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Genetic evidence confirms severe extinction risk for critically endangered swift parrots: implications for conservation management

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Abstract

Mobile species pose major challenges for conservation because of their unpredictable, large scale movements in response to fluctuating resources. If locations with critical resources overlap with threats, large proportions of a mobile population may be exposed to threats. Critically endangered and nomadic swift parrots *Lathamus discolor* nest wherever food is most abundant in their breeding range, but concern exists that nest predation from an introduced predator may severely affect their population. Although swift parrots nest on predator-free offshore islands, population viability analysis indicates that is land nesting alone may be insufficient to offset extinction risk from high mainland predation rates assuming that the species is a single panmictic population. We test the assumption that swift parrots act as a single conservation unit. We undertook a population genetic analysis using seven microsatellite loci and samples obtained over 6 years from across the breeding range of swift parrots. We found no evidence of departure from Hardy–Weinberg expectations across the species and both Analysis of Molecular Variance and Bayesian Structure analyses failed to detect any evidence for genetic differentiation across the samples both spatially and temporally. These results, supported by simulations, indicate panmixia and a lack of population genetic structure in swift parrots. Unlike a sedentary or site philopatric species, the majority of the swift parrot population may be at risk of exposure to predation when unpredictable resources draw individuals away from islands. These findings support a key assumption of population viability models that predict an extreme reduction in population size for swift parrots, and address a major gap in knowledge of the species' ecology. Our study has implications both for the development of effective conservation management strategies and for the longer-term evolution of avoidance of predator-infested habitat in swift parrots.

Introduction

Conservation of mobile species is complicated by their variable movements because these increase the proportion of the total population potentially exposed to threatening processes (Runge *et al.*, 2015, 2016). The consequences of threats may be particularly severe if they occur at critical locations where resources are limiting (Runge *et al.*, 2014; Maron *et al.*, 2015), and thus may act as ecological traps that increase extinction risk (Robertson & Hutto, 2006; Robertson, Rehage & Sih, 2013). However, the degree of extinction risk may depend on whether the mobile species behaves as one or more genetically discrete subpopulations (hereafter: conservation units). The existence of multiple conservation units may reduce the likelihood of species extinction when the impact of threats is severe (Runge *et al.*, 2014).

The number of conservation units for a species can depend on the scale of individual movements (Newton, 2006*a*; Canales-Delgadillo, Scott-Morales & Korb, 2012), variation in resource availability across the geographic range (Roshier, Doerr & Doerr, 2008) and the spatial scale at which gene flow occurs (Haig *et al.*, 2011). Whether individual movements correspond to gene flow (i.e. resulting in new breeding sites) is critical to how different conservation units may be defined. Some widespread mobile species exhibit local adaptation where food is reliable and these adaptations may assist differentiation of separate conservation units. For example, crossbills *Loxia* spp. undertake continental scale movements to exploit masting of a few food tree species in forests where seed production is unpredictable (Newton, 2006*b*). Some crossbill populations exploit more reliable food trees (e.g. trees that seed annually or are serotinous) and have evolved into distinct lineages (Benkman, 1993) that can be considered separate conservation units. Reliable food enables evolutionary divergence of local

crossbills from mobile populations that live in less predictable environments (Parchman, Benkman & Britch, 2006; Edelaar *et al.*, 2012). Low resource reliability also appears to be closely linked with low population genetic structure in other comparable systems, for example irruptive owls (Marthinsen *et al.*, 2009) and seed-eating passerines (Mason & Taylor, 2015). Understanding genetic consequences of resource fluctuations and movement patterns may be key to defining conservation units for widespread mobile species.

We use data from a multi-year study to evaluate whether one or more conservation units exist for a mobile resource specialist. Swift parrots *Lathamus discolor* are nomadic migrants that breed in Tasmania (including two major offshore islands) and winter on the Australian mainland (Higgins, 1999). The entire population moves to breed in different locations each year depending on the configuration of key resources across the potential range (Webb *et al.*, 2017). Swift parrots are critically endangered, and introduced sugar gliders *Petaurus breviceps*, a small arboreal, volant marsupial, are a major cause of mortality of nests and breeding female parrots (Heinsohn *et al.*, 2015). The small nest cavities preferred by swift parrots protect against native Tasmanian predators, but sugar gliders are not excluded by this passive nest defence (Stojanovic *et al.*, 2017). Tasmanian offshore islands (where sugar gliders do not occur) are important population sources, whereas Tasmanian mainland sites can act as sinks for swift parrots due to predation pressure (Stojanovic *et al.*, 2014).

On the basis of population-level movements of swift parrots (Webb *et al.*, 2017), population viability analysis (PVA) of extinction risk have assumed that the species acts as a single panmictic conservation unit (Heinsohn *et al.*, 2015), and that no island-philopatric subpopulations exist. Under these assumptions, Heinsohn *et al.* (2015) estimated that swift parrots may decline by 94% in three generations because breeding success on islands cannot offset predation mortality on the Tasmanian mainland.

