



A severe predator-induced population decline predicted for endangered, migratory swift parrots (*Lathamus discolor*)



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ABSTRACT

Identifying the impact of introduced predators on endangered prey populations is critical for conservation management. Population viability analysis (PVA) becomes a valuable tool for quantifying such impacts when high quality life history data are available but, surprisingly, predictions from PVA of future population decline have seldom been used directly to assess conservation status. Here we synthesise new research on the unusual life history of the endangered swift parrot *Lathamus discolor*, an austral migrant that breeds in Tasmania, Australia. Swift parrots are challenging to monitor because (1) spatio-temporal fluctuation in food availability causes them to select entirely different breeding sites each year over a 10,000 km² range, and (2) they suffer high but variable rates of predation from introduced sugar gliders *Petaurus breviceps* depending on where they breed. 50.9% of nesting females on the main island of Tasmania were killed by sugar gliders while incubating eggs, but there was no predation from this source on offshore islands. Over four years 16.5% (0–29%) of the population bred on offshore islands. We use PVAs to examine the likely extent of future population decrease due to sugar glider predation, and demonstrate that the remaining swift parrot population is likely to decrease by 78.8–94.7% (mean over four models = 86.9%) over only three generations (12–18 years). Our models offer a rare example of the use of PVAs for assessing impending population decline and conservation status in species that are challenging to monitor. In this case they support a change of status for swift parrots from “Endangered” to ‘Critically Endangered’ under IUCN criteria.

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1. Introduction

In anthropogenically altered landscapes, predators can have serious consequences on the viability of prey populations. Globally, introduced predators are a major driver of extinction (Clavero and Garcia-Berthou, 2005; Salo et al., 2007), but native predators can also have serious effects (Millus et al., 2007; Roemer et al., 2001). In modified landscapes, multiple threatening processes often occur in tandem (Brook et al., 2008), so that synergistic interactions between different threats (e.g., predation and habitat loss) accelerate prey population declines. Island endemics are particularly vulnerable to predators and have suffered high rates of extinction following the introduction of predators to their habitats (Duncan and Blackburn, 2007).

Identifying the causes of mortality and understanding their impacts on prey population viability is critical to successful conservation management (Lavers et al., 2010; Moorhouse et al.,

2003; Whitehead et al., 2008). These impacts must be considered in the context of life history parameters (Bode and Brennan, 2011; McLoughlin and Owen-Smith, 2003). Detailed life history data are not available for most species (Morais et al., 2013; Norris, 2004), which is a problem for understanding how best to arrest decline in threatened populations (Christensen et al., 1996; Martin et al., 2012; Regan et al., 2005). However, when life history data are available, tools like population viability analysis (PVA) become valuable for understanding how animal populations might respond to environmental change (e.g., inflated mortality or habitat loss) and to identify where the best management options lie (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 likelihood of extinction (Beissinger and Westphal, 1998). PVAs are recognised as a potentially powerful tool in the assessment process for species conservation status (IUCN, 2012) and have been used to develop management strategies for several species (Crouse et al., 1987; Heinsohn et al., 2004). Somewhat surprisingly, predictions from PVA of future population decline based on current demographic

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data and the impact of threatening processes have seldom been used directly to assess conservation status.

Here we synthesise new research on the life history and distribution of endangered swift parrots *Lathamus discolor* (BirdLife International, 2008) and assess their population trajectory and conservation status using PVA. Swift parrots are austral migrants that breed on the large island of Tasmania to the south of continental Australia and over-winter in the south-east of the Australian mainland. They have a contentious conservation history (Allchin et al., 2013), are the subject of an Australian National Recovery Plan, and analysis of population viability has been identified as a key recovery action (Saunders and Tzaros, 2011). Until recently, few detailed demographic or ecological data have been available to help in understanding their population trajectory or conservation status. However recent research has revealed two important details about swift parrot ecology. First, spatio-temporal fluctuation in food availability drives unpredictable annual movements by swift parrots, causing the population to select entirely different breeding sites each year across a breeding range of approximately 10,000 km² (Webb et al., 2014). Second, nesting swift parrots suffer intense predation by sugar gliders *Petaurus breviceps* (Stojanovic et al., 2014b). Sugar gliders are native to continental Australia, but there is evidence to indicate that they were introduced to Tasmania as early as the 19th century (Gunn, 1851; Lindenmayer, 2002; Munks et al., 2004; Rounsevell et al., 1991). Webb et al. (2014) and Stojanovic et al. (2014b) highlighted that both the habitat requirement of swift parrots and the threatening processes occur over unusually complex spatio-temporal scales. Importantly, sugar gliders are present at all swift parrot breeding sites thus far monitored on the main island of Tasmania, but are absent from two smaller offshore islands (Bruny and Maria Islands) where the swift parrots sometimes breed (Fig. 1).

