Policy analysis

Slow breeding rates and low population connectivity indicate Australian palm cockatoos are in severe decline

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ABSTRACT

Dispersal dynamics can determine whether animal populations recover or become extinct following decline or disturbance, especially for species with slow life-histories that cannot replenish quickly. Palm cockatoos (*Probosciger aterrimus*) have one of the slowest known reproductive rates of any parrot, and they face steep decline in at least one of three populations comprising the meta-population for the species in Australia. Consequently, we estimated demographic rates and population connectivity using data from published field studies, population genetics, and vocal dialects. We then used these parameters in a population viability analysis (PVA) to predict the trajectories of the three regional populations, together with the trajectory of the meta-population. We incorporated dispersal between populations using genetic and vocal data modified by landscape permeability, whereby dispersal is limited by a major topographical barrier and non-uniform habitat. Our PVA models suggest that, while dispersal between palm cockatoo populations can reduce local population decline, this is not enough to buffer steep decline in one population with very low breeding success. The small population size and likely decrease in the meta-population of greater than 50% over three generations (49 years) supports a change of conservation status for Australian palm cockatoos from 'Vulnerable' to 'Endangered' under IUCN criteria. Our research provides an important demonstration of how PVA can be used to assess the influence of complex meta-population scale processes on the population trajectory of species that are challenging to monitor.

1. Introduction

Natural or human-induced fragmentation of species distributions creates separate, small populations that are vulnerable to decline from local threats or stochastic fluctuations in numbers (Frankham, 2005). However, local declines can be buffered by immigration from connected populations, thus increasing the effective population size and lowering the probability of extinction. The dynamics between small and partially connected populations are important in determining which populations recover or disappear following dramatic changes in distribution due to disturbance (Hanski, 1998; Sunnucks, 2011). Detailed life history data including dispersal rates are often not available (Morais et al., 2013), which can hinder effective management of threatened populations (Martin et al., 2012; Regan et al., 2005). Conversely, when life history data are available, population viability analysis (PVA) is valuable for understanding how animal populations respond to environmental change (e.g. habitat loss) and to identify the best management options

(Crouse et al., 1987; Drechsler et al., 1998). PVAs are computer simulation models that use demographic data to make quantitative predictions about population size over time and the probability of extinction (Beissinger and Westphal, 1998). PVAs are recognized as a powerful tool for developing management strategies for declining species, and have been used successfully as such for several species (Crouse et al., 1987; Heinsohn et al., 2009; IUCN, 2019; Williams et al., 2017). Surprisingly, predictions from PVA of population decline are rarely used to assess the conservation status of species (Heinsohn et al., 2015)

A disproportionate number of species in the order Psittaciformes (hereafter parrots) are threatened with extinction, with habitat loss and fragmentation the main threatening processes (Olah et al., 2016). Of the 398 extant parrot species, 28% are threatened with extinction ('critically endangered', 'endangered' or 'vulnerable' according to IUCN criteria, IUCN, 2019), constituting a greater proportion than in the three largest avian orders *Passeriformes* (5913 spp., 10%), *Caprimulgiformes* (593 spp., 9%), and *Piciformes* (484 spp., 7%). Parrot species at most risk are those

with large body size, slow reproduction, dependence on forest, and small historical distributions (Olah et al., 2016; Toft and Wright, 2015). Many cockatoo species (family *Cacatuinae*) fit this description, with over half threatened with extinction (Juniper and Parr, 1998; Snyder et al., 2000).

Palm cockatoos (*Probosciger aterrimus*) are the largest cockatoo, reaching 1.2 kg and 65 cm in length (Forshaw, 2002), and occur in lowland New Guinea, the Aru Islands, and Cape York Peninsula north of 14.5°S on mainland Australia. The global conservation status of palm cockatoos under IUCN criteria is 'least concern' but within Australia they are listed as 'vulnerable' due to the slow reproductive rates recorded for the population on eastern Cape York Peninsula, altered habitat availability due to changed fire regimes and large scale vegetation
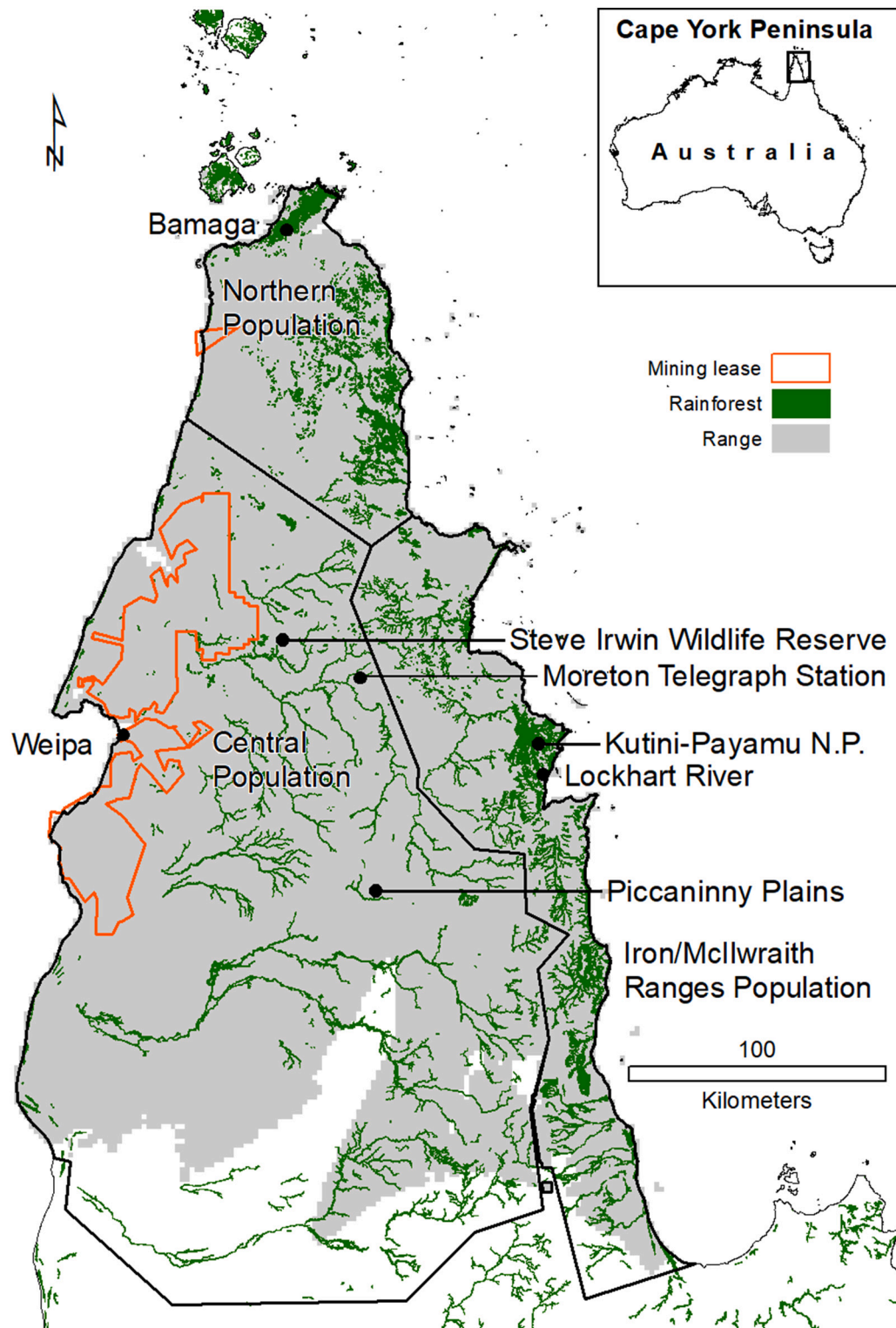