This critical assumption of panmixia in the PVA of Heinsohn *et al.* (2015) has not been tested, despite the conservation significance of potential island refuges assuming population differentiation exists. Therefore, in this study we address this knowledge gap by applying population genetic analysis and simulations to answer four questions: (1) Does the species fit expectations consistent with a single panmictic conservation unit? (2) Is there genetic differentiation among populations from islands and the Tasmanian mainland? (3) Is there temporal genetic differentiation among years? (4) Is there evidence for sex-biased dispersal? We consider these results in the context of PVA of the species and evaluate the implications for the conservation of mobile species.

Materials and methods

Study system and species background

This study was conducted across most of the swift parrot breeding range between 2010 and 2016 (Fig. 1). Genetic samples for this study were not available for Maria Island or northern Tasmania, but all other sites considered by Heinsohn *et al.* (2015) were included here. Swift parrots require the co-occurrence of both food (nectar from *Eucalyptus globulus* and *Eucalyptus ovata* flowering) and nesting habitat (tree cavities) for successful breeding (Webb *et al.*, 2017). Breeding occurs anywhere in Tasmania where flowering and suitable nesting habitat occur together, including two offshore islands, but the specific location of breeding varies over time depending on local resource abundance (Fig. 2). In any given breeding season due to the variation in food availability, only a fraction of the potential range is occupied (Webb *et al.*, 2017). Swift parrots move to breed where tree flowering is most abundant (Fig. 2), and in years when food is locally unavailable, birds are absent from islands (Webb *et al.*, 2017). Heinsohn *et al.* (2015) reported that the proportion of the swift parrot population that settled to breed on islands varied between 0 and 29% in any given year. Based on these high rates of movement of individuals among island and Tasmanian mainland breeding sites, Heinsohn *et al.* (2015) treated the population as a single conservation unit for the purposes of PVA.

Sample collection

Swift parrot nests were identified across the study area during standardized monitoring (Webb *et al.*, 2014) and unstructured searches. Nests were identified using behavioural cues of swift parrots and accessed using single rope climbing techniques (Stojanovic *et al.*, 2015). Nestling swift parrots were temporarily removed from their nest cavities (Stojanovic *et al.*, 2015) and blood was collected using brachial venepuncture. Blood was stored on FTA paper (Whatman™). Adult swift parrots were captured during nestling provisioning and either blood (collected as above) or feathers (plucked from the flank and stored in 95% ethanol) were collected. Tissue was taken from dead swift parrots (adult females and nestlings killed by sugar gliders, and an injured wild bird that was euthanized after entering care) and these were stored in 95% ethanol.

Our swift parrot samples were drawn from two geographic groups (referred to as 'regions' in our AMOVA analysis, see below): 'mainland' Tasmania and 'island', with spatially aggregated samples within regions treated *a priori* as 'populations'. In an additional analysis of genetic differentiation among sampling years, we defined 'temporal populations' on the basis of the year in which they were collected (i.e. 2010–2015 breeding seasons, Table 1).

DNA extraction and microsatellite genotyping

We used two methods to extract DNA depending on the type of sample. DNA extraction from blood stored on FTA paper was performed following the standard procedure for nucleated erythrocytes (Smith & Burgoyne, 2004). DNA was extracted from feather and tissue samples using the Qiagen DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA) following manufacturer instructions with some modifications (Olah *et al.*, 2017).

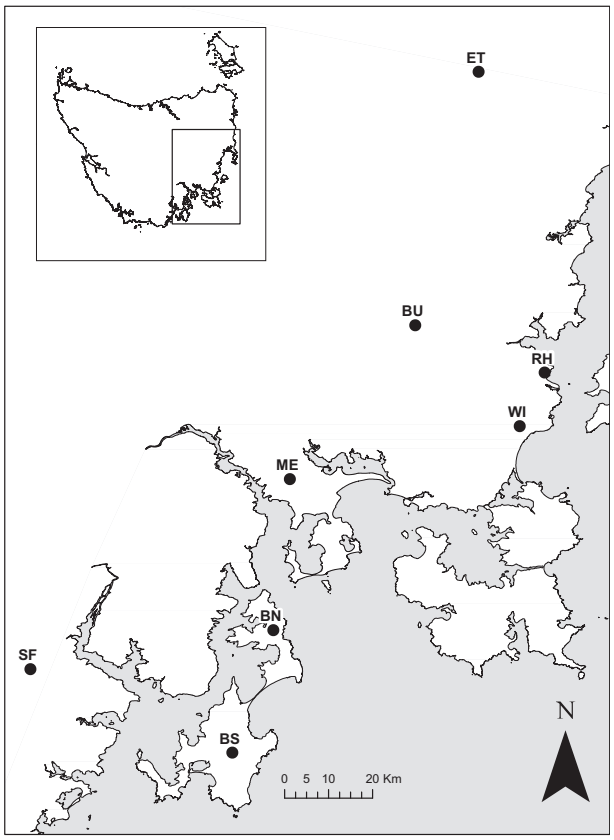

Figure 1 Map of the study area in Tasmania, Australia. Populations where swift parrot genetic samples were collected were: North (BN; $N = 32$ genetic samples) and South Bruny Island (BS; $N = 23$), Buckland (BU; $N = 13$), Eastern Tiers (ET; $N = 16$), Meehan Range (ME; $N = 8$), Rheban (RH; $N = 5$), Southern Forests (SF; $N = 6$), and Wielangta (WI; $N = 6$).

