

Long-term ecological data confirm and refine conservation assessment of critically endangered swift parrots

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Keywords

population viability analysis; conservation assessment; swift parrot; *Lathamus discolor*; nest survival; introduced predator; forest landscape integrity.

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Editor: Rahel Sollmann

Associate Editor: Miguel Acevedo

Received 10 April 2022; accepted 31 October 2022

doi:10.1111/acv.12834

Abstract

Conservation assessments of threatened species are often limited by scarce data and parameter uncertainty. Predictive models, designed to incorporate this uncertainty, may be the only tool available to inform conservation assessments for data-deficient species, but they are used surprisingly rarely for this purpose. The swift parrot *Lathamus discolor* is the only critically endangered bird to be listed in Australia based on population viability analysis (PVA). We aimed to evaluate the accuracy of the 2015 conservation assessment, which used sparse information, by incorporating new detailed and long-term data. First, we updated a range of life history parameter estimates, and then we repeated the same PVA as per the original conservation assessment. This process confirmed our earlier finding that swift parrot nests were more likely to survive in places with high mature forest cover. We identify that high forest landscape integrity and abundant hollow-bearing trees best predict nest daily survival rates. Based on the updated PVA, we predict a 92.3% population decline over three generations (11 years). This supported the predictions of the original conservation assessment, and the main benefit of the additional data was improved confidence in projections (the magnitude and direction of the population decline were similar between the original and updated PVAs). Our results demonstrate that meaningful trends can be inferred for species with imperfect information about their life history. Using predictive models like PVAs can help managers identify which life history parameters impact most on demographic trends. This information can guide targeted data collection so that 'draft' models can be later updated to improve certainty around population predictions.

Introduction

Conservation assessments determine the status of a species based on past and predicted future trends and extinction risk (Rodrigues *et al.*, 2006). Ranking of species into threat categories, particularly in global frameworks such as the Red List of the International Union for Conservation of Nature (IUCN), enables prioritisation of conservation actions and funding. Rankings affect species recovery actions, support legislative protection and inform land-use decisions. Therefore, it is important that these rankings are accurate and up-to-date to reflect new knowledge. Re-evaluations are useful to identify whether population trends and/or threats have changed between assessment periods (e.g. the Red List Index; Stuart *et al.*, 2006; Szabo *et al.*, 2012) and regular re-examination of evidence is necessary to assess whether the species is progressing towards the recovery objectives.

Conservation assessments should ideally be made using high-quality data, but rare and threatened species are likely to be data-deficient (Possingham, Grantham, & Rondinini, 2007; Morais *et al.*, 2013). In such cases, demographic models may be necessary for conservation

assessments (Norris, 2004). Demographic models provide the flexibility to test scenarios, evaluate parameter uncertainty and to forecast changes to ultimately inform decisions despite limited information. Surprisingly, demographic models are rarely used to inform conservation assessments – 3.25% of critically endangered species on the IUCN Red List are listed based on models (Criterion A3) (IUCN, 2021) (Supporting Information Table S1). Conversely, 12.55% of critically endangered species have been listed based on direct observations of past declines (Criteria A1 and A2) and 10.26% are listed based on past/future observed or predicted population declines (Criterion A4) (IUCN, 2021). Overall, 16.26% of critically endangered species include Criteria A (i.e. an 80% population size reduction over the longer of three generations or 10 years) within their conservation assessment (Supporting Information Table S2). Of the 17 critically endangered bird species in Australia, only one has a demographic model as the basis of its conservation assessment (Commonwealth of Australia, 2021).

Why are predictive models so rarely used in conservation assessments? Models are, by necessity, simplifications of natural processes and when underlying demographic data are

weak, this results in high parameter and model uncertainty. However, these uncertainties can be quantified and re-evaluated as new information is uncovered and remodelled to strengthen population predictions (Brook *et al.*, 2002). Underutilisation of demographic models for conservation assessments means that for many species, limited data is a barrier to adequate conservation protections.

Population viability analyses (PVAs) are widely used demographic models for conservation to estimate population trends, identify management priorities and explicitly account for the impacts of stochastic and ecological variation on species demography (e.g. Ferreras *et al.*, 2001; Heinsohn *et al.*, 2004). Because PVAs draw information from species' ecological traits, they are suitable for holistic conservation assessments (Akçakaya & Sjögren-Gulve, 2000; Burgman & Possingham, 2000). Some demographic parameters (e.g. rates of births and deaths) are disproportionately influential on modelled population growth rates, so ensuring that data on these traits is robust is crucial (Beissinger & Westphal, 1998). Generation length also has a significant scaling effect on population trends and extinction risk (O'Grady *et al.*, 2008), but these have only recently been systematically estimated for birds (Bird *et al.*, 2020). Understanding the magnitude of impacts that uncertain parameters have on simulations can be highly informative when deciding on research and conservation priorities.

For bird population conservation, nest survival analyses complement PVA by (1) identifying key predictors of nest success (e.g. nest age, habitat features, climate and time) and by (2) estimating key parameter data (i.e. clutch and brood size, number of offspring fledged and mortality of adult nesting birds). Predation is the predominant cause of nest failure for birds globally (Ricklefs, 1969; Lima, 2009) and variation in nest fate is often predicted by habitat features that may influence predation risk (Newmark & Stanley, 2011; Smith *et al.*, 2018). Many bird species form nesting aggregations and this also may have positive (e.g. group mobbing of predators or competitors, diluted predation effects, increased foraging efficiency) (Clark & Robertson, 1979; Brown, 1988; Hernandez-Matias, Jover, & Ruiz, 2009) or negative (e.g. locally elevated predator activity) (Dunn, 1977; Krama & Krams, 2005) density-dependent effects on breeding outcomes. Where PVA identifies steep population declines, nest survival and spatial analyses may explain broader ecological processes that enhance or limit survival and therefore inform mitigation approaches.