Fig. 1. Map of Cape York Peninsula showing the bioclimatic range of palm cockatoos, major rainforest patches, and the boundaries delineating the three populations in this study. Also shown are the main study sites (Bamaga, Piccaninny Plains, Steve Irwin Reserve, Moreton Telegraph Station, and Kutini-Payamu National Park) and mining lease boundaries.

clearing by mining operations (Garnett et al., 2011; Gould, 2011). At Kutini-Payamu National Park at the northern end of the Iron and McIllwraith Ranges on eastern Cape York Peninsula, females were found to produce just 0.11 offspring per year on average due to small, infrequent clutches (a single egg every 2.2 years on average) and high predation of eggs and nestlings (Murphy et al., 2003). Subsequent population viability analysis forecast rapid decline for this population (Heinsohn et al., 2009).

The conclusions concerning likely steep population decline of the Iron/McIllwraith population were based on two key assumptions. First, the models showed that the population could only be stable if a substantial proportion of the birds lived close to 100 years. The conclusion that this is unlikely was based on known lifespans of captive and wild cockatoo species (Heinsohn et al., 2009). The second assumption was that the Iron/McIllwraith population is largely disconnected from other populations on Cape York Peninsula. While it is possible that dispersal from adjacent populations helps maintain numbers at the Iron/McIllwraith Ranges, recent published evidence regarding genetics and vocal dialects suggests that connectivity with other regions on Cape York Peninsula is at least partially limited. Genetic differentiation (Keighley et al., 2018), some distinct components of vocal dialects (Keighley et al., 2016; Zdenek et al., 2015), and a higher frequency of manufacture of a unique tool type (Heinsohn et al., 2017) by the palm cockatoos at Iron/McIllwraith Ranges compared to elsewhere on Cape York Peninsula are explained by landscape resistance models. These models incorporated elevated terrain and non-uniform habitat as a barrier to connectivity between populations (Keighley et al., 2019).

Here we use our previously published estimates of demographic rates and connectivity between populations in population viability analysis to (a) explore whether the observed extent of connectivity between populations revealed by recent genetic and vocal data is sufficient to improve the predicted trajectory of the Iron/McIllwraith Range population, and (b) to use new knowledge of inter-connectivity between populations to determine the likely trajectory and conservation status of the entire meta-population of Australian palm cockatoos.

2. Methods

2.1. Study species and populations

Palm cockatoos feed on the seeds of rainforest and woodland tree species, and for nesting require tree hollows, which they prefer in woodland less than 300 m from rainforest (Murphy et al., 2003). Fig. 1 shows the bioclimatic range of palm cockatoos on Cape York Peninsula, however the distribution of rainforest (also shown) provides the best predictor of their patchy distribution. Palm cockatoos face varying threatening processes throughout their range. They compete with sulphur-crested cockatoos (*Cacatua galerita*) for nests, and suffer high rates of nest predation by varanid lizards (*Varanus* spp.), white-tailed rats (*Uromys caudimaculatus*), black butcherbirds (*Cracticus quoyi*) and amethystine pythons (*Morelia amethistina*) (Murphy et al., 2003). Altered fire regimes affect recruitment and persistence of nest-trees (Murphy et al., 2003; Murphy and Legge, 2007), and tropical cyclones can temporarily decrease the availability of trees for nesting and feeding. Mining for bauxite on the western side of Cape York Peninsula (Fig. 1) involves complete vegetation clearing, and palm cockatoos avoid mine-sites for at least 23 years post rehabilitation (Gould, 2011).