Using a subset of randomly selected high-quality DNA samples ($n = 30$) we screened previously described microsatellite loci ($n = 30$) that were known to be informative in other parrot species. Based on this pilot study we selected eight informative loci for further analysis (all were dinucleotide repeats): Cfor1415, Cfor2627, Cfor3031 (Chan *et al.*, 2005), pCl3 (White *et al.*, 2009), and SCMA 01, SCMA 04, SCMA 07, SCMA 29 (Olah *et al.*, 2015).

Laboratory analysis followed Olah *et al.* (2017), but briefly, M13 PCR tags were attached to all forward primers (Schuelke, 2000) and we amplified all loci individually. PCR products were multiplexed in the same lane using different fluorescent tags and genotyped on an ABI 3130XL sequencer (Applied Biosystems, Foster City, CA, USA). We used water instead of DNA extract as a negative control for contamination checking and with each genotyping run, in one out of 16 capillaries we always included the same sample as positive control to ensure consistent size scoring across all genotyping runs. Results were scored using Geneious version R6 (Kearse *et al.*, 2012) with full genotypes constructed across 8 loci. Approximately, 25% of the samples were repeated to estimate genotyping errors. Loci were screened for the presence of null alleles across all samples with MicroChecker 2.2.3 (Van Oosterhout *et al.*, 2004). Samples with more than four missing loci were excluded from subsequent analysis.

Population genetic structure analyses

We tested for deviations from Hardy–Weinberg Equilibrium in GenePop 3.4 (Raymond & Rousset, 1995*b*) using an exact probability test (Markov chain parameters were set to 100 batches with 1000 iterations per batch). We first treated the entire sample set as a single population representative of the entire species. We also performed separate analyses for island and mainland subsets. We combined the exact P values using Fisher's method and report the chi-square test across all loci and populations. We used GenAlEx 6.5 (Peakall & Smouse, 2006, 2012) to calculate allele frequencies, observed and expected heterozygosities, inbreeding coefficients, G-statistics, probability of identity (PI), and probability of identity for siblings (PI_{sibs}). We also used the analysis of molecular variance (AMOVA) framework offered within GenAlEx to partition genetic variation within and among *a priori* defined populations and regions (defined above). This AMOVA analysis provided estimates of overall and pairwise population genetic differentiation (F_{ST}), differentiation among regions (F_{RT}), differentiation among populations within regions (F_{SR}) (Excoffier, Smouse & Quattro, 1992; Peakall, Smouse & Huff, 1995), and their standardized (0,1) equivalents (Meirmans, 2006; Meirmans & Hedrick, 2011). We performed tests for departure from the null hypothesis of no genetic differentiation using 1000 random permutations and interpolated the missing data (Peakall & Smouse, 2006).

To identify potential population genetic structure in the absence of any *a priori* grouping of the samples, we used the Markov chain Monte Carlo (MCMC) Bayesian clustering approach implemented in the program STRUCTURE 2.3.4 (Pritchard, Stephens & Donnelly, 2000). For this analysis we ran the admixture model, with correlated allele frequencies and no location priors (Falush, Stephens & Pritchard, 2003). Burn-in was set to 50 000 iterations, followed by 50 000 MCMC iterations replicated 10 times for each value of the number of genetic clusters (K) from 1 to 10. We used STRUCTURE Harvester (Earl & vonHoldt, 2012) and the 'CorrSieve' package of R (Campana *et al.*, 2011) to determine K (Evanno, Regnaut & Goudet, 2005).

We used GenAlEx to test for isolation-by-distance across the study area using a Mantel test (Mantel, 1967) based on individual genotypes. We used 10 000 random permutations at the individual level to test for departure from the null hypothesis (no spatial genetic relationships).

Relatedness estimates

We tested the possibility that related individuals may prefer to nest together using the '*compareestimators*' function of the '*related*' package in R (Pew *et al.*, 2015) to compare the performance of four relatedness estimators simulated from the original dataset. Given similar performance [Pearson's