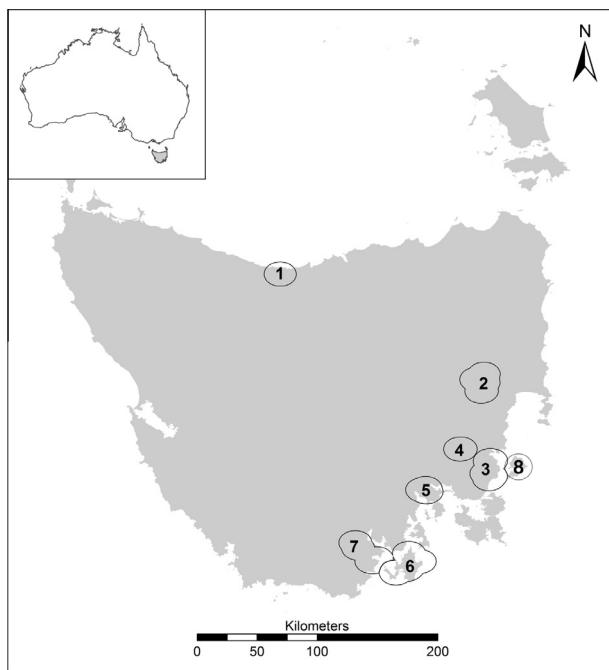


Fig. 1. Map of the study area, showing the regions where swift parrot nests were monitored in eastern Tasmania. The inset shows Tasmania (shaded) in relation to continental Australia. The regions and years in which they were utilised for nesting by swift parrots are: (1) Devonport; 2011, 2013 (2) the Eastern Tiers; 2011, 2013 (3) Wielangta; 2010 (4) Buckland; 2010, 2013 (5) the Meehan Range; 2010 (6) Bruny Island; 2011, 2012, 2013 (7) the Southern Forests; 2012, and; (8) Maria Island; 2010, 2011, 2012, 2013. Sugar gliders are known to occur in all regions except Bruny Island (6) and Maria Island (8).

In this study, we build on Stojanovic et al. (2014b) and Webb et al. (2014) by presenting PVAs incorporating up-to-date information concerning the highly variable and site-specific reproductive success and mortality of swift parrots. We specifically examine: (1) the impact of sugar glider predation on swift parrot population viability, and; (2) whether the current listing of swift parrots as ‘Endangered’ is still appropriate given these advances in knowledge. Our data and analyses are of broad importance because they show how PVA can be used for predicting severe population decline, and early assessment of conservation status, in species that are challenging to monitor because they are mobile, cryptic or uncommon across a large range.

2. Materials and methods

2.1. Study species

The swift parrot is a small (60–80 g), migratory bird whose main food is the nectar from several patchily distributed ephemeral flowering *Eucalyptus* spp (Higgins, 1999). Apart from a sea crossing to arrive at or depart from their Tasmanian breeding grounds, spatiotemporal variation in food availability causes the timing, direction, distance and destination of their movements to be highly irregular and unpredictable. Their over-wintering range is approximately one million square kilometres, and they can utilise *Eucalyptus* forest over approximately 10,000 square kilometres of eastern Tasmania for breeding (Saunders and Heinsohn, 2008; Webb et al., 2014). Swift parrots nest in tree cavities in the east coast forests of the Tasmanian mainland and nearby offshore islands (Stojanovic et al., 2012; Webb et al., 2012) within the distribution of their primary food trees (blue *Eucalyptus globulus* and black gums *Eucalyptus ovata*) (Brown, 1989). On the Tasmanian mainland where sugar gliders occur, Stojanovic et al. (2014b) reported that 83% of swift parrot nests failed due to predation compared to no losses from predation on glider-free offshore islands. Most cases (80.0%) of sugar glider predation at nests also resulted in the death of the adult female parrot in addition to her eggs. In this analysis we include an additional year of mortality data that has become available since the analysis presented in Stojanovic et al. (2014b).