Swift parrots *Lathamus discolor* are the only Australian bird listed as critically endangered based on a PVA (Heinsohn *et al.*, 2015; Commonwealth of Australia, 2021). The species was predicted to decline by 94% in three generations (Heinsohn *et al.*, 2015) based on estimated mortality and reproductive rates (Stojanovic *et al.*, 2014b). The status of swift parrots has major implications for managing the impact of logging on Tasmanian forests where the parrots breed (Webb, Stojanovic, & Heinsohn, 2019). Due to data deficiency, Heinsohn *et al.* (2015) made several necessary assumptions about population size, generation length and the variation in predation rates. Nest survival where predators

occur (i.e. introduced sugar gliders *Petaurus notatus*) is known to vary with forest extent (Stojanovic *et al.*, 2014b) but it is unknown how discrete habitat features or spatial aggregations of nests may predict nest fate. Monitoring of swift parrots continued for another 6 years after Heinsohn *et al.* (2015), so here we evaluate the performance of the original model against fully updated PVAs based on a decade of field data. Nest predation rates had a large impact on the earlier PVAs (Heinsohn *et al.*, 2015, 2018), but data deficiency resulted in low confidence for the earlier estimates. By revising our models, we advance our knowledge of ecological factors that predict nest predation.

In this study we specifically: (1) update nest survival estimates, which are a critical PVA parameter, using long-term nest monitoring data; (2) verify the impact of habitat variables and nest location on nest fate (i.e. glider predation); (3) refit the preferred PVA of Heinsohn *et al.* with updated parameters and; (4) evaluate whether the conservation listing of the swift parrot as "Critically Endangered" based on a decline greater than 80% over three generations was accurate based on our new knowledge.

Materials and methods

Study system

Swift parrots are hollow-nesting, nectarivorous migrants that breed in eastern Tasmania, Australia and its offshore islands. Breeding locations vary between years in response to food (i.e. flowering eucalypts) (Webb, Holdsworth, & Webb, 2012) and nesting site availability (Stojanovic *et al.*, 2014a; Webb *et al.*, 2017). Swift parrots occupy only a fraction of their potential breeding range in any given year (Webb *et al.*, 2014), and exist as one panmictic population (Stojanovic *et al.*, 2018b). Swift parrots have a socially monogamous mating system with high levels of shared paternity (Heinsohn *et al.*, 2018). Females lay 3–6 eggs and undertake all incubation and initial care of the nestlings (~30 days) (Heinsohn *et al.*, 2018), making them more vulnerable to predation in the nest hollow. The nesting period takes ~60 days from egg laying to fledging.

Nest predation

Swift parrot nests on the Tasmanian mainland suffer predation from invasive sugar gliders *P. notatus* [synonyms *P. breviceps*, Krefft's glider (Cremona *et al.*, 2021)]. Sugar gliders are a small, gliding marsupial that were introduced to Tasmania (Campbell *et al.*, 2018) and also use tree hollows (Suckling, 1984). They occur across the swift parrot breeding range except for the offshore islands and predation pressure varies locally (Stojanovic *et al.*, 2014b). Stojanovic *et al.* (2014b) estimated over 3 years of monitoring that nest failure rates were 83% on mainland Tasmania and 0% on islands. An additional year of data revised this estimate to 78.5% and 2.4%, respectively (Heinsohn *et al.*, 2015). Of nests that failed due to gliders, 64.9% of mothers were killed (Heinsohn *et al.*, 2015). Predation pressure was negatively

correlated with mature forest cover extent (Stojanovic *et al.*, 2014b).

Habitat predictors of sugar gliders

It is likely that variation in nest fate may be explained by habitat factors that predict sugar glider occurrence and density. Sugar gliders are adaptable omnivores (Smith, 1982; Stojanovic *et al.*, 2014b) that occupy a wide range of eucalyptus forest types and utilise both the upper canopy and understorey for foraging, locomotion and nesting (Davey, 1984). In Tasmania, there is limited knowledge of sugar glider ecology but elsewhere they are primarily associated with abundant hollow-bearing trees, favoured food plants (e.g. *Banksia* and *Acacia* species) and forest connectivity (Smith, 1982; Jackson, 2000; Lindenmayer *et al.*, 2017). Sugar gliders den in hollows with the same entrance size as swift parrots (Stojanovic *et al.*, 2017), thereby acting both as their competitors and predators.

Sugar gliders persist in disturbed forests provided there are hollow-bearing trees, and their probability of occurrence increases after landscape logging (Lindenmayer *et al.*, 2021) but may decrease with fire (Quin, Smith, & Green, 2004; Lindenmayer *et al.*, 2021). Disturbance may impact the scale at which sugar gliders utilise the landscape due to variation in habitat connectivity, resources and competition. Gliders may travel further in fragmented landscapes where resources (i.e. food, hollows) are patchy or limiting (Goldingay, Sharpe, & Dobson, 2010; Stobo-Wilson *et al.*, 2021a). Conversely they may move less if confined by barriers to dispersal (Jackson, 2000). Territorial home ranges are typically 0.35–6 ha (Quin *et al.*, 1992; Quin, 1995; Gracanic & Mikac, 2022) although some records indicate sugar gliders can travel approximately 1 km in a single night (Gracanic & Mikac, 2022), and much further (2–14 km) over longer periods of dispersal (Suckling, 1984; Gracanic & Mikac, 2022). Spatial ecology of sugar gliders in Tasmania remains uncertain.