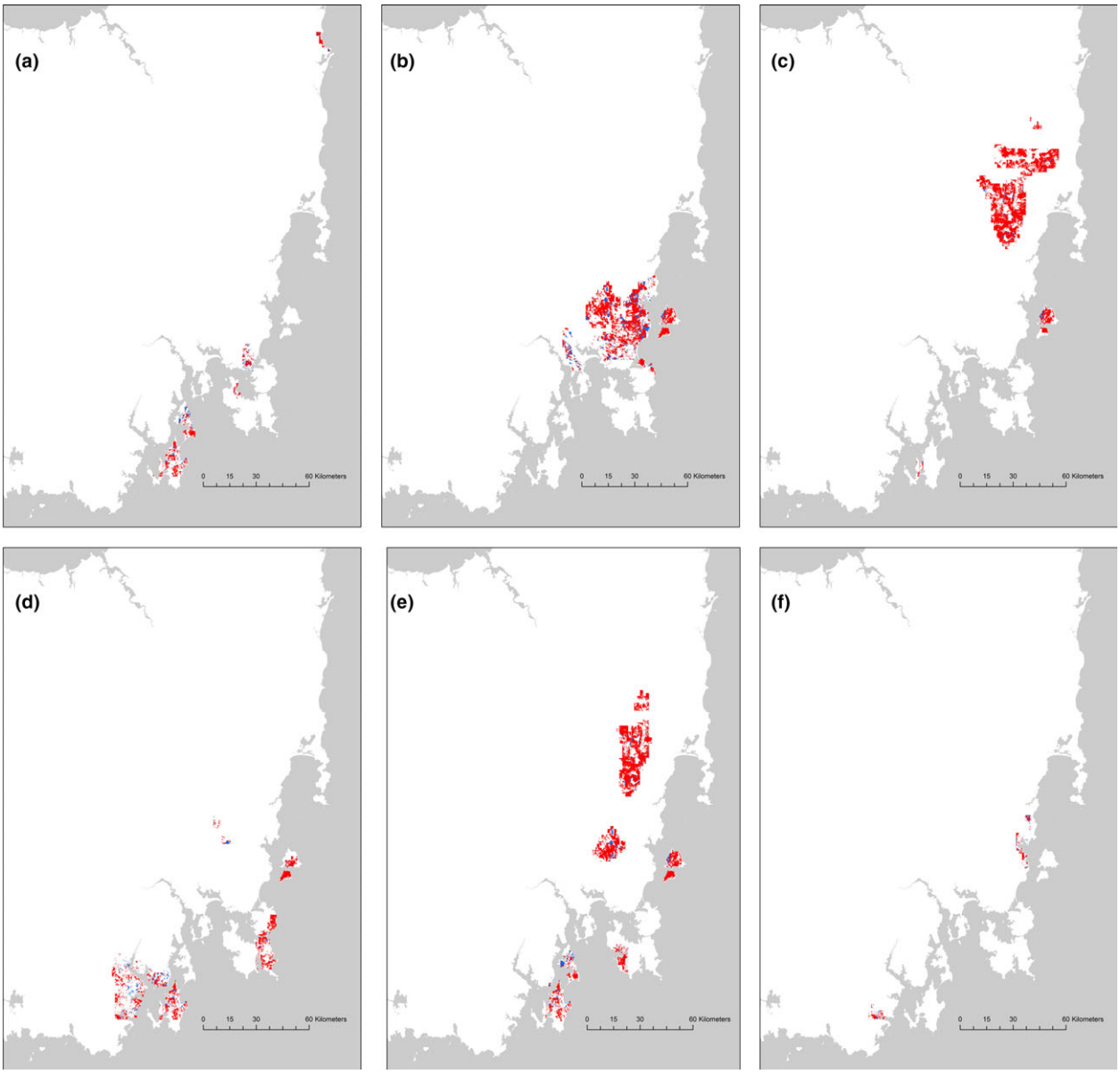

Figure 2 Locations and areas of habitat occupied by breeding swift parrots based on occupancy models (red = nesting habitat, blue = foraging habitat) in eastern Tasmania, Australia between (a) 2009, (b) 2010, (c) 2011, (d) 2012, (e) 2013 and (f) 2014. The location of nesting by the swift parrot population varies annually depending on where food is available, and <30% of the swift parrot population settles to breed on predator-free islands in any given year. Reproduced with permission from Webb *et al.* (2017).

correlation coefficients between observed and expected values: Wang (2002) = 0.707, Li, Weeks & Chakravarti (1993) = 0.709, Lynch & Ritland (1999) = 0.717, Queller & Goodnight (1989) = 0.696], we selected the Lynch & Ritland (1999) estimator (Supporting Information Fig. S1) and used the '*grouprel*' function to analyse relatedness within populations using 1000 iterations.

We used GenAlEx to calculate mean pairwise relatedness (Lynch & Ritland, 1999) of each pair of individuals within our sample compared to mean relatedness among all samples, and estimated the 95% confidence interval for mean pairwise r values via bootstrapping (Beck, Peakall & Heinsohn, 2008). We used random permutation of the data to generate a distribution for the null hypothesis (no relatedness within groups) and test for significance (process performed 1000 times). We included a control group of 15 siblings from five nests. We also used individual-focused multilocus spatial autocorrelation analysis for each sex to investigate potential sex-biased dispersal.