To run the PVAs, we used detailed demographic data from a three year study of palm cockatoos from the Iron/McIllwraith Ranges population on Cape York Peninsula, Australia (Murphy et al., 2003), together with genetic and vocalization data describing the extent of connectivity

with other major populations. The three populations used in this study inhabit 1) the Iron/McIllwraith Ranges on the eastern side of Cape York Peninsula, 2) the smaller but inter-connected patches of rainforest on the western side of the Great Dividing Range, and 3) forest patches closer to the tip of Cape York Peninsula (Fig. 1). The Iron/McIllwraith Ranges population is considered to be one contiguous population. Some connectivity occurs between the Iron/McIllwraith population and the western population on Cape York Peninsula via gallery forest corridors that occur along major rivers to the west of the mountain ranges (Fig. 1). However, studies of population genetics and vocal characteristics have shown that the Iron-McIllwraith Ranges population is at least partially distinct from other palm cockatoos on Cape York Peninsula. Palm cockatoos living in rainforest on the central river systems and small patches of rainforest on the west coast and tip of Cape York Peninsula are more similar in this regard. See Zdenek et al. (2015), Keighley et al. (2016), Keighley et al. (2018), and Keighley et al. (2019) for a full description of field sites and genetic and vocal datasets.

2.2. Population viability analysis

2.2.1. Modelling approach and parameters

VORTEX software is an individual-based simulation program of the deterministic and stochastic forces that affect the persistence of small populations. We used VORTEX (Lacy et al., 2014) to model population trajectories from individuals' sequential life history events (e.g. birth, death, reproductive success, dispersal) based on data from field studies. Where good quality data were not available for certain parameters, we made conservative assumptions (informed by other similar species where possible) so that output trajectories reflected the 'best case' scenarios for our study system (i.e. where the true situation is likely to be worse). Model outputs typically summarize population growth, extinction probability over the simulated time period, time until extinction, as well as the average size and genetic variation in extant populations. The available data were most suitable for deterministic evaluations of population growth or decline rather than extinction probability; we use this output primarily as a means of assessing conservation status according to IUCN criteria concerning rates of population decline (IUCN, 2019).

We ran 1000 simulations for each VORTEX model, with extinction occurring when only one sex remained. Simulations were run with a timeframe of three generations for palm cockatoos (estimated at 48.9 years) (Bird et al., 2020), as this figure is used as a benchmark for rates of population decline under IUCN criteria for threatened species listings (IUCN, 2019). VORTEX models require an estimate of the level of concordance between reproductive success and mortality. We assumed low concordance because field observations suggest that, although palm cockatoos may fail to breed, this has no apparent effect on their survival (Murphy et al., 2003).

The population of palm cockatoos on Cape York Peninsula has been estimated at 2600 (Storch, 1996) and 3000 individuals (Garnett et al., 2011). We use the larger of these estimates divided into the three sub-populations shown in Fig. 1 but caution that this is optimistic. We used the estimate in Heinsohn et al. (2009) for the population of palm cockatoos at Iron/McIllwraith Ranges (1000 individuals: 500 males, 500 females) and allocated 1700 individuals to the central population and 300 individuals to the smaller patches of habitat in the north. We allowed population size to fluctuate widely by calculating carrying capacities in each population as being 1.5 times larger than the initial population size. We included inbreeding in the models using the default value used in VORTEX of 6.29 lethal equivalents (genetic load of recessive genes that would kill homozygous individuals) (O'Grady et al., 2006). Unless otherwise specified, demographic values used in our

Table 1

Demographic values used in models.

Parameter	Value
Initial population size (carrying capacity)	Iron/McIlwraith Ranges 1000 (1500) Northern 300 (450) Central 1700 (2550) (Garnett et al., 2011; Heinsohn et al., 2009; Storch, 1996)
Age of first reproduction by males/females	4 (Murphy et al., 2003)
Maximum age	100 (Heinsohn et al., 2009)
Mortality	See Table 2
Maximum progeny per year	1 (Murphy et al., 2003)
Proportion males (sex-ratio) at hatching	0.5 (Murphy et al., 2003)
Percentage adult females breeding	Limited by fluctuating hollow availability (Heinsohn et al., 2009)
No. of offspring per female per year	0.11 ± 0.02 Iron/McIlwraith Ranges (all models), Other Cape York Peninsula populations (Models *1, 2, 3 & 4*) (Murphy et al., 2003) 0.30 ± 0.04 Other Cape York Peninsula populations (Models 5–9)
Environmental variation (%)	10
Percentage of males in breeding population	100
Mating system	Long-term monogamy (Murphy et al., 2003)
Dispersal	(See Table 3)

Table 2

Estimated mortality rates (percentage) and standard deviation for males and females over five age-classes (years) (Heinsohn et al., 2009; Saunders, 1982).

	Mortality	Standard deviation
Female age		
0–1	16.6%	3.4%
1–2	8.8%	1.8%
2–3	9.0%	1.8%
3–4	9.4%	1.7%
4+	9.4%	1.7%
Male age		
0–1	16.6%	3.4%
1–2	8.8%	1.8%
2–3	9.0%	1.8%
3–4	6.8%	1.7%
4+	6.8%	1.7%

simulations follow Heinsohn et al. (2009) and are given in Table 1.

2.2.2. Mortality

Palm cockatoos are very long-lived and no age-specific mortality data exist for the species. Mortality schedules including sensitivity analyses were evaluated by Heinsohn et al. (2009) in previous PVAs. These were based on mortality data from Carnaby's black-cockatoos (*Calyptorhynchus latirostrus*), which are the most extensive for any cockatoo species (Saunders, 1982). Here we used a method for background adult mortality rate (*m*) specific to palm cockatoos which we derived from generation time where Generation time = $(1/m)$ + age of maturity. Generation time has been determined via expert elicitation to be 16.3 years and age of maturity is 4 years (Bird et al., 2020). This yields an annual adult mortality rate of 8.1% per annum. This method has been shown to produce baseline mortality rates that were consistent with field observation of similar species (Heinsohn et al., 2015). Here the mortality rates derived from generation time accord well with the values shown by Heinsohn et al. (2009) to be the most plausible. However the study with the best mortality data for a black cockatoo species (Saunders, 1982) showed that females suffer slightly higher mortality than males. We

consequently adjusted our mean adult mortality so that females had slightly higher mortality in proportion to sexual differences shown by Saunders (1982) (Table 2). The age distribution using these data are shown in Fig. 2.