Nesting data

Our updated dataset more than doubled the number of nests available for analysis and consists of 293 breeding attempts with confirmed fates between 2010 and 2019 across seven study regions in Tasmania, Australia (Stojanovic *et al.*, 2014b, 2018b) (Fig. 1). Nest hollows were used between one and five times by swift parrots over the study. Nests occurred on the Tasmanian mainland ($n = 97$) and offshore islands ($n = 196$) and included 196 new nests between 2014 and 2019 (mainland = 30, island = 166; Table 1) in addition to our earlier sample (Stojanovic *et al.*, 2014b; Heinsohn *et al.*, 2015). The date when the first egg was laid was known for 150 of these nests and two or more observations were recorded for 289 nests. We monitored nest fate with cameras (Reconyx HC600) and with manual checking from their point of discovery until fledge/failure. All nests were checked at least twice. We estimated unknown laying dates using the date of hatching or fledging (Stojanovic

et al., 2014b), or using models of nestling growth (Stojanovic *et al.*, 2019). We counted fledglings and we considered nests successful if a chick fledged. We only recorded female mortality when there was evidence of predation (cass, camera images).

Habitat data

To explore relationships between habitat and nest success, we took a multi-scale approach to explore the relative importance of site and landscape effects (Manning *et al.*, 2006) that may influence sugar glider predation of swift parrot nests. We selected covariates based on forest structural and habitat attributes that are relevant for both swift parrot and sugar glider ecology (all covariates are described in Table 2). We derived our landscape scale habitat data from geographic information systems, and at fine scales from field surveys.

Landscape scale data – Regional mature forest cover predicts swift parrot nest survival (Stojanovic *et al.*, 2014a). Here, we again use the ‘mature habitat availability map’ (Koch & Baker, 2011; Forest Practices Authority, 2016) to identify nesting habitat for both parrots and sugar gliders, that is areas of hollow-bearing forest (Stojanovic *et al.*, 2014b). We used this map at two spatial scales: (1) a 5-km radius around nests (as per the preferred model in Stojanovic *et al.*, 2014b, which corresponded to recommended logging management prescriptions around nests and potential swift parrot foraging range during breeding), and (2) a 1-km radius around nests, to correspond to maximum sugar glider movements (finer site-level data were not publicly available). We used the combined extent of ‘high’ and ‘medium’ mature habitat availability as potential cavity-bearing trees are more likely to occur in these categories than in the ‘low’ category (Stojanovic *et al.*, 2014b).

For the year each nest was active, we calculated the surrounding proportion of total forest canopy cover at 500-m, 1-km, 5-km scales to capture multi-scale effects using the global forest change layer (Hansen *et al.*, 2013). This layer includes spatially explicit information on the annual extent of global deforestation since 2000 across land tenures. Nests used in multiple years had different scores of forest cover if deforestation occurred locally during the study.

We used the global Forest Landscape Integrity Index (FLII) (Grantham *et al.*, 2020), to test if cumulative impacts of anthropogenic forest modification affect nest survival. The FLII integrates four spatial datasets on: (1) current forest extent, (2) observed anthropogenic pressures at <3 km and <12 km scales, (3) inferred anthropogenic pressures associated with forest edges, and (4) loss of forest connectivity (Grantham *et al.*, 2020). FLII scores (range 0–10) are at a pixel resolution of 300 m and represent three broad categories of forest integrity: low (≤ 6.0); medium (> 6.0 and < 9.6); and high integrity (≥ 9.6) (Grantham *et al.*, 2020). We used the FLII value for each pixel around each nest as an empirical index of local forest quality.

We derived forest structural complexity covariates from light detection and ranging (LiDAR) aerial laser scanning data per LaRue *et al.* (2019) (Supporting Information