Swift parrots rarely nest in the same places between years, and the population usually moves *en masse* to breed in entirely new localities (see Fig. 1 for inter-annual variability of breeding site choice). Thus they are likely to be exposed to different rates of mortality between years depending on whether or not sugar gliders are present. By monitoring sites spread across the entire Tasmanian breeding range of the swift parrot, Webb et al. (2014) showed that the proportion of birds nesting on islands (low predation habitat) versus the Tasmanian mainland (high predation habitat) varies annually. There is no evidence to suggest that the island breeding birds comprise a separate population. The proportion of the population that breeds on islands varies greatly between years because patterns of settlement across the study area by swift parrots mirrors the spatial configuration of food in a given year (Webb et al., 2014). Here, we use an additional year of spatial breeding data (2013/14) that has become available since Webb et al. (2014).

2.2. Mortality and fledging data

Swift parrot mortality and nesting success were estimated from the sample of 63 nests used in the mark analysis published by Stojanovic et al. (2014b). We updated these results by including one additional year of nest monitoring ($n = 48$ nests) in the analysis (i.e., four consecutive breeding seasons, 2010/11, 2011/12, 2012/13, 2013/14). We used the same analytical approach outlined in

Stojanovic et al. (2014b) to estimate swift parrot nest survival for 114 swift parrot nests. The sample of nests analysed here included three additional nests that failed for reasons other than sugar gliders to provide a more realistic estimate of swift parrot nest survival (note that one of these nests occurred on an island). All nests included in the sample were monitored on more than one occasion, making them suitable for analysis in mark, and calculation of daily survival rates. We calculated fledging success for these same nests, and for all but two nests (both of which occurred on Bruny Island), we were able to determine the final number of fledglings.

2.3. Proportion of the population exposed to predation

The proportion of the population using Tasmanian mainland habitat versus island habitat for each year of the study was estimated using the spatially explicit occupancy models presented in Webb et al. (2014, Figure 3a). Area of occupancy is commonly used as a surrogate for abundance in wildlife studies (MacKenzie and Nichols, 2004). The models presented by Webb et al. (2014) were intersected with a map of mature forest cover (Forest Practices Authority, 2011) in ArcMap 10.2. The mature forest layer was used as an indicator of the presence of old hollow bearing trees across the landscape. The layer is also used for conservation management decision making to assess the availability of swift parrot nesting habitat across the landscape. Therefore, this new spatial layer provided an estimated probability of swift parrot occupancy in potential nesting habitat. We calculated: (1) the overall area of occupied nesting habitat for each year and, (2) the proportion of occupied mainland Tasmania habitat versus offshore island habitat. We used an occupancy threshold of 0.5, so that the probability of a location being occupied by swift parrots exceeded the probability of absence (Vance et al., 2003).

2.4. Modelling approach

We used *VORTEX 10* (Lacy et al., 2014; Lacy and Pollak, 2012) to model swift parrot population trajectories via the discrete, sequential events that happen to individuals (e.g., births, deaths, reproduction, environmental changes). *vortex* is an individual-based simulation of the deterministic and stochastic forces affecting populations, and is primarily used to model population trends, the probability of extinction of small populations and the relative effects of different impacts and threatening processes. We used data gained from our intensive four-year field study of demography, predation rates, and variation in nesting habitat use. The following analyses focus on the mean projected size of populations after three generations.

2.5. Initial population size, carrying capacity, inbreeding and sex ratios

Population estimates for swift parrots are, at best, approximate. We use the largest recent estimate of the swift parrot population of 2158 individuals (Garnett et al., 2011). We allow a carrying capacity of 10,000 birds (± 300 S.D. to allow for environmental variation across years, Table 1) although the true carrying capacity is likely to be lower than this due to ongoing habitat loss across Tasmania and annual variation in the availability of flowering. We have not explicitly considered the impact of inbreeding, largely because of the short time frames of our model projections. We also assume an even adult sex ratio based on an unbiased nestling sex ratio observed in the field thus far (Stojanovic, Unpublished Data). Taken together, the large initial population size and carrying capacity, lack of inclusion of some likely sources of mortality (see below) and possible deleterious effects of inbreeding as the population becomes small, mean that our population projections are conservative, and represent 'best case' scenarios.

Table 1

Demographic values \pm SD used in all simulations. SDs are the annual variation in the model due to environmental fluctuations, except for the SD in number of offspring per female, which is the variation among females in brood size.