Population genetic simulations

In order to test the power of the microsatellite markers to detect potential population genetic structure ($F_{ST} > 0$ = 'genetic

Table 1 Source of swift parrot samples per region and per season

Region/Year	2010	2011	2012	2013	2014	2015	Total per Region
North Bruny Island (BN)	–	1	–	10	–	21	32
South Bruny Island (BS)	–	2	12	4	–	5	23
Buckland (BU)	3	–	–	9	1	–	13
Eastern Tiers (ET)	–	8	1	6	1	–	16
Meehan Range (ME)	8	–	–	–	–	–	8
Rheban (RH)	–	–	–	–	5	–	5
Southern Forests (SF)	–	–	3	–	3	–	6
Wielangta (WI)	6	–	–	–	–	–	6
Total per Year	17	11	16	29	10	26	109

differentiation'), and given the constraints on the total sample size, we implemented the program POWSIM v4.1 (Ryman & Palm, 2006). This program creates simulated populations of an expected divergence without the effects of migration or mutation, based on specific demographic parameters. As input we provided total allele frequencies from our study to simulate the process of genetic drift, at these starting allele frequencies, and defined effective population size(s). The program then subsamples the simulated populations at specified generations for given sample sizes, and performs a genetic homogeneity test for equivalent allele frequencies ($F_{ST} = 0$). The proportion of significant outcomes offers an estimate of the power of a given marker set to detect genetic differentiation, given the sampling frame. We set the effective population size (N_e) to 1000 and repeated the entire process of drift, sampling and statistical testing 10 000 times.

Using POWSIM, we first estimated the type I (α) error (i.e. falsely rejecting the null hypothesis of $F_{ST} = 0$ no differentiation) by setting drift to zero (sampling directly from the base population) and using different sample sizes (n = 10, 25, 50 and 100) from two generated populations (i.e. mainland and island). Second, we assessed the power to detect different F_{ST} values (N_e = 1000, t = 10, F_{ST} = 0.005; or N_e = 1000, t = 20, F_{ST} = 0.01) between two populations using different sample sizes (n = 10, 25, 50 and 100). We report Pearson's chi-square and Fisher's exact test, following the calculation in GENEPOP 3.4 (Raymond & Rousset, 1995*a*,*b*). In order to show the effect of allelic losses during the simulations, we report separate results from both runs where all original alleles were preserved and also runs where allelic loss had occurred (Ryman *et al.*, 2006).

In a complementary simulation approach, we also used the program EASYPOP v2.0.1 (Balloux, 2001) to estimate how many generations of restricted gene flow would be required to develop genetic differentiation similar to that found in our empirical dataset. We used equivalent parameter settings to POWSIM to simulate two populations (each including 250 males and 250 females, i.e. N_e = 1000) with mating set to monogamy with 40% extra pair copulation events (as observed in the wild swift parrot populations, R. Heinsohn unpublished data) isolated over 100 generations with different migration rates (m). We used Wright's island model to simulate isolation, using seven unlinked microsatellite loci (with mutation rate of 0.0005) and five possible allelic states (matching the average effective allele number of our loci), setting maximum variability in the initial populations (randomly assigned alleles).

In the first group of models, we simulated panmixia in the first 10 generations (m = 0.75 for both males and females), before setting a different migration rate for another 100 generations (m = 0, 0.001, 0.01, 0.05 and 0.1). In the second group of models, we simulated two divergent populations with F_{ST} = 0.02 (m = 0 for 40 generations), and then set different migration rates for another 70 generations as above. We then calculated the average unbiased F_{ST} values for each simulated generation based on 100 repeats.

Results

We obtained genetic data for 109 individuals (Table 1), comprising 63 males and 46 females (one sample per nest).

Microsatellite validation

For the locus Cfor3031 the software MicroChecker indicated the presence of null alleles (estimate of Oosterhout frequency of null alleles = 0.166), hence we excluded it from further analyses. Based on repeated genotypes, across the seven loci the average scoring error was 0.5% (range: 0–2.2%), and the average allelic dropout was 12.9% (range 8.6–19.4%). Across all seven loci the allele number ranged from 3 to 20 per locus.

Tests for Hardy–Weinberg Equilibrium

We found no deviation from Hardy–Weinberg Equilibrium across all seven loci at the species level (Fisher's χ^2 = 9.55, d.f. = 14, P = 0.795), or evidence for heterozygote deficit (P = 0.326, SE = 0.029) or heterozygote excess (P = 0.674, SE = 0.029) (Table S1). Only the locus Cfor3031 showed significant deviation from Hardy–Weinberg Equilibrium, but we excluded it based on the MicroChecker analysis for null alleles (Table S1). We found no deviation from the Hardy–Weinberg Equilibrium when the Tasmanian mainland (Fisher's χ^2 = 13.83, d.f. = 14, P = 0.463) and the offshore island populations (Fisher's χ^2 = 6.15, d.f. = 14, P = 0.963)

were considered separately. Mean expected heterozygosity among populations was 0.685 and observed heterozygosity values ranged from 0.42 to 0.9 (mean 0.679). The overall average fixation index was 0.007 (Table 2), consistent with Hardy–Weinberg Equilibrium. The five most variable loci ($PI_{sibs}(5) = 0.009$) were predicted to recover all unique genotypes, given the sample size.