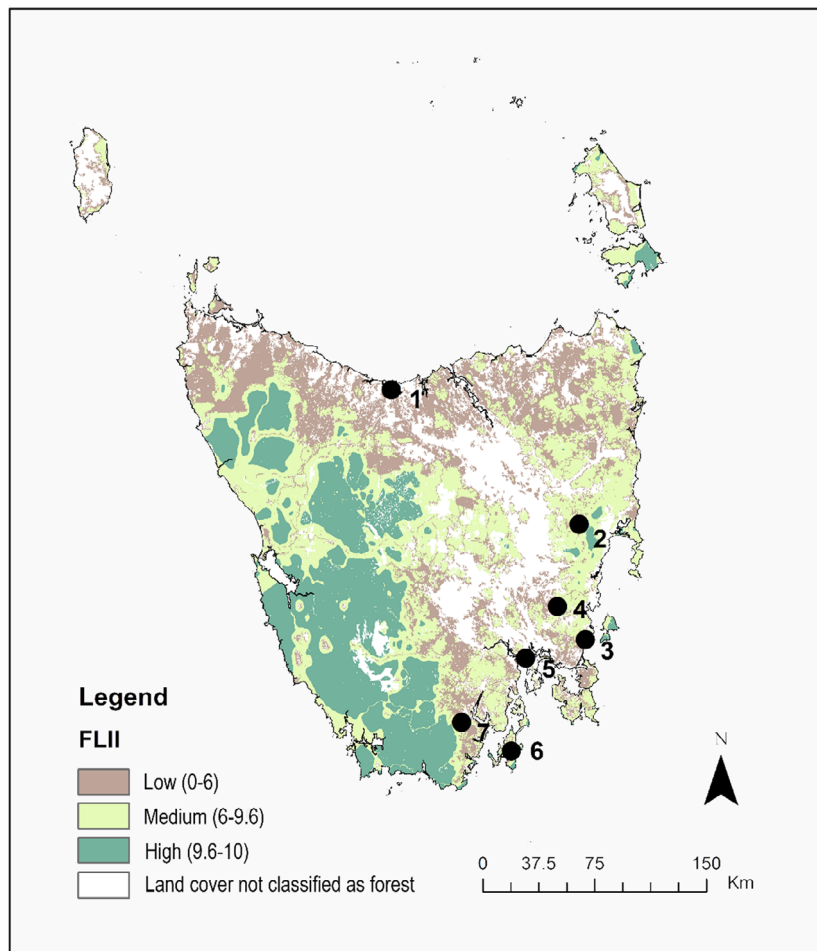


Figure 1 Forest landscape integrity index (FLII) (range 0–10) of Tasmanian forests derived from Grantham *et al.* (2020), with the study regions where swift parrot nesting data were collected between 2010 and 2019. Regions represent: (1) Devonport, (2) Eastern Tiers, (3) Wielangta, (4) Buckland, (5) Meehan Range, (6) Bruny Island and (7) the Southern Forests.

Table 1 Annual swift parrot nest survival records in Tasmania and offshore islands per season and per region with confirmed nest fate

Region/year	2010	2011	2012	2013	2014 ^a	2015 ^a	2016 ^a	2017 ^a	2018 ^a	2019 ^a	Total per region
1. Devonport	-	6	-	4	-	-	-	-	-	-	10
2. Eastern Tiers	-	13	-	8	2	1	-	1	-	-	25
3. Wielangta	8	-	-	-	5	-	-	9	-	-	22
4. Buckland	3	-	-	12	1	-	-	3	-	-	19
5. Meehan Range	8	-	-	-	-	-	-	-	-	-	8
6. Bruny Island	-	3	12	15	-	31	65	-	28	42	196
7. Southern Forests	-	-	5	-	2	-	3	2	-	1	13
Total per year	19	22	17	39	10	32	68	15	28	43	293

^aIndicates years of additional data collection since the original population viability analysis (PVA) (2014–2019).

Methods S1) for nests with coverage (73% of nests). LiDAR is increasingly used to characterise wildlife habitat (García-Feced, Tempel, & Kelly, 2011; Carrasco *et al.*, 2019; Tweedy *et al.*, 2019; Stobo-Wilson *et al.*, 2021b; Smith *et al.*, 2022) and provides precise measurements of features that may predict wildlife use or movement (see Supporting

Information Table S3 for a full list of covariates used). Due to incomplete coverage of the study area, we only used LiDAR data in an exploratory analysis. LiDAR-based covariates had poor explanatory power, so we excluded these variables from further analysis (Supporting Information Table S4).

Table 2 Covariates included in swift parrot nest survival models for nesting data between 2010 and 2019 on the Tasmanian mainland and offshore islands

	Covariate	Description
Breeding data	Location	Spatial location of nest (latitude and longitude coordinates)
	Nest age	Age of nest in days since date of initiation (first egg laid)
	Time	Julian date of nest within overall breeding season (August 30 to February 26)
	Year	Ten-level factor: 1 – 2010, 2 – 2011, 3 – 2012, 4 – 2013, 5 – 2014, 6 – 2015, 7 – 2016, 8 – 2017, 9 – 2018, 10 – 2019
	Region	Seven-level factor: 1 – Devonport, 2 – Eastern Tiers, 3 – Wielangta, 4 – Buckland, 5 – Meehan Range, 6 – Bruny Island, 7 – Southern Forests
Landscape -scale	Canopy cover	Percent tree cover >5 m height in the year of each nesting attempt within 500-m, 1-km and 5-km radius of each nest [(Global Forest Change, Hansen <i>et al.</i> , 2013)]
	Mature forest cover	Percent estimated mature forest (i.e. hollow-bearing trees) crown cover within 1 km and 5 km of each nest. [Mature Habitat Availability Map, (Forest Practices Authority, 2016)]
	Forest Landscape Integrity Index (FLII)	Index value (1–10) of forest landscape integrity (forest extent + anthropogenic pressure + lost forest connectivity) at nest location (Grantham <i>et al.</i> , 2020)
	Dominant forest species	Eight-level factor: 1 – <i>Eucalyptus pulchella</i> , 2 – <i>Eucalyptus globulus</i> , 3 – <i>Eucalyptus obliqua</i> , 4 – <i>Eucalyptus amygdalina</i> , 5 – <i>Eucalyptus delegatensis</i> , 6 – <i>Eucalyptus pauciflora</i> , 7 – <i>Eucalyptus ovata</i> , 8 – <i>Eucalyptus tenuiramis</i> (TASVEG 4.0; Department of Primary Industries, Parks, Water and Environment, 2020)
Fine-scale	Eucalypt basal area	Stand basal area of <i>Eucalypt</i> spp.
	Acacia basal area	Stand basal area of <i>Acacia</i> spp.
	Banksia basal area	Stand basal area of <i>Banksia marginata</i>
	Hollow-bearing trees	Count of trees with visible hollows from the ground
	Acacia stem density	Count of <i>Acacia</i> spp. stems (<i>A. dealbata</i> , <i>A. mearnsii</i> , <i>A. verticillata</i> , <i>A. melanoxylon</i> , <i>A. longifolia</i> var. <i>sophorae</i>)
	Banksia stem density	Count of <i>Banksia</i> spp. stems (<i>B. marginata</i>)
	Canopy cover	Estimated percentage tree cover within 50 m of the nest
	Canopy height	Mean canopy height (m) measured with a Nikon Forestry Pro II rangefinder
	Canopy connectivity	Four-level factor: 1 = low; 2 = moderate; 3 = high; 4 = very high
	Midstorey connectivity	Four-level factor: 1 = low; 2 = moderate; 3 = high; 4 = very high
	Understorey connectivity	Four-level factor: 1 = low; 2 = moderate; 3 = high; 4 = very high
	Elevation	Elevation (m) above sea level at nesting site
	Slope	Degree (0–90°) of slope at nesting site
	Aspect	Aspect of slope face (0–360°) at nesting site