Initial population size	2158
Carrying capacity	10,000 \pm 300 SD
<i>Age of first reproduction by males and females</i>	
Models 1–3	2
Models 4–5	1
Maximum age	9
Juvenile mortality (0–1 years)	45.0% \pm 8.07 SD
<i>Background adult mortality (no additional predation)</i>	
Model 1 (No additional predation)	29.4% \pm 8.1 SD
Model 2 (Predation by sugar gliders)	29.4% \pm 8.1 SD
Model 3 (Predation but longer generation time)	25.0% \pm 8.1 SD
Model 4 (Predation, shorter generation time)	33.3% \pm 8.1 SD
Model 5 (Predation, shorter generation time, orange-bellied parrot mortality)	35.0% \pm 8.1 SD
<i>Total adult female mortality</i>	
Model 1 (No additional predation)	29.4% \pm 8.1 SD
Model 2 (Predation by sugar gliders)	56.4% \pm 8.1 SD
Model 3 (Predation, longer generation time)	53.7% \pm 8.1 SD
Model 4 (Predation, shorter generation time)	58.7% \pm 8.1 SD
Model 5 (Predation, shorter generation time, orange-bellied parrot mortality)	59.9% \pm 8.1 SD
Maximum progeny per year	5 (single clutch)
Proportion males (sex-ratio) at hatching	0.5
Percentage adult females breeding	90
Percentage adult males available for breeding	100
No. of offspring per female per year – (Model 1 – no additional nest predation)	3.14 \pm 1.70 SD
No. of offspring per female per year – additional nest predation (Models 2–5)	1.87 \pm 1.71 SD
Mating system	Monogamy

2.6. Reproductive rates and mortality

We initially use the generation time of 5.4 years and time to maturity of 2 years, both derived from expert elicitation (Garnett et al., 2011). However we also explore the possible effect of a higher (6 year) or lower (4 year) generation time on population projections.

We first used generation time of 5.4 years to calculate background adult mortality rates of 29.4% per annum (where Gen time = $1/m + \text{age at first reproduction}$; $m = \text{annual adult mortality rate}$). We used the juvenile (fledging to one year) mortality rate (45% per annum) recorded for the similar, endangered migratory orange-bellied parrot *Neophema chrysogaster* (Holdsworth et al., 2011) but leave the sub-adult (1–2 year) mortality rate equal to the adult rate (Heinsohn et al., 2009).

We use field data for reproductive success and adult mortality recorded over four breeding seasons, including the three breeding seasons reported by Stojanovic et al. (2014b) to model multiple scenarios based on differing rates of predation.

2.7. Models

2.7.1. Model 1

Model 1 is based on our field data from offshore islands (Bruny and Maria Islands) where sugar gliders are absent (Stojanovic et al., 2014b). Although this model does not reflect observed patterns of

predation over the whole breeding range, it is included as a baseline model for comparison to other models with sugar glider predation included. Importantly it shows that potential population growth (r) is high in the absence of heightened predation by sugar gliders. The parameters used in all models are given in Table 1.

2.7.2. Model 2. Predation by sugar gliders

Model 2 (our preferred model based on up to date knowledge) incorporates observed mean rates of reproductive success and predation when the impact of sugar gliders on swift parrots on the Tasmanian mainland is included (Stojanovic et al., 2014b) over four years of nest monitoring. Mean reproductive success (fledging success) for Bruny and Maria Islands was 3.14 ± 1.70 S.D. and for the Tasmanian mainland 1.62 ± 1.71 S.D. (Stojanovic, Unpublished Data). Our published analysis of nest predation using mark indicated an overall failure rate due to sugar gliders on the Tasmanian mainland of 83% (Stojanovic et al., 2014b). Here we incorporate an additional year of data (including three nests that failed for reasons other than predation) yielding a failure rate on the mainland of 78.5%, and 2.4% on islands. Stojanovic et al. (2014b) found that in 80% of cases where nests were predated the breeding female also died, but the extra year of data lowered the proportion of females killed to 64.9%. Using the updated dataset, we estimate that 50.9% (i.e., $0.649 * 0.785 = 0.509$) of females that initiate nests on mainland Tasmania are killed. In Model 2 and all subsequent models we are careful only to apply this rate to the females still alive after background annual mortality (29.4% when generation time is 5.4 years) has been applied (see below). The proportion killed is further reduced to reflect that not all (90%) adult females attempt to nest each year.

We used spatially explicit occupancy models (Webb et al., 2014) to estimate the proportion of the overall swift parrot population that nested on the Tasmanian mainland versus offshore islands each year. These proportions of predator-free and predator-infested habitat used each year by the birds were used to estimate the mean fledging success and adult mortality across the entire population each year. These values are given in Table 2 below.