Genetic differentiation in space and time

We failed to detect any evidence of population genetic structure in swift parrots. The genetic distance based AMOVA analysis partitioned only 0.17% of genetic variation between the mainland versus island regions ($F_{RT} = 0.002$, $F'_{RT} = 0.006$, $P = 0.258$) and 0.22% among populations within these regions ($F_{SR} = 0.002$, $F'_{SR} = 0.007$, $P = 0.325$; Table S2). Furthermore, no significant differences in F_{ST} were detected for any pairwise comparison between the populations (AMOVA: $F_{ST} = 0.004$, $P = 0.175$; Table S2), or over time (AMOVA: 0.37% among years, $F_{ST} = 0.004$, $F'_{ST} = 0.013$, $P = 0.201$). Using alternative allele frequency based G-statistics analysis also failed to detect any significant genetic differentiation (overall $G_{ST} = 0.002$, $P = 0.333$; overall $G''_{ST} = 0.009$, $P = 0.332$),

The STRUCTURE analysis outcome was consistent with the AMOVA and G-statistics analyses, indicating a single genetic cluster and no detectable population boundaries (Supporting Information Fig. S2, Table S3). Finally, at the level of individual genotypes, no significant isolation-by-distance was detected across the study (Mantel test >180 km, $N = 109$, $r = 0.048$, $P = 0.096$), nor within mainland Tasmania (Mantel test >180 km, $N = 54$, $r = 0.362$, $P = 0.362$).

Relatedness and sex-biased dispersal

Mean pairwise relatedness estimates (Lynch & Ritland, 1999) did not indicate higher than expected relatedness at any nesting site in either the 'related' (Supporting Information Fig. S3) or in the GenAlEx (Supporting Information Fig. S4) analyses. We also did not detect significant local individual-by-individual spatial genetic structure when females and males were considered separately (Fig. 3), indicating no evidence for a strong sex-biased dispersal pattern (Banks & Peakall, 2012).

Population genetic simulations

The PowSim results confirmed that risk of type I errors was below 5% across the full range of sample sizes that characterized this study (10–100; Supporting Information Fig. S5a). For our sample of individuals from mainland and island populations respectively, the simulation results indicated almost complete power (96%) to detect genetic differentiation if the real F_{ST} was 0.01 and reasonable power (67%) to detect differentiation if the real F_{ST} was 0.005 (Supporting Information Fig. S5b).

The EasyPop simulations confirmed that genetic differentiation develops quickly in the absence of any gene flow, as expected (even under the one-migrant-per-generation scenario with $m = 0.001$). With extensive gene flow of $m = 0.1$ per generation, a stable and low level of differentiation developed and persisted at $F_{ST} \sim 0.001$ (Supporting Information Fig. S6a). Conversely, when we started the EasyPop simulation at $F_{ST} \sim 0.02$, differentiation declined to a similar low level of $F_{ST} \sim 0.001$ at $m = 0.1$ per generation (Supporting Information Fig. S6b). Under more restricted gene flow of $m \geq 0.01$, F_{ST} exceeded 0.01 in the later generations of the simulation (Supporting Information Fig. S6).

Discussion

In this study, we present the first population genetic data for the critically endangered swift parrot. PVAs predict swift parrot population decline by 94% over just three generations (Heinsohn *et al.*, 2015), prompting recent revision of the species conservation status (BirdLife International, 2016; Threatened Species Scientific Committee, 2016). The assumptions underlying PVAs must be rigorously tested, particularly given the implications of Heinsohn *et al.* (2015) for swift parrot conservation and forest management. Here, we confirm a key assumption of Heinsohn *et al.* (2015), that is, the entire swift parrot population is a single, panmictic

Table 2 Population statistics for seven microsatellite markers of dinucleotide repeats for swift parrots. Column headings (from left to right) are: locus name, number of samples (N), fragment size range (bp), number of alleles (N_a), effective number of alleles (N_e), observed heterozygosity (H_O), expected heterozygosity (H_E), fixation index (F)

Locus	N	bp	N_a	N_e	H_O	H_E	F
Cfor1415[a]	112	204–214	6	3.221	0.652	0.689	0.055
Cfor2627[a]	111	142–180	17	6.397	0.874	0.844	−0.036
pCl3[b]	112	112–122	4	1.664	0.429	0.399	−0.074
SCMA 01[c]	110	160–206	20	10.364	0.9	0.904	0.004
SCMA 04[c]	99	251–291	17	7.054	0.848	0.858	0.011
SCMA 07[c]	106	283–301	8	2.946	0.632	0.661	0.043
SCMA 29[c]	100	220–224	3	1.787	0.42	0.441	0.047
Mean			10.7	4.776	0.679	0.685	0.007

Species of origin for the genetic markers were: [a]*Cyanoramphus forbesi* (Chan *et al.*, 2005), [b]*Calyptorhynchus latirostris* (White *et al.*, 2009), and [c]*Ara macao* (Olah *et al.*, 2015).