Field Surveys – Fine-scale vegetation assessments were completed in 2020 for habitat features associated with sugar gliders (Table 2). Data were collected along 50 × 10 m transects from the nest tree in a random cardinal direction. We recorded a count of hollow-bearing trees (Smith & Lindenmayer, 1988), stem count and basal area of *Acacia* spp. (Smith, 1982; Suckling, 1984; Slater, 1987; Jackson, 2000), *Banksia marginata* (Howard, 1989; Quin *et al.*, 2004) and *Eucalyptus* spp. (Lindenmayer *et al.*, 1991; Crane *et al.*, 2008) (Table 2). Canopy height was measured with a Nikon Forestry Pro II rangefinder, and basal area was obtained with the angle-count sampling method (Van Laar, 1970). To assess barriers to sugar glider movement, the connectivity-index methods of Nelson *et al.* (2017) were adapted where canopy connectivity represents the potential ease of movement for sugar gliders through the forest strata. Forest habitat covariates selected were considered to be representative of habitat at the time of nesting (e.g. compared to rapidly changing seasonal environments like grasslands). However, if sites were partially deforested since the nesting attempts, transects were purposefully aligned in remaining intact forest surrounding the nest tree, rather than by random

cardinal direction. In two locations affected by firewood harvesting and bushfire, mature trees were included retrospectively in hollow-bearing tree counts by evidence of cut stumps (<10 years) and knowledge of their form at time of nesting.

Survival analysis

Nest survival

We followed the same approach as Stojanovic *et al.* (2014b). We estimated daily survival rate (DSR) of swift parrot nests with nest survival models (Dinsmore, White, & Knopf, 2002) using programme MARK (White & Burnham, 1999), via the interface 'RMark' v.2.2.7 (Laake, 2013) in programme R v.3.6.3 (R Core Team, 2021). The data were not censored. When models were comparable (i.e. within delta AICc <2 of the top model) (Burnham & Anderson, 2002), we selected the most parsimonious model and used the estimates and confidence intervals from these in PVA.

We standardised the season length from August 30th (day 1) to February 26th (day 181) based on the earliest egg laying and

last fledging. We used all nests with complete encounter histories ($n = 289$) per Dinsmore *et al.* (2002) and excluded four nests that had already failed due to predation at the first visit. Swift parrots are one population (Stojanovic *et al.*, 2018b), so we included all nests but undertook the analysis in several steps. First, we analysed the survival of nests across islands and mainland Tasmania to obtain discrete DSRs. Second, to detect potential habitat predictors of nest predation by invasive sugar gliders, we modelled nest survival separately for the 91 mainland nests with habitat and breeding covariates (Table 2). Pearson's r pairwise correlation coefficients were computed for habitat covariates and correlated coefficients above 0.7 were assessed and one covariate was removed (i.e. banksia basal area was correlated with stem count and basal area removed; mid-storey connectivity was correlated with canopy connectivity and removed). We also conducted supplementary analyses to determine whether outcomes of nests were spatially autocorrelated (i.e. whether nearby nests were more likely to share the same fate than nests further away) (Supporting Information Methods S2).

Population viability analyses

We aimed to update earlier population viability analyses (Heinsohn *et al.*, 2015) using the software VORTEX

10.5.5.0 (Lacy, Miller, & Traylor-Holzer, 2021; Lacy & Polak, 2021) by integrating new information on mortality, fledging success and generation length estimates (Bird *et al.*, 2020). VORTEX is an individual-based, stochastic population simulation programme typically used to model population trends, extinction risk and the different impacts of threats or mitigation approaches (Lacy, 2000). We calculated adult female mortality rates and fledging success, with and without sugar glider predation pressure, following Stojanovic *et al.* (2014b) and Heinsohn *et al.* (2015). We adapted the preferred model (Model 2) from Heinsohn *et al.* (2015) as our baseline model. We updated all values detailed in Heinsohn *et al.* (2015) (Table 3).