2.2.3. Dispersal between populations

VORTEX models exchange of individuals between populations via specification of the rate between each pair of populations in the meta-population. Palm cockatoos are largely sedentary and use the same territories between years (Murphy et al., 2003), but it is unknown how old they are, or how far they go, when juveniles disperse. A recent genetic study indicated higher rates of exchange among palm cockatoos from different areas on Cape York Peninsula west of the Great Dividing Range, but less movement between the eastern population and all other populations (Keighley et al., 2018). We tested four dispersal scenarios and always assumed survival of dispersing individuals in keeping with our deliberate bias towards best case scenarios.

Our first dispersal model was based on information from other cockatoo species. We used detailed information from Major Mitchell's cockatoos (*Cacatua leadbeateri*) and galahs (*Cacatua galerita*). In both species roughly 7.5% of individuals between two and four years old disperse more than 20 km (Rowley, 1983; Rowley and Chapman, 1991). We assumed that this proportion of long-distance dispersers is similar for palm cockatoos and used this figure to model the proportion of individuals that inter-change between breeding populations each year. In our first model we therefore designated 7.5% of individuals between two and four years old as switching populations every year in total, spread evenly between the populations without any restriction (3.75% from each population to each other population, Table 3: Model 1).

The second dispersal model incorporated recent evidence suggesting major restrictions on connectivity to the Iron Range from the Central/Western population on Cape York Peninsula. This evidence includes variation between populations in genomic and mitochondrial single nucleotide polymorphisms (Keighley et al., 2018) and acoustic contact calls (Keighley et al., 2016). Iron/McIlwraith Ranges palm cockatoos differ the most, both genetically and acoustically, to others on Cape York Peninsula, whereas the birds in other areas tend to be more similar to each other. In the second dispersal scenario we recognize the impedance due to steep elevation change westwards from Iron/McIlwraith Ranges and by the pattern of limited suitable inter-connecting habitat in the form of discreet rainforest corridors (Keighley et al., 2019). We standardized the resistance values of the elevation and habitat surfaces used in Keighley et al. (2019) to the same range and added them to form a combined 'habitat and elevation' resistance surface. Output resistance values were obtained using the method in Keighley et al. (2019) and were averaged between the three populations, inverted to imply connectivity rather than resistance and standardized to between 0 (low connectivity) and 1 (high connectivity). See Table 4 for average resistance and connectivity values between populations. The product of the connectivity values and the dispersal proportions used in the first dispersal model formed the second dispersal scenario (Table 3: Model 2).

The third dispersal model recognized that dispersal between Iron/McIlwraith Ranges and other populations may be largely one-way, i.e. into Iron/McIlwraith Ranges. This is based on the steep decline of the population at Iron/McIlwraith Ranges and the likelihood that it creates a 'sink' for the meta-population, and is supported by the presence of unique mitochondrial haplotypes in the Iron/McIlwraith Ranges population (Murphy et al., 2007). We therefore conducted simulations using the dispersal values of Model 2 above but without dispersal out of Iron/McIlwraith Ranges (Table 3: Model 3).

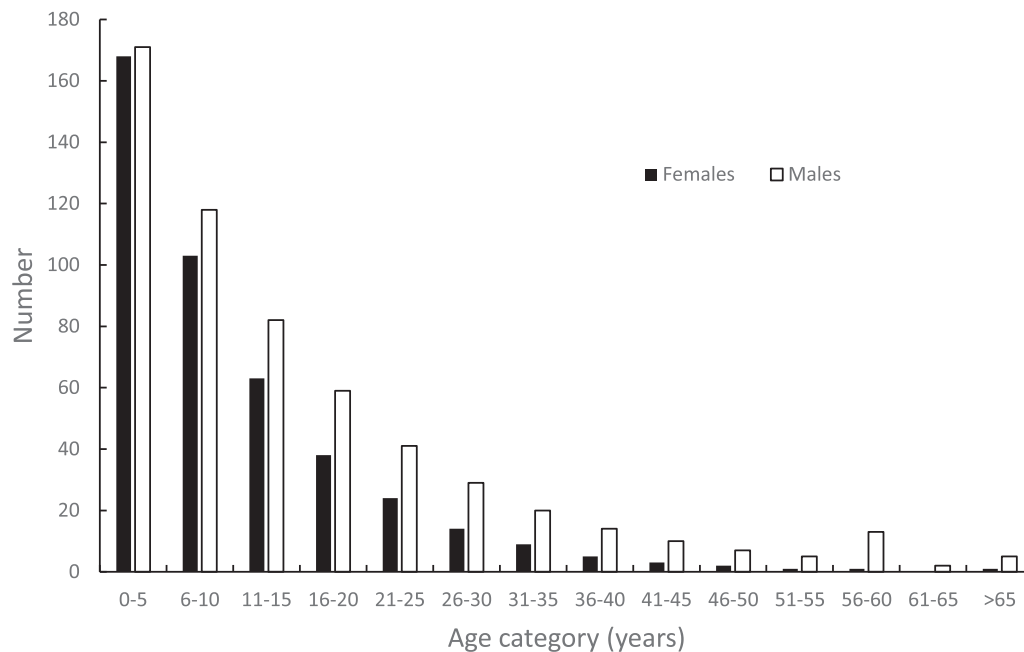Our fourth dispersal model tested the hypothetical situation of much

Fig. 2. The simulated age structure of the palm cockatoo population, divided by sex, using mortality rates derived from generation time (Bird et al., 2020) and other cockatoo species (Saunders, 1982). The oldest female in this analysis was 66 years, whereas there were males aged 67, 71, 74, 79, 87, and 106 years.