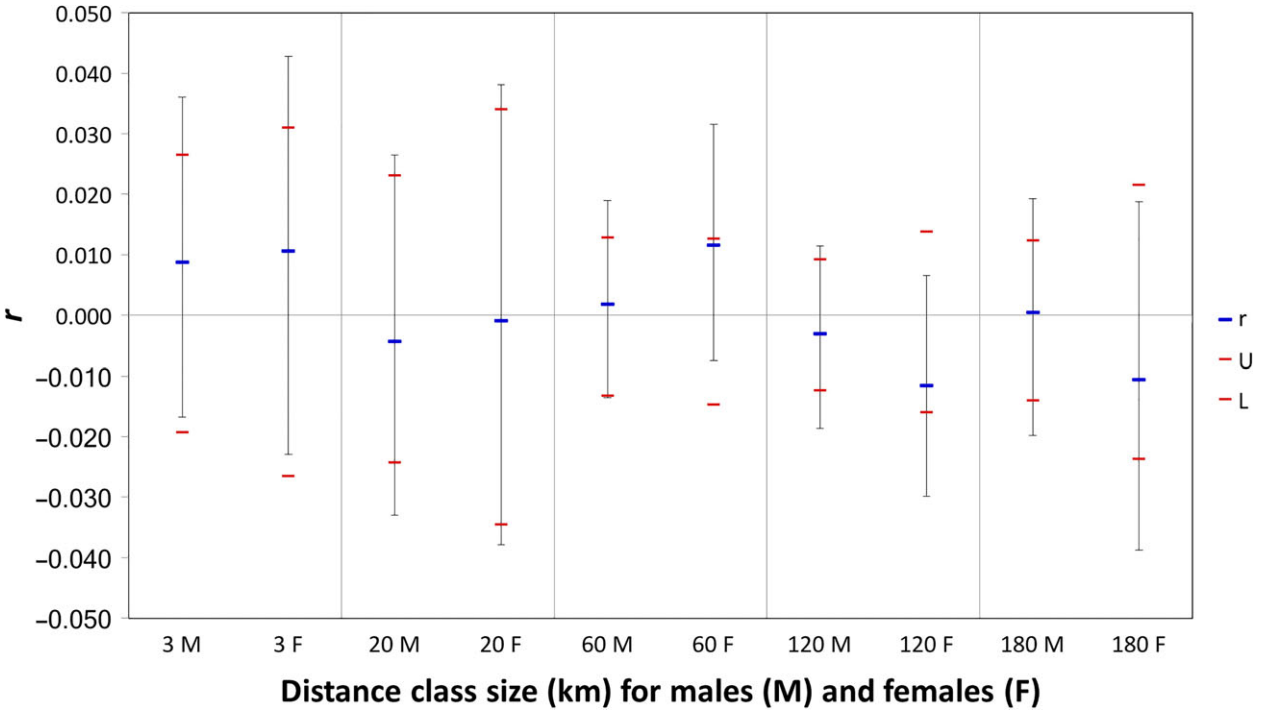

Figure 3 Sex-specific spatial genetic autocorrelation analysis for swift parrots comparing correlations for females versus males across study sites. The figure shows pairwise genetic distance (*rc*) for increasing distance class sizes (blue), 95% confidence intervals (red) about the null hypothesis of a random distribution and 95% confidence error bars about *rc* as determined by bootstrapping (black).

conservation unit and that isolated subpopulations do not exist on predator-free islands.

Our multifaceted population genetic analysis, which included robust tests for Hardy–Weinberg Equilibrium, and multiple tests for population genetic structure including AMOVA, G-statistics, Structure analysis and Mantel tests, found congruent and highly consistent results. No significant deviation from Hardy–Weinberg Equilibrium expectations was detected at either the species or regional levels (island vs. mainland), consistent with a very low average inbreeding coefficient ($F'_{SR} = 0.007$). We found no evidence for any significant population genetic structure across geographically defined regions, or among populations defined by space or time. Neither was any isolation-by-distance detected at the individual genotype level.

Our PowSim simulation confirmed that despite the challenges of collecting enough genetic material from a critically endangered nomadic population, we had adequate power to detect genetic structure ($F_{ST} > 0$) if it existed between islands and the Tasmanian mainland. However, the simulation drift process used in our method is not intended to replicate the true demography of the studied population, but to simulate their evolutionary history by randomly distributing the original alleles in a biologically reasonable way (Ryman *et al.*, 2006).

We found that F_{ST} was not significantly different from zero for swift parrots (mean $F_{SR} = 0.002$, $P < 0.325$). The EasyPop simulations indicated that high levels of contemporary gene flow best explain the observed lack of genetic differentiation. For example, at migration rates of $m = 0.01$ or less, genetic differentiation developed quickly in the simulations and reached a stable $F_{ST} > 0.01$ (Supporting Information Fig. S6a). Similarly, when starting the simulations at $F_{ST} = 0.02$, differentiation quickly declined at higher migration rates ($m = 0.01$ or more; Supporting Information Fig. S6b). We note that the high migration rates associated with the lower levels of differentiation are at least an order of magnitude higher than one migrant per generation ($m = 0.001$). The one migrant per generation rule of conservation genetics is considered a minimum level of gene flow to avoid loss of heterozygosity among populations (Wang, 2004). However, our simulations support the well-known caveat that one migrant per generation does not imply panmixia of different populations (Mills & Allendorf, 1996).