We calculated mean annual fledging success (*FledSuc*) as 1.87 ± 1.71 S.D (Eq. (1)) and mean annual mortality of adult females due to sugar glider predation (*FemMort*) as **0.383** (or **38.3%**) (Eq. (2)).

$$FledSuc = \frac{\sum_{2013}^{2010} ((Island_i \times N_{off}) + (Mainland_i \times N_{off, pred}))}{4} \quad (1)$$

$$FemMort = \frac{\sum_{2013}^{2010} (Mainland_i \times 0.509) \times 0.9}{4} \quad (2)$$

where $Island_i$ = proportion of birds breeding on offshore islands in year i , $Mainland_i$ = proportion of birds breeding on the mainland in year i , N_{off} = number of offspring in the absence of predation, $N_{off, pred}$ = number of offspring where predation occurs; 0.509 = estimated probability of mortality of females that initiate nests on the

mainland. In Eq. (2), the proportion killed is further reduced to reflect that not all (90%) adult females attempt to nest each year. Note – $Island_i$ does not appear in Eq. (2) because there is no sugar glider predation on offshore islands.

Therefore the overall proportion of breeding females *OverallFemMort* killed by sugar gliders can be represented by:

$$OverallFemMort = FemMort \times 0.706 = 0.27 \quad (3)$$

where '0.706' is the proportion of the population remaining after annual background mortality (0.2941% or 29.41%) has been applied.

Total mortality of breeding aged (2+) females in Model 2 was then calculated by summing background mortality and mortality from sugar glider predation: $29.4\% + 27.0\% = 56.4\%$.

Simulations were run 1000 times, the primary time frame used in Models 1 and 2 was 16 years to reflect three generations for swift parrots (where generation time = 5.4 years) primarily to address criteria for a 'Critically Endangered' listing under the IUCN Red List (IUCN, 2012).

2.7.3. Model 3. Predation by sugar gliders, longer generation time

Given the uncertainty around a definitive generation time (Garnett et al., 2011), we ran three additional models to investigate variation in predictions for longer (Model 3) and shorter (Models 4 and 5) generation times. In Model 3 we used the same basic parameters of Model 2 to investigate population projections when generation time is 6 years (age at first breeding remains 2 years). Using the same methods as above, annual mortality of breeding age (2+) females in this case is calculated as $(FemMort * 0.75) + 0.25 = 0.537$ (or 53.7%).

2.7.4. Models 4 and 5. Predation by sugar gliders, shorter generation time

Models 4 and 5 examine the population trajectory if generation time is shorter and breeding age is lower. Model 4 uses the basic parameters of Model 2 to investigate population projections when generation time is 4 years (age at first breeding is 1 year). Using the same method as above, annual mortality of breeding age females (in this case aged 1+) is calculated as $(FemMort * 0.67) + 0.33 = 0.5866$ (or 58.66%).

Model 5 uses published parameters for orange-bellied parrots, a parrot with similar life-history, to provide a further estimate of the likely impact of heightened predation if generation time is in fact closer to four years, and age at first breeding is one year. The availability of data from a similar species allows important independent verification that our inferred mortality rates based on generation time derived from the expert elicitation process (Garnett et al., 2011) yield population projections that are broadly consistent with values gained from field observation. Background mortality for this species has been estimated at 35% (Holdsworth et al., 2011). Using the same method as above, annual mortality of breeding age female swift parrots (in this case aged 1+) is calculated as $(FemMort * 0.65) + 0.35 = 0.599$ (or 59.9%). The time-frame for Models 4 and 5 was 12 years to reflect three generations.

3. Results

Our PVAs demonstrate that the swift parrot population will be reduced by up to 94.7% over three generations (range over models with sugar glider predation included = 78.8–94.7%, mean = 86.9%, Table 3). The probability of complete extinction $P(E)$ was zero in all models but we do not emphasise this finding here because of likely data limitations and conservative nature of our analyses (see discussion). Instead we emphasise the more deterministic projection of population size over three generations to directly

Table 2

Proportion of swift parrots nesting in island or Tasmanian mainland habitat, derived from spatially explicit zero inflated binomial models of swift parrot occupancy (Webb et al., 2014) using a 0.5 occupancy threshold.