Table 3

Dispersal values for two to four year old palm cockatoos between populations. Model 1: Dispersal based on other cockatoo species (7.5% of 2–4 year old individuals disperse to two other populations) (Rowley, 1983; Rowley and Chapman, 1991). Model 2: dispersal adjusted for landscape permeability based on elevation and habitat (Keighley et al., 2018; Keighley et al., 2019; Keighley et al., 2016). Model 3: one-way dispersal into Iron/McIllwraith Ranges. Model 4: hypothetically high dispersal (50% of 2–4 year old individuals disperse evenly between populations).

Source	Destination		
	Iron/McIlwraith	Northern	Central/West
Model 1			
Iron/McIllwraith		3.75%	3.75%
Northern	3.75%		3.75%
Central/West	3.75%	3.75%	
Model 2			
Iron/McIllwraith		1.93%	2.53%
Northern	1.93%		2.76%
Central/West	2.53%	2.76%	
Model 3			
Iron/McIllwraith		0	0
Northern	1.93%		0
Central/West	2.53%	2.76%	
Model 4			
Iron/McIllwraith		25%	25%
Northern	25%		25%
Central/West	25%	25%	

Table 4

Mean pairwise resistance and connectivity values between three populations of palm cockatoos on Cape York Peninsula (Keighley et al., 2019).

	Iron/McIllwraith range	Northern	Central/west
Average resistance			
Iron/McIllwraith	13.78854	177.4557	117.1249
Northern	177.4557	0	127.6351
Central/west	117.1249	127.6351	125.2801
Connectivity			
Iron/McIllwraith	0.958985	0.472152	0.651608
Northern	0.472152	1	0.620345
Central/west	0.651608	0.620345	0.62735

higher rates (50%) of individuals between the ages of two and four years old dispersing between populations (Table 3: Model 4). This model was included to see if higher levels of dispersal between populations could ameliorate the downward trajectory at Iron/McIllwraith Ranges (Heinsohn et al., 2009).

2.2.4. Reproductive success, sexual maturity and mating system

We used the same parameters as Heinsohn et al. (2009) for palm cockatoo reproductive success, sexual maturity, and mating system (Table 1). Heinsohn et al. (2009) established that the low reproductive rate at Iron/McIllwraith Ranges meant that the birds would have to be extraordinarily long-lived for the population to be stable. It is currently unknown whether reproductive success at Iron/McIllwraith Ranges is similar to other populations on Cape York Peninsula. Baseline models for the Iron/McIllwraith population can be found in Heinsohn et al. (2009).

For this study, we initially used the reproductive rate calculated for Iron/McIllwraith Ranges (0.11 $\pm$ 0.02 offspring per year, Heinsohn et al., 2009) as the baseline for our simulations for all populations (Models 1 to 4, Table 5). We then allowed for the possibility that reproductive success is higher in populations outside of Iron/McIllwraith Ranges by iteratively increasing the reproductive rate until these populations (if isolated) were stable ($r = 0$). The reproductive rate at which the populations became stable was 0.30 $\pm$ 0.04 offspring per year. Thus, Models 5 to 8 correspond to Models 1 to 4 but differed in the use of higher reproductive rates for the other (non- Iron/McIllwraith Ranges) populations.

We included one further model (Model 9) to test the impact on the meta-population if the Central/west population is in fact much larger and therefore a greater 'source' via dispersal for the declining Iron/McIllwraith Ranges population. In this model the initial population size for the Central/west population is 3000 individuals.

We used the method in Heinsohn et al. (2009) to model the effect of gradual loss of nest hollows due to fire, wind and decay, their creation by cyclones when high winds break branches and open the inside of the tree to rot and termite activity, and the impact of this process on the number of breeding females. Our models set the percentage of females (F) that bred each year according to the number of available hollows (H) using the VORTEX formula MIN (1; H/F)*100 where MIN takes the minimal value of either 1, where 100% of females get a breeding hollow, or H/F,

Table 5

The stochastic annual population growth rate (*r*) and change (%) over three generations (49 years) under nine modelled scenarios for three inter-connected populations of Australian palm cockatoos, and the meta-population. Models 5–8 examine the effects of increased reproductive success for all populations outside of Iron/McIlwraith Ranges, and correspond to Models 1–4 in all other values. Model 9 examines the impact on the meta-population if the Central/west population is larger.

	Population	*r*	Decrease
Model 1	Iron/McIlwraith Ranges	−0.056	−93.4%
(dispersal based on data from other species)	Northern	−0.017	
	Central/west	−0.059	
	Meta-population	−0.055	−94.1%
Model 2	Iron/McIlwraith Ranges	−0.055	−92.9%
(dispersal adjusted for landscape permeability)	Northern	−0.017	
	Central/west	−0.058	
	Meta-population	−0.055	−93.8%
Model 3	Iron/McIlwraith Ranges	−0.053	−92.2%
(one-way dispersal into Iron/McIlwraith Ranges)	Northern	−0.028	
	Central/west	−0.059	
	Meta-population	−0.055	−93.9%
Model 4	Iron/McIlwraith Ranges	−0.057	−93.8%
(high dispersal between populations)	Northern	0.003	
	Central/west	−0.064	
	Meta-population	−0.055	−94.5%
Model 5	Iron/McIlwraith Ranges	−0.033	−79.8%
(Model 1 + higher reproductive success outside Iron/McIlwraith Ranges)	Northern	0.071	
	Central/west	−0.014	
	Meta-population	−0.013	−59.9%
Model 6	Iron/McIlwraith Ranges	−0.036	82.9%
(Model 2 + higher reproductive success outside Iron/McIlwraith Ranges)	Northern	0.065	
	Central/west	−0.010	
	Meta-population	−0.012	−55.1%
Model 7	Iron/McIlwraith Ranges	−0.033	−80.3%
(Model 3 + higher reproductive success outside Iron/McIlwraith Ranges)	Northern	0.069	
	Central/west	−0.011	
	Meta-population	−0.012	−55.6%
Model 8	Iron/McIlwraith Ranges	−0.030	−76.9%
(Model 4 + higher reproductive success outside Iron/McIlwraith Ranges)	Northern	0.090	
	Central/west	−0.038	
	Meta-population	−0.021	−79.5%
Model 9	Iron/McIlwraith Ranges	−0.028	−74.2%
(Model 6, larger Central/west population)	Northern	0.089	
	Central/west	−0.001	
	Meta-population	−0.009	−46.7%