We conclude that our genetic findings collectively and consistently support the null hypothesis of a randomly mating, single panmictic swift parrot population. These genetic findings support predictions based on the monitoring of landscape scale fluctuation in food availability and population settlement patterns by swift parrots (Webb *et al.*, 2014, 2017). Those studies showed major fluctuation in the proportion of the swift parrot population that settled in island or Tasmanian mainland breeding habitats in any given year, as a consequence of annual variation in food availability (Fig. 2). For example, in some years breeding mainly occurs on the Tasmanian mainland (Fig. 2b, c, f) with few or no birds breeding on islands. In other years both the mainland

and islands are used (Fig. 2e), whereas in some year breeding is almost exclusively on islands (Fig. 2a, d). Such variable patterns of breeding indicate extensive gene flow among these habitats, consistent with the genetic results.

Our findings contrast with studies of other parrots, which typically show some degree of significant population genetic structure over space (White *et al.*, 2014; Olah *et al.*, 2017), but not always (Wright & Wilkinson, 2001; Wright, Rodriguez & Fleischer, 2005). However, our results are broadly consistent with the few other genetic studies of mobile resource specialists, for example comparable nectarivores (Kvistad *et al.*, 2015), owls (Marthinsen *et al.*, 2009) and seed eating passerines (Questiau *et al.*, 1999), where population genetic structure is limited or absent. Given the ecological similarities between our study system and those of other mobile resource specialists, swift parrots may be a good model species for understanding how resource fluctuation and encounters with threatening processes impact mobile populations more generally.

Our study highlights the potential population-level consequences of spatial overlap between unpredictable resource pulses (Webb *et al.*, 2017) and a widespread predator (Stojanovic *et al.*, 2014). Predator-free islands support <30% of the swift parrot population in a given year (Heinsohn *et al.*, 2015), but our study shows that these birds do not comprise a genetically isolated subpopulation. When food availability is limited on islands, most swift parrots settle on the Tasmanian mainland (Fig. 2) where, at some locations, sugar glider nest predation rates can be as high as 100% (Stojanovic *et al.*, 2014). When mobile species operate as a single conservation unit, localized threats may, given enough time, impact the entire population (Runge *et al.*, 2014). Therefore, it follows that conservation action in predator infested mainland habitats will be critical to prevent extinction of swift parrots. This must include limiting deforestation in breeding habitat (which may be related to predation severity, Stojanovic *et al.*, 2014), augmenting nesting habitat on islands, and protecting parrot nests in sugar glider infested forests.

For mobile species in unpredictable environments, lack of isolated subpopulations and few conservation units increases overall extinction risk when resources overlap with threats. Our results support the argument that in addition to targeting conservation action for mobile species at broad spatial scales (Cottee-Jones, Matthews & Whittaker, 2016), conservation efforts for mobile species should focus on reducing the likelihood that resources could attract animals into areas where threatening processes occur (Runge *et al.*, 2014). Where this is unavoidable due to low habitat availability, targeted conservation action at critical sites may be necessary to alleviate population level impacts of threatening processes.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Hardy–Weinberg Equilibrium (HWE) tests in GenePop for the swift parrot population.

Table S2. Pairwise population genetic differentiations of swift parrot samples originating from discrete breeding sites.

Table S3. STRUCTURE output and implementing the Evanno method (Earl & vonHoldt, 2012).

Figure S1. Performances of four non-likelihood relatedness estimators (L&L – Li *et al.*, 1993; L&R – Lynch & Ritland, 1999; Q&G – Queller & Goodnight, 1989; and W – Wang, 2002) on simulated datasets with the same locus characteristics as our own data.

Figure S2. Results from STRUCTURE Harvester (Earl & vonHoldt, 2012) indicating that a single genetic cluster best explains population genetic structure of swift parrots (*Lathamus discolor*) across their breeding range in Tasmania.

Figure S3. Histograms of the expected relatedness values within each population, using the 'related' package of R (Pew *et al.*, 2015).

Figure S4. Pairwise relatedness among different nesting sites of swift parrots across their breeding range (blue) with 95% confidence intervals (red) around the null hypothesis of zero relatedness using GenAlEx (Peakall & Smouse, 2012).

Figure S5. Simulated estimates (10 000 runs) of (a) type I error and (b) power when scoring seven microsatellite markers and sampling *N* individuals from two populations of swift parrots (*Lathamus discolor*).

Figure S6. EasyPop simulations for two swift parrot (*Lathamus discolor*) populations (each with 250 males and 250 females) with different migration rates (*m*).