Year	Island	Tasmanian mainland (%)
2010/11	10%	90
2011/12	0	100
2012/13	29%	71
2013/14	27%	73

Table 3

Models 1–5, including time-frame, stochastic rate of population increase r (\pm SE), final mean extant population size (\pm S.D.), and percentage increase/decrease of sugar glider population over three generations. The probability of extinction was zero in all models.

Model	Time-frame (3 generations) (years)	Mean r	Final mean population	Percentage change
1. No sugar glider predation	16	0.143 ± 0.001	9449 ± 939	+339
2. Sugar glider predation	16	-0.197 ± 0.001	115 ± 87.9	-94.7
3. Longer generation time	18	-0.153 ± 0.001	169 ± 120.0	-92.2
4. Shorter generation time	12	-0.151 ± 0.002	457 ± 330.4	-78.8
5. Shorter generation time, orange-bellied parrot mortality	12	-0.161 ± 0.001	395 ± 285.6	-81.7

address IUCN criteria pertaining to the extent of the estimated population decline.

We suggest that the most appropriate model is Model 2 as this includes data from a published analysis of sugar glider predation on swift parrots that accounts for predated nests that were likely to have been missed in surveys (Stojanovic et al., 2014b) together with an additional year of mortality data. This model forecasts a severe population decline over three generations of 94.7% (Fig. 2). Compared with the strong growth projections from Model 1 (i.e., without predation from sugar gliders incorporated, see Table 3), Model 2 highlights sugar glider predation at swift parrot nests as a key driver of likely severe population decline.

Our investigation of the effects of shorter and longer generation times (Models 3–5) similarly demonstrate that population size will decrease dramatically in all cases. Model 3 (longer generation

time) shows a 92.2% decrease over three generations whereas Models 4 (shorter generation time) and Model 5 (using orange-bellied parrot demographic rates) show decreases over three generations of 78.8% and 81.7% respectively (Fig. 2, Table 3). The mean population decrease over all models incorporating sugar glider predation was 86.9%.

4. Discussion

Our PVAs indicate that the conservation status of swift parrots is worse than previously supposed. When evaluated against the framework of the IUCN Red List and the Australian Government Environment Protection and Biodiversity Conservation Act criteria, the >80% population decline within three generations projected by all but one of our models (mean across all models = 86.9%), and the extreme value of 94.7% in our preferred model, support a change of status for swift parrots from 'Endangered' to 'Critically Endangered' under Criterion 1A3 (IUCN, 2012). Our projections indicate that even when other known threatening processes that contribute to additional mortality (e.g., collisions with human-built structures, disease, habitat loss) are ignored, predation by sugar gliders on nesting females is so severe that it is likely to result in swift parrot population collapse within three generations. Of particular concern is that the high survival of swift parrots that sometimes breed on offshore islands free of sugar gliders appears to be insufficient to buffer the population against decline. Below we evaluate the assumptions and validity of our PVAs and the necessity of high quality, spatially explicit, field data when assessing the conservation status of mobile and cryptic species such as swift parrots.

4.1. Evaluation of assumptions

Although there is some debate about the reliability of PVAs for predicting accurate population trajectories, there is an emerging consensus that they are useful for detecting trends in populations, and formulating management strategies, where high quality demographic data are available (Ball et al., 2003; Brook et al., 2002, 1997, 2000; Lahoz-Monfort et al., 2014; Lindenmayer and McCarthy, 2006). As for any modelling exercise, however, the assumptions and quality of data used in PVAs must be explicitly evaluated (Coulson et al., 2001). In our simulations all assumptions were conservative, ensuring that the population projections represented 'best case' scenarios (i.e., the population is probably worse off than indicated by our models). This provided added confidence to our assertions that the population is in severe decline. Here we evaluate five key influences on our interpretation of the models used.

First, we did not include any increases in anthropogenically caused mortality such as collision with human-made structures even though this is likely to be a major source of mortality (Saunders and Tzaros, 2011). Nor did we include any likely effect of human-induced climate change, which is likely to influence eucalypt flowering, or natural or human induced 'catastrophes' (e.g., disease, drought, bush fires). We allowed a generous carrying capacity roughly five times the optimistic initial population size and did not incorporate any effect of continuing loss of habitat,