where a lower proportion of females get to breed because there are enough hollows for them all. This formula has the property of allowing all adult females to breed if there are sufficient hollows, or only as many females as there are available hollows. The initial number of available hollows was set for each population following Heinsohn et al. (2009), whereby each male in a pair defends 1.5 hollows on average, meaning that fewer are available for breeding. Two processes captured the loss and creation of hollows. Field data have shown that the loss of breeding hollows due to fire, wind and decay is ~1% per year (calculated from data in Murphy et al., 2003). Offsetting the loss of hollows is the episodic creation of potential new hollows when high winds during cyclones break branches, leading to rot and termite activity (Murphy and Legge, 2007). However, it is important to note that 1) the number of these new hollows that actually became nesting hollows, and how long the process takes, are unknown, and 2) the number of nest trees destroyed in the cyclone was unknown. Following Heinsohn et al. (2009) we included cyclones as occurring approximately every 20 years. The gradual loss and episodic addition of nesting hollows was programmed in VORTEX by first creating a 'catastrophe' that occurs every 20 years on average, and second, creating a function for each population that allowed both loss of hollows at 1% per year combined with the addition of new hollows when each cyclone occurred. New hollows were assumed to be available the year following the cyclone. The number of hollows thus

available each year was then used to determine the proportion of breeding females described above.

3. Results

The simulations presented here predict severe declines in the meta-population ranging from 46.7–94.5% over three generations (49 years) and in the Iron/McIllwraith population from 74.2–93.8%. The probability of extinction within 49 years for the meta-population *P*(*E*) was zero in all cases. Models 1–9 and their output are summarized in Table 5. It is important to note that baseline models presented in Heinsohn et al. (2009) showed that the very low reproductive success of the Iron/McIllwraith population is causing severe population decline. That analysis examined the mortality rates and age structure that would be necessary to maintain population stability, and the authors concluded that the birds would need unrealistically long lifespans for that to occur. This study uses the low reproductive rates at Iron/McIllwraith Ranges and new measures of probable lifespan based on generation time, but also explores the implications if reproductive rates at the other populations are higher.

Our simulations were primarily aimed at determining rates of population decline that specifically address IUCN criteria regarding the extent of predicted population decline over three generations. We
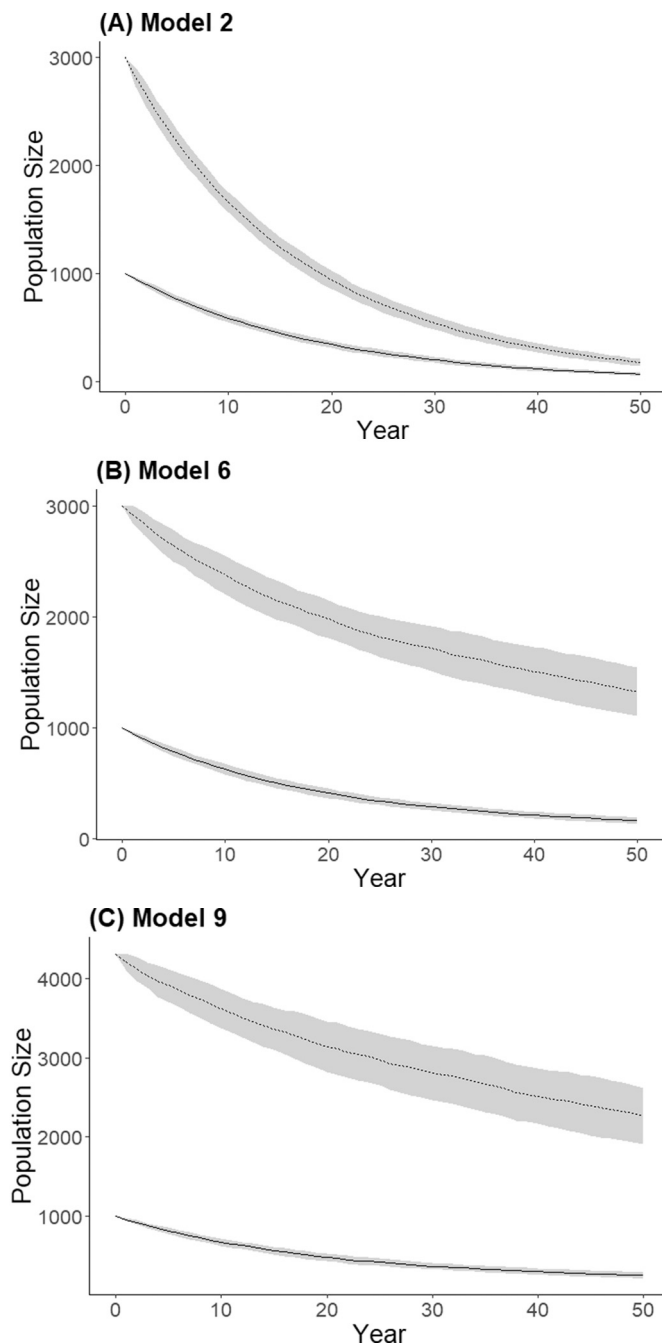
Fig. 3. A selection of predicted population trajectories for Iron/McIlwraith population and the meta-population. The reference year (Year 0) is 2018. In all models, upper (dotted) line = meta-population and lower (unbroken) line = Iron/McIlwraith population. Standard deviations, shown as ribbons, are given for each year of predictions. Model 2 shows dispersal adjusted for landscape permeability. Model 6 is based on Model 2 but allows higher reproductive success outside the Iron/McIlwraith Ranges. Model 9 is based on Model 6 but has a larger Central/west population. See Table 5 for full descriptions of the models.

