151(3):1211–1216
Miller S, Harper C, Bloomer P, Hofmeyr J, Funston P (2015) Fenced and fragmented: conservation value of managed metapopulations. PLoS ONE 10(12):1–16. https://doi.org/10.1371/journal.pone.0144605
Murray J, Low Choy S, McAlpine C, Possingham H, Goldizen A (2008) The importance of ecological scale for wildlife conservation in naturally fragmented environments: a case study of the brush-tailed rock-wallaby (*Petrogale penicillata*). Biol Cons 141(1):7–22. https://doi.org/10.1016/j.biocon.2007.07.020
Nei M (1972) Genetic distance between populations. Am Nat 106(949):283–292
Norbury G (1986) Twins in the western grey kangaroo, *Macropus fuliginosus* (Marsupialia: Macropodidae), in north-western Victoria. Aust Mammal 10(1–2):33
O'Leary S, Puritz J, Willis S, Hollenbeck C, Portnoy D (2018) These aren't the loci you'e looking for: principles of effective SNP filtering for molecular ecologists. Mol Ecol 27(16):3193–3206. https://doi.org/10.1111/mec.14792
Olivieri I, Michalakis Y, Gouyon P (1995) Metapopulation genetics and the evolution of dispersal. Am Nat 146(2):202–228
Perrin N, Mazalov V (1999) Dispersal and inbreeding avoidance. Am Nat 154(3):282–292
Piry S, Alapetite A, Cornuet J, Paetkau D, Baudouin L, Estoup A (2004) GENECLASS2: a software for genetic assignment and first-generation migrant detection. J Hered 95(6):536–539

Pope L, Sharp A, Moritz C (1996) Population structure of the yellow-footed rock-wallaby *Petrogale xanthopus* (Gray, 1854) inferred from mtDNA sequences and microsatellite loci. Mol Ecol 5(5):629–640

Pope L, Sharp A, Moritz C (1998) The genetic diversity and distinctiveness of the yellow-footed rock-wallaby *Petrogale xanthopus* (Gray, 1854) in New South Wales. Pac Conserv Biol 4(2):164–169

Potter S, Cooper S, Metcalfe C, Taggart D, Eldridge M (2012) Phylogenetic relationships of rock-wallabies, *Petrogale* (Marsupialia: Macropodidae) and their biogeographic history within Australia. Mol Phylogenet Evol 62(2):640–652

Potter S, Neaves L, Lethbridge M, Eldridge M (2020) Understanding historical demographic processes to inform contemporary conservation of an arid zone specialist: the yellow-footed rock-wallaby. Genes 11(154):1–25

Pritchard J, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155(2):945–959

Rannala B, Mountain J (1997) Detecting immigration by using multilocus genotypes. Proc Natl Acad Sci 94(17):9197–9201

RAPAD, QFPI (2018) RAPAD cluster fencing project round 1: march 2016–april 2018 final report: section 3. RAPAD and QFPI report to Queensland Government: Australia

Robertson A (1965) The interpretation of genotypic ratios in domestic animal populations. Anim Sci 7(3):319–324

Ruykys L, Lancaster M (2015) Population structure and genetic diversity of the black-footed rock-wallaby (*Petrogale lateralis* MacDonnell Ranges race). Aust J Zool 63(2):91–100

Schroeder M (2019) Cheetah (*Acinonyx jubatus*) mortality and survival in fenced reserves as part of a managed metapopulation across South Africa. (Doctoral Thesis), University of Cape Town, South Africa

Sharp A (2002). The ecology and conservation biology of the yellow-footed rock-wallaby. (Doctoral Thesis), University of Queensland, Australia

Sharp A (2011) Drinking behaviour of yellow-footed rock-wallabies (*Petrogale xanthopus celeris*) in semiarid Queensland. Aust Mammal 33(2):189–194

Smith D, Allen B (2021) Habitat use by yellow-footed rock-wallabies in predator exclusion fences. J Arid Environ. https://doi.org/10.1016/j.jaridenv.2020.104329

Smith D, King R, Allen B (2020a) Impacts of exclusion fencing on target and non-target fauna: a global review. Biol Rev. https://doi.org/10.1111/brv.12631

Smith D, Lethbridge M, Allen B, Andrew R (2020b) Data from: inferring inter-colony movement within metapopulations of yellow-footed rock-wallabies using estimates of kinship. https://doi.org/10.5281/zenodo.7412787

Smith D, Waddell K, Allen B (2020c) Expansion of vertebrate pest exclusion fencing and its potential benefits for threatened fauna recovery in Australia. Animals. https://doi.org/10.3390/ani10091550

Spencer P, Marsh H (1997) Microsatellite DNA fingerprinting confirms dizygotic twinning and paternity in the allied rock-wallaby, *Petrogale assimilis* (Marsupialia: Macropodidae). Aust Mammal 19:279–280

Stevens L, Salomon B, Sun G (2007) Microsatellite variability and heterozygote excess in *Elymus trachycaulus* populations from British Columbia in Canada. Biochem Syst Ecol 35(11):725–736

Telfer W, Griffiths A, Bowman D (2008) The habitat requirements of four sympatric rock-dwelling macropods of the Australian monsoon tropics. Austral Ecol 33(8):1033–1044

Threatened Species Scientific Committee (2016a) Conservation advice for *Petrogale xanthopus xanthopus*, yellow-footed rock-wallaby (SA and NSW) created by Threatened Species Scientific Committee (Australia)

Threatened Species Scientific Committee (2016b) Conservation advice: *Petrogale xanthopus celeris*, yellow-footed rock-wallaby (central-western Queensland). Canberra, Australia: Threatened Species Scientific Committee. Retrieved from http://www.environment.gov.au/biodiversity/threatened/species/pubs/87608-conservation-advice-05052016b.pdf

van Oorschot R, Cooper D (1989) Twinning in the genus *Macropus*, especially *M. Eugenii* (Marsupialia: Macropodidae). Aust Mammal 12(1–2):83–84

Wahlund S (1928) Composition of populations and correlation appearances viewed in relation to the studies of inheritance. Hereditas 11:65–106

Waples R (2015) Testing for Hardy-Weinberg proportions: have we lost the plot? J Hered 106(1):1–19

Weir B, Cockerham C (1984) Estimating F-statistics for the analysis of population structure. Evolution 38(6):1358–1370

Wells J, Richmond M (1995) Populations, metapopulations, and species populations: what are they and who should care? Wildl Soc Bull 23(3):458–462

Wickham H (2006) An introduction to ggplot: an implementation of the grammar of graphics in R. Statistics

Wright S (1922) Coefficients of inbreeding and relationship. Am Nat 56(645):330–338

Zheng X (2013). Package 'SNPRelate' (Version 0.9.15). Retrieved from http://corearray.sourceforge.net/