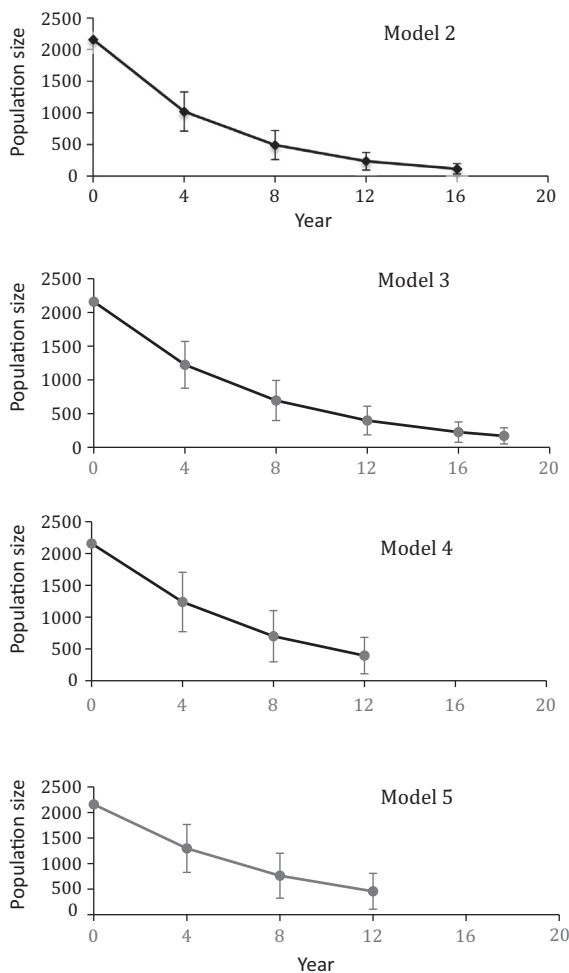


Fig. 2. PVA population projections (\pm S.D.) over three generations for all models incorporating predation from sugar gliders: Model 2 (three generations = 16 years), Model 3 (three generations = 18 years) and Models 4 and 5 (three generations = 12 years).

despite strong evidence that resources like tree cavities may be limiting (Stojanovic et al., 2014a, 2012). Nor did we factor in the likely negative impacts on survival and reproduction in years when flowering is poor across the breeding range (Webb et al., 2014). The latter effect may be particularly important, and emerging data from the 2014/15 breeding season indicates that food limitation when flowering is poor may severely curtail breeding opportunities (Webb and Stojanovic, unpublished data). One result of these omissions was that our basic model (Model 1) without sugar glider predation showed a high population growth rate which is probably unrealistic. We do not claim that Model 1 is a reflection of reality when sugar glider predation is absent. Rather we use it as a careful starting point to demonstrate that the population is clearly not in decline from background sources.

Second, we did not incorporate any effects of density dependence in our population trajectories even though these are likely. For example, our field observations suggest gregarious (possibly colonial) nesting habits and a high degree of gregariousness while on migration. It is likely that the swift parrots benefit by travelling and breeding in large groups (e.g., via better defence against predation), and that harmful Allee effects will apply at low population size (Kokko and Sutherland, 2001). Conversely the extent and concentration of flowering is a major driver of population density among breeding swift parrots (Webb et al., 2014). Tree cavities are known to be a limiting resource (Stojanovic et al., 2014a, 2012; Webb et al., 2012) suggesting severe curtailment of nesting opportunities per individual at high population densities (Webb et al., 2014). Incorporation of the impact of either of these density dependent factors in models would be likely to increase the severity of projected population declines. Another potentially negative consequence of small population size not included in our models is inbreeding, which we assumed had minimal impact over the relatively short time frame (three generations) of the population projections.

Third, we assumed constant rates of predation by sugar gliders regardless of swift parrot density. This differs from some models of hunting in which search effort for particular prey decreases as they become more scarce and harder to catch (Bomford and Caughley, 1996). Sugar gliders appear to be opportunistic omnivores that search for multiple types of prey (Stojanovic et al., 2014b) and only occasionally have swift parrots nesting in their region. Given the unreliability of swift parrots as staple prey, it is likely that sugar glider populations are regulated independently of swift parrot occurrence and abundance. Further, the likelihood of a swift parrot nest being found and predated is unlikely to be affected by swift parrot density because sugar gliders are consistently searching for multiple prey types and can only attack and kill nesting swift parrots opportunistically. However we cannot rule out other types of interaction between sugar glider and swift parrot populations. Spatial configuration of a common food source (nectar from flowering eucalypts) could affect predation rates by concentrating both species in the same habitat.