suggest the most appropriate models to use for assessment of conservation status are Models 6 and 7 (Table 5). These use conservative estimates of dispersal based on habitat distribution and topographic influences on movement (Keighley et al., 2019). They also conservatively assume that populations outside Iron/McIlwraith Ranges have more than two and half times the reproductive success of the Iron/McIlwraith population. In spite of presenting such best-case scenarios,

Models 6 and 7 predict a 55.1–55.6% meta-population decline and 80.3–82.9% decline in the Iron/McIlwraith Ranges population within three generations. Models that used higher rates of dispersal (Models 4 and 8) predicted higher rates of decline for the meta-population (79.5% and 94.5%). Representative population trajectories for the meta-population and Iron/McIllwraith Ranges are shown in Fig. 3.

In general, we found that altering the dispersal scenario affected population trajectories only slightly, whereas the rate of meta-population decline was reduced when higher rates of reproduction were applied to populations outside of the Iron/McIllwraith Ranges. The trajectory of the Iron/McIllwraith Ranges population was also little affected by different dispersal scenarios, unless other populations had higher reproduction. In that case, the scenario of higher dispersal (Model 8) improved the trajectory of the Iron/McIllwraith population. Model 9 showed how the size of the population neighbouring Iron/McIllwraith Ranges (the potential 'source' population) affects the meta-population trajectory. When the Central/west population was increased in the model from 1700 to 3000 individuals, the decrease in the meta-population over three generations went from 55.1% to 46.7% (Table 5).

4. Discussion

Our PVA models suggest that the conservation status of palm cockatoos in Australia is much worse than suggested by their current 'Vulnerable' status (Garnett et al., 2011). The >50% meta-population decline over three generations (49 years) predicted over all our models, except one with overly optimistic population size (Model 9), supports a change in conservation status for Australian palm cockatoos to 'Endangered' according to Red List Criterion A3b (IUCN, 2019). The likely small population size (now <2500 individuals) combined with continual decline also supports a revision to "Endangered" status under Red List Criterion C1. Our models are best-case scenarios, so in reality the true rate of population decrease is likely to be higher. The analysis was optimistic because five of the models (Models 5–9) assume that the Central/west and Northern populations both have substantially higher (>2.5 times) reproductive rates than those observed at Iron/McIllwraith Ranges, to the extent that they would be stable if isolated ($r = 0$). Further research on the reproductive rates of the non-Iron/McIllwraith populations is clearly required. If these estimates prove (as is likely the case) overly optimistic, the appropriate level of listing for the meta-population may in fact be "Critically endangered' as suggested by the models that used lower reproductive rates (Models 1–4, decrease over three generations, 93.8–94.5%). Our model with a larger Central/west population demonstrates that meta-population decline may be slower in that case, suggesting that better estimates of population size are also required.

The analysis presented here builds on previous PVAs showing that the population of Australian palm cockatoos on the east coast of Cape York Peninsula (Iron/McIlwraith Ranges) is in steep decline due to low reproductive success (Heinsohn et al., 2009). Low reproductive rates are typical of large parrot species (Olah et al., 2016), but palm cockatoos have especially slow recruitment to the population because they lay just one egg every two years on average, with infertile eggs contributing to low reproductive success, and most eggs and nestlings eaten by predators (Murphy et al., 2003). However, as noted by Heinsohn et al. (2009) it was not clear whether the declining population at Iron/McIlwraith Ranges is buffered by connections to other, possibly more productive, populations on Cape York Peninsula. The present analysis uses new, informative genetic and vocal dialect data to estimate the extent of connectivity between the three major palm cockatoo populations. The present PVA models show that population connectivity does little to alter the severe downward trajectory of the Iron/McIlwraith population, and that even optimistic scenarios show the meta-population is steeply declining.

Despite ongoing debate about the accuracy of PVA population trajectories, it is broadly accepted that the trends they predict are reliable for formulating management strategies when good quality demographic

data are available (Ball et al., 2003; Brook et al., 1997; Brook et al., 2000; Lahoz-Monfort et al., 2014; Lindenmayer and McCarthy, 2006). However the quality of the data and any assumptions require explicit evaluation (Coulson et al., 2001). We used conservative assumptions in our simulations so that our population projections represent best-case scenarios. The real-world trajectories are likely to be worse, which adds confidence to our prediction that Australian palm cockatoos are in severe decline. Our simulations follow from those of Heinsohn et al. (2009) with key data and assumptions regarding longevity, reproductive senescence, and age of first breeding evaluated there. Here we evaluate five key assumptions unique to the current study.

First, we used high quality genetic (Keighley et al., 2018) and vocal dialect data (Keighley et al., 2016; Zdenek et al., 2015) to estimate population connectivity and dispersal. Our initial model was based on robust data from other cockatoo species (Rowley, 1983; Rowley and Chapman, 1991), however these rates were adjusted further for land-scape permeability values calculated in Keighley et al. (2019) based on the mosaic pattern of the birds' preferred rainforest habitat. Genetic and vocal dialect data showed that the greatest difference between populations on CYP is between the Iron/McIllwraith population and elsewhere. This difference is very likely to be because the Iron/McIllwraith population is partially isolated by the Great Dividing Range with connections only via major rivers (e.g. Pascoe and Wenlock Rivers, Fig. 1). By comparison, the northern and central/west populations differ less genetically and in terms of vocal dialects, and this appears to be because they are more connected (no major topographic barriers).