Based on the updated data, we fitted two new PVAs: model A – incorporating a starting population size of 2158 (the population estimate modelled in the prior PVA of Heinsohn *et al.*, 2015), and model B – incorporating a starting population size of 750 (the contemporary population estimate as of 2020) (Webb *et al.*, 2021). We ran models from the current in time when the population size estimates were current (Model A: 2015, Model B: 2020) so that changes in population size over time were considered. All models were simulated over 11 years, representing three generations of swift parrots (Bird *et al.*, 2020), noting that the estimate of generation time has been revised down from the value of

Table 3 The best available demographic values \pm SD for the Australian swift parrot used in a published population viability analysis from 2015 (Heinsohn *et al.*, 2015) and in the year 2022

Demographic parameter	2015	2022	Citation
Reproductive system			
Age of first reproduction by males and females	2	2	
Maximum age of reproduction	9	10	Bird <i>et al.</i> (2020)
Maximum lifespan	9	11	Bird <i>et al.</i> (2020)
Mating system	Monogamy	Polyandry	Heinsohn <i>et al.</i> (2018)
Generation length	5.4	3.7	Bird <i>et al.</i> (2020)
Reproduction rates			
Maximum progeny per year (single clutch)	5	6	^a
Proportion males (sex-ratio at hatching)	0.5	0.52	Heinsohn <i>et al.</i> (2021)
Percentage adult females breeding	90	90	
Percentage adult males available for breeding	100	100	
No. of offspring per female per year – (no additional nest predation)	3.14% \pm 1.7	3.29% \pm 1.44	^a
No. of offspring per female per year – additional nest predation	1.87% \pm 1.71	1.85% \pm 1.54	^a
Mortality rates			
Background adult female and male mortality (no predation by sugar gliders)	29.4% \pm 8.1	40.5% \pm 8.1	Bird <i>et al.</i> (2020)
Total adult female mortality (predation by sugar gliders)	56.4% \pm 8.1	52.8% \pm 8.1	^a
Juvenile mortality (0–1 year)	45% \pm 8.1	48.5% \pm 8.1	Stojanovic <i>et al.</i> (2020a)
Initial population size (N)			
Model A – prior population estimate	2158	-	Garnett, Szabo, & Dutson (2011)
Model B – contemporary population estimate (as of the year 2020)	-	750	Webb <i>et al.</i> (2021)

Contemporary simulations (Models A and B) use the demographic values from 2022 and differ only by initial population size. Standard deviations (SD) are the annual variation in the model due to stochastic environmental effects, except for the SD in number of offspring per female, which is the variation in brood size among females. Citations are provided for demographic values updated since 2015. Shading denotes the base demographic variables used in all models that have been updated using information we present in this study.

^aDenotes values derived from 10 seasons of breeding data collected between 2010 and 2019.

5.4 years used by Heinsohn *et al.* (2015) to 3.7 years (Table 3). Carrying capacity was set at 10 000 [± 300 standard deviation (SD)], per Heinsohn *et al.* (2015), and simulations were run 1000 times.

We applied the same equations as Heinsohn *et al.* (2015) to calculate mean rates of reproductive success and mortality with and without predation pressure (Supporting Information Methods S3). As the swift parrot is a single panmictic population, we used the proportion of swift parrots nesting on the offshore islands versus the Tasmanian mainland calculated by Heinsohn *et al.* (2015) to derive mean values including predation pressure across years. Mean reproductive success (fledglings per female) for the Tasmanian mainland was 1.56 ± 1.68 SD and for offshore islands 3.29 ± 1.44 SD. Our published PVA analysis (Heinsohn *et al.*, 2015) using 4 years of data estimated failure rates of 78.5% on the mainland and 2.4% on islands. Our additional data (Table 1) resulted in lower nest failure rates (71.4%) on the Tasmanian mainland but higher rates (10.2%) on islands. Sugar gliders were the cause of failure for 89.8% of nests on the Tasmanian mainland (only five nests failed for reasons other than predation). The proportion of failed nests where the mother died was estimated as 64.9% with only 4 years of data (Heinsohn *et al.*, 2015). We updated this estimate to 38.6% with 10 years of data. Using all data, we estimated that 27.6% ($0.386 \times 0.714 = 0.276$) of females that initiate nests on the Tasmanian mainland are killed. In our models we applied this rate only to remaining females once background annual mortality (41.4% when generation time is 3.7 years) (Bird *et al.*, 2020) has been applied. We estimated that not all females breed each year (90%), further reducing mortality in our models (Table 3). We used the historical juvenile (fledging to 1 year) mortality rate for the similar, migratory orange-bellied parrot *Neophema chrysogaster* (Stojanovic *et al.*, 2020b) and applied the background adult (2 years+) mortality rate of swift parrots (Bird *et al.*, 2020) to subadults (1–2 years). We retained the mating system as monogamous rather than polyandrous (Heinsohn *et al.*, 2018) as there is no option to model polyandry within the Vortex modelling framework.

Following the procedures in Heinsohn *et al.* (2015) we calculated mean annual fledging success per female (*Fled-Suc*) as 1.85 ± 1.54 SD and mean annual female mortality due to predation by sugar gliders (*FemMort*) as 0.207 (20.7%) (Supporting Information Methods S3). The proportion of breeding females that die from predation annually, assuming 90% of females breed, was 12.3%. Total mortality of breeding females was 52.8% (background mortality + mortality from predation).

Prior to selecting our parameter values (Table 3), we conducted a sensitivity test to explore impacts of parameters for which we lacked field data or that differed from the previous modelling. This is an important step to evaluate which parameters have the greatest influence on model projections. We applied a latin-hypercube sampling approach in VORTEX, with 500 samples and 500 iterations in a population-based sensitivity test, with Model B as a base (Table 3). We modelled extreme variation of each parameter and recorded

the stochastic population growth rate and mean population size at the end of simulations. Parameters tested were: adult female mortality (range: 42.8–62.8), proportion of females that breed annually (range: 20–100), initial population size (range: 250–2250), juvenile mortality (range: 30–80%) per rates for the orange-bellied parrot (Stojanovic *et al.*, 2020b, 2022), adult male mortality (range: 31.4–51.4%) and carrying capacity (range: 2000–12000). Iteration data were collated with package ‘vortexR’ v.1.1.7 (Pacioni & Mayer, 2017). We used linear regression and model averaging in the package ‘MuMIn’ v. 1. 43. 17 (Barton, 2020) in R to identify impactful parameters on stochastic growth rate and population size after three generations (full results presented in Supporting Information Methods S4). The sensitivity test showed that variation in female breeding rates and juvenile mortality were most important. Female mortality impacted strongly on stochastic growth rate (full model-averaged coefficients: $\beta -7.990e-03$, $P < 0.001$) whereas initial population size did not ($\beta -6.89e-134$, $P = 1$) and instead was associated with the substantial variation of population size after three generations. From these results, we applied optimistic or our best-supported values (Table 3), but caution that our parameter selection and model predictions represent a best-case scenario.

Results

Nest survival

For nest survival across the entire breeding range, our best-supported model included an effect of whether swift parrots bred on islands or the Tasmanian mainland ($\Delta AICc = 75.29$ versus the null model). The DSR estimate for islands was 0.998 ± 0.0004 [95% confidence interval (CI) 0.997–0.999] and 0.979 ± 0.003 (95% CI 0.972–0.984) for the Tasmanian mainland. Over a 60-day nesting period, this resulted in an overall nest survival probability of 0.90 (95% CI 0.83–0.94) for island nests and 0.29 (95% CI 0.19–0.39) for mainland nests.

For mainland Tasmanian nests, our best-supported model included additive effects of the Forest Landscape Integrity Index and count of hollow-bearing trees near nests (Table 4). We show estimates and confidence intervals from this model in Fig. 2. DSR was positively correlated with both forest

Table 4 Top-ranked nest-survival (S) models for swift parrot nests on the Tasmanian mainland between 2010 and 2019

Nest survival model parameters	N. Par.	$\Delta AICc$
S(~Forest landscape integrity + Hollow-bearing trees)	3	0.00
S(~Forest landscape integrity \times Hollow-bearing trees)	4	1.99
S(~Forest landscape integrity + Nest age)	3	2.27
S(~Forest landscape integrity \times Nest age)	4	3.72
S(~Forest landscape integrity)	2	4.39
S(~Null)	1	18.08

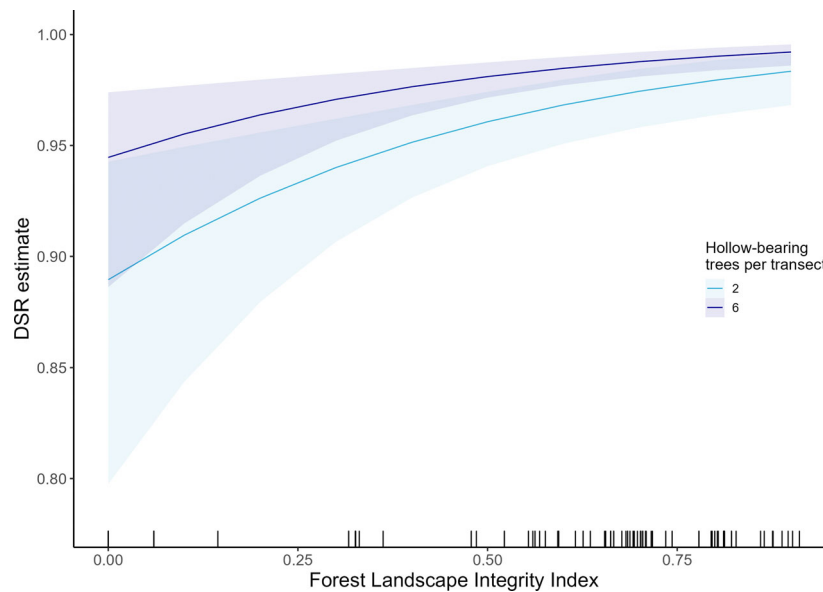


Figure 2 Modelled daily survival rates (DSR) of mainland Tasmanian swift parrot nests ($\pm 95\%$ confidence intervals) observed over 10 years (2010–2019) as a function of Forest Landscape Integrity Index (FLII) values and the count of hollow-bearing trees per 50×10 m transect adjacent to the nest tree. DSR were calculated with nest survival models (Dinsmore *et al.*, 2002) using programme MARK (White & Burnham, 1999), via the interface 'RMark' v.2.2.7. (Laake, 2013). Tickmarks indicate FLII values of nests.

landscape integrity and the number of hollow-bearing trees near nests. Small sample sizes at low values of forest landscape integrity resulted in low confidence, but confidence improved for medium to high values of forest landscape integrity. Overall nest survival probability reached 0.5 when the FLII exceeded 0.8. Nest success was spatially autocorrelated at distances up to 500 m, even after accounting for predictors of nest success, indicating that nearby nests have similar fates (Supporting Information Figure S1; Supporting Information Table S5).

Population viability analyses

Compared to the PVA by Heinsohn *et al.* (2015), the model in which we updated life history parameters but used the same high starting population size (Model A) had a more negative mean population growth rate [-0.2582 ± 0.002 standard error (SE)] but a larger mean extant population size (147.15 ± 82.98 SD) at the end of the simulation (Fig. 3) than previously estimated (-0.197 ± 0.001 SE; mean extant $N = 115 \pm 87.9$), due to the shorter timeframe of 11 versus 16 years (three generations). The fully updated model (Model B) had a more negative mean stochastic growth rate (-0.2495 ± 0.002 SE) than the baseline model but was only marginally different to model A. Combined with the smaller population size at the start of the simulation, model B predicted a more severe population collapse (Fig. 3; mean extant $N = 58.08 \pm 36.01$ SD, 92.3% decline) and supported the current conservation assessment of swift parrots as 'Critically Endangered' because the rate of decline exceeded 80% over three generations.

Discussion

Predictive demographic models are essential tools to identify population trends and extinction risk but species with limited data present analytical challenges. Our updated and expanded results reaffirm our previous PVA estimates of the rate and extent of population decline in swift parrots. Better quality input data resulted in predictions of a faster decline than previously modelled. We doubled the sample size of nests used in our prior assessments, but the results support the trends predicted by Heinsohn *et al.* (2015). The fully updated model predicts that the population will decline to 58 individuals over 11 years without drastic conservation interventions and supports the species' status as 'Critically Endangered' under Red List Criterion 1, A3. We also support our earlier findings that mature forest cover predicts nest survival (Stojanovic *et al.*, 2014a). Forest landscape integrity and the number of hollow-bearing trees near nests were important in predicting the survival of parrot nests. Furthermore, nest fates were spatially autocorrelated at small scales (<500 m) but fate is dependent on surrounding forest integrity. This supports our earlier findings that within some regions most nests fail, whilst elsewhere the opposite is true. Together, these results show that conservation planning should prioritise actions that preserve the integrity of swift parrot habitat, especially in locations where sugar glider predation is already low.

Swift parrots nesting on the Tasmanian mainland were nearly three times less likely to be successful than those on islands. Although the proportion of mainland nests monitored by Heinsohn *et al.* (2015) was relatively less than that

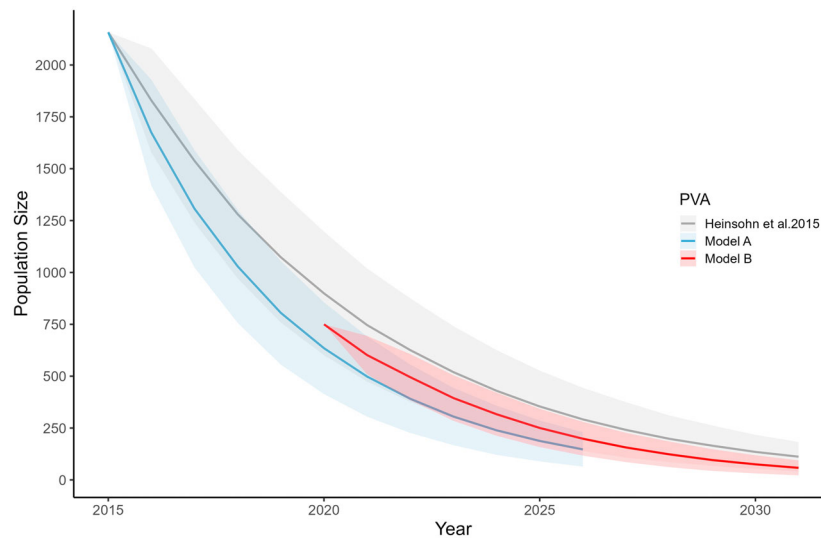


Figure 3 Population viability analysis population projections (\pm standard deviation) for the Australian swift parrot *Lathamus discolor* over three generations from a prior population model with original (Heinsohn *et al.*, 2015 'Model 2') and updated parameters (Model A; initial population = 2158) and a contemporary model with updated parameters (Model B; initial population = 750). Plot lines commence in the year when population estimates were current.

of island nests, more island nest data improved confidence in estimates of background nest survival and brood size. We expand on prior findings that landscape metrics of mature forest cover are important in predicting the nest survival of swift parrots with fine-scale habitat data specifically associated with sugar glider ecology. Other potential habitat resources of sugar gliders (e.g., food plants like *Acacia* and *Banksia*) did not explain parrot nest fate. Low forest integrity indicates high levels of fragmentation, forest connectivity loss and proximity to anthropogenic sources of disturbance (Grantham *et al.*, 2020). The interactive impacts of invasive species from habitat-mediated disturbance (e.g. land clearing, apex predator loss, fire, altered food resources) on threatened species has been well documented (Didham *et al.*, 2007; Doherty *et al.*, 2015; Geary *et al.*, 2018). These processes may affect sugar gliders, for example, by limiting dispersal and increasing population densities, in turn resulting in a higher probability of sugar gliders encountering parrot nests as hollow resources become more limited. Elsewhere, sugar gliders are more abundant in logged than undisturbed landscapes (Lindenmayer *et al.*, 2021), and occur in higher densities in fragmented forests than in continuous forests (Jackson, 2000), and where mature eucalypts are prevalent (Quin *et al.*, 2004). Although sugar gliders are often associated with flowering shrubs as food resources, this is not necessarily a key determinant of their occupancy or density (Quin *et al.*, 2004; Goldingay *