Fourth, we tested the likely sensitivity of our estimates of key demographic variables on model results using alternative approaches. We initially used the generation time of 5.4 years and time to maturity of 2 years, arrived at via the expert elicitation process (Garnett et al., 2011), and used juvenile (fledging to one year) mortality rates of a similar migratory parrot species (Holdsworth et al., 2011). We also explored the possible effect of higher (6 year) or lower (4 year) generation times (including an earlier age of breeding) on population projections. We further tested our models using endangered orange-bellied parrot juvenile and adult mortality rates, as these birds share several traits with swift parrots (small, migratory, cavity nesting parrots). The model using generation time of four years with breeding age of one year showed the smallest decrease in population size (78.8%) which was

just below the 80% threshold required to qualify as Critically Endangered under IUCN criteria. However the very similar model for generation time of four years using orange-bellied parrot demographic rates showed a similar decrease after three generations of 81.7% which was slightly greater than the 80% threshold. We emphasise that the model we consider most realistic (Model 2) showed a drastic decrease of 94.7%, and that the mean population decrease across all models with sugar glider predation was 86.9%.

Fifth, our PVAs are valuable for demonstrating the deterministic trend of the population but do not provide useful estimates of the probability of extinction because of inadequate measures of the variability around some parameters. Whereas the standard deviation around fledging success is likely to reflect true variability because of our large sample size of nests under observation, calculations of variation in mortality rates between years and sites were by necessity more limited and likely to underestimate the true variation (Lacy et al., 2014). Our studies on breeding habitat use by swift parrots and the impact of sugar gliders are ongoing, and it is likely that the measure of variation in mortality between years will continue to improve.

4.2. Necessity of high quality, spatially explicit, field data

Swift parrots are challenging to monitor because they are mobile, cryptic and relatively uncommon across their breeding range. As a consequence, detecting population trends from field surveys alone is difficult and a decline in their population size may easily go undetected. Reliable PVAs for swift parrots would not have been possible without the incorporation of high quality data from recent innovative field studies aimed at capturing the unusual variability in their use of breeding habitat with differing levels of predation pressure. The studies by Webb et al. (2012) and Webb et al. (2014) have been highly efficacious in developing methods for tracking the variable use of ephemeral nesting habitat by the entire remaining swift parrot population across eastern Tasmania. In particular, the spatially explicit occupancy models presented in Webb et al. (2014), here supplemented by an additional year of data, allowed estimation of the proportion of the population that used offshore islands compared to mainland Tasmanian breeding habitat each year. The three-year studies by Stojanovic et al. (2014a), Stojanovic et al. (2014b) and Stojanovic et al. (2012), again supplemented by an additional year of data, used the spatially explicit data from Webb et al. (2014) to determine key demographic parameters of swift parrots each year, including reproductive success and the site-specific rates of predation by sugar gliders.

These data revealed that predation on breeding females, eggs and nestlings was extraordinarily high across all mainland Tasmanian sites (where 78.5% of nests, and 64.9% of breeding females fell victim to sugar gliders). By contrast, nest predation was low on the offshore islands and there was no recorded loss of breeding females to predation at these sites. Over all, the less frequent use of island versus Tasmanian mainland habitat across the study period (Table 2) indicates that on average (over a 4 year period) approximately 83.5% of the population faced high predation from sugar gliders. There is little doubt that this pressure will be exacerbated by increasing habitat loss across the breeding range, effectively forcing sugar gliders and swift parrots into smaller patches of suitable habitat.

4.3. Conclusions

The PVAs presented here provide a strong indication of the long term deterministic effect of high predation on nesting swift parrots by sugar gliders. Our results should be interpreted as an early

warning that swift parrots are more severely threatened than previously realised. When our results are reviewed in the framework of the IUCN Red List and the Australian Government Environment Protection and Biodiversity Conservation Act criteria, it is clear that reconsideration of the current 'Endangered' listing is warranted. The >80% population decline within three generations projected by all but one of our models support a strong case for listing swift parrots as 'Critically Endangered' under Criterion 1A3 (IUCN, 2012).

Our data and analyses provide an important demonstration of how PVA can be used to predict the population trajectory of species that are challenging to monitor because they are mobile, cryptic or uncommon across a large range. When high quality demographic data are available PVA can be an effective tool for predicting severe population decline, and early assessment of conservation status. In some cases, this may enable conservation action before an endangered species has been reduced to very low numbers.

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Glossary

- PVA:** Population viability analysis: computer simulation models that use demographic data to make quantitative predictions about population size over time and the likelihood of extinction