Second, we note that the age of dispersing individuals determines the overall proportion of individuals moving between populations, but we suggest that modifying the overall proportion of two to four year old birds moving between populations gives a realistic picture of how dispersal dynamics shape populations. Our models erred towards best-case scenarios by assuming that individuals disperse only once (palm cockatoos appear to be philopatric) (Murphy et al., 2003), always survived the dispersal journey, and did not suffer reduced success in the new population. However, cultural differences such as vocal dialects have been shown to influence social integration in wild parrots (Salinas-Melgoza and Wright, 2012), so it is possible that birds dispersing between Iron/McIllwraith Ranges and the other populations would fare less well until they had time to modify their vocal dialects. We also assumed no sex-specific dispersal e.g. (Wright et al., 2005) because there is limited evidence to suggest this occurs in palm cockatoos (Keighley et al., 2018; Murphy et al., 2003).

Third, although demographic data for the Iron/McIllwraith Ranges population was of high quality, we had limited data for the other populations, apart from anecdotal accounts of decline of the central/west population (Gould, cited in Garnett et al., 2011, Heinsohn et al., 2009). Working from the hypothesis that Iron/McIllwraith Ranges are a 'sink' population (Pulliam, 1988), we tested scenarios (Models 5–9) in which the constraint imposed by low reproductive success at Iron/McIllwraith Ranges was relaxed in other populations. However, the use of reproductive rates more than two and a half times those of Iron/McIllwraith Ranges in the other populations only lifted the trajectory of Iron/McIllwraith Ranges slightly (Table 5). The meta-population in these circumstances had an improved but still declining trajectory.

Fourth, the average adult mortality rates derived here used generation time from expert elicitation (Bird et al., 2020). Use of these data was found to be appropriate, as they were similar to the mortality rates in Model 3 in Heinsohn et al. (2009) which were evaluated to be most plausible for the species. We could not use the mortality rates reported by Saunders (1982) for Carnaby's Cockatoos, as these were probably unnaturally elevated due to poor survival of wing-tagged birds (Saunders, 1988). However we modified slightly the sex and age-specific rates according to differences among juveniles and adults observed in a study of wing-tagged Carnaby's cockatoos (Saunders, 1982). Despite occupying a different habitat type, Carnaby's cockatoos have similar life-history traits to palm cockatoos in their small clutch size (two eggs,

usually one survivor) and high rates of breeding failure.

Fifth, the population estimates used here are the best available for the meta-population but the total was somewhat arbitrarily apportioned between the three sub-populations. If Iron/McIllwraith Ranges acts as a sink and the Central/west population as a source, then the relative size of the two populations may be important. We tested the impact on the meta-population trajectory of the Central/west population being much larger (3000 individuals compared with 1700) in Model 9 and found that this improved the trajectory. It is important to note however that Model 9 used the much higher reproductive rate (0.3 offspring per year) of Models 5–8 and is thus very optimistic for both population size and reproductive rate. We also used generous carrying capacities (1.5 times the initial population size) to allow populations to fluctuate without much restriction so that initial population sizes were less likely to mask overall trends. Again, our models highlight the necessity for further research on population size and reproductive rates.

4.1. Conclusion

Our PVA provides strong evidence of the severe and negative impact on the meta-population of Australian palm cockatoos of unusually low reproductive success known to occur in one of the three major interconnected populations. These analyses have been made possible by detailed studies of both population genetics (Keighley et al., 2018) and vocal dialects (Keighley et al., 2016; Zdenek et al., 2015) across Cape York Peninsula. They draw attention to a major landscape barrier, the Great Dividing Range, that limits dispersal between sub-populations. The Iron/McIllwraith Ranges on the eastern seaboard has the best demographic data available, and this indicates that the population is in steep decline, and that connections to the other populations do not improve its viability. When viewed against the framework of the IUCN Red List and Australian Government criteria, clearly the current listing of palm cockatoos as 'Vulnerable' is inadequate. This is because it is not representative of either the meta-population or the somewhat genetically and vocally distinct Iron/McIlwraith Ranges population. The >50% population decline within the next three generations predicted by our models (based on probably unrealistic best-case scenarios) supports the need for immediate change in status at least to 'Endangered' for the Australian meta-population of palm cockatoos and the Iron/McIllwraith Ranges population under Criteria A3 and C1 (IUCN, 2019). In the future, addressing the knowledge gaps that we highlight here may be cause for future revisions of this status to 'Critically endangered' based on predictions from our less optimistic models. Dispersal between the eastern and other populations is unlikely to buffer local declines and highlights the importance of further investigation and relieving of local threatening processes. In the east, changed fire regimes that reduce nest hollow availability, as well as factors that may have caused predation at nests to increase, require further investigation and mitigation. In the west, palm cockatoo habitat is subject to major losses and disturbance from extensive bauxite mining. Mining leases cover approximately 5300 km^2, much of which is potential palm cockatoo habitat, and rehabilitated mine sites are not quickly recolonized by palm cockatoos (Gould, 2011).

Our study reinforces the value of population viability analyses that utilize robust life history data for empirically assessing species conservation status. Our study shows that, for long-lived species, severe population declines may only be detectable using PVA, given that collecting real-world data over ecologically relevant time scales may take so long that declines are irreversible. This is an under-appreciated aspect of species conservation, particularly in cases where knowledge gaps and short-term data limit the reliability of expert opinion in assessing threat status. We show that PVA, with clearly identified assumptions and caveats, can provide important demographic insights that might otherwise be missed.

Declaration of competing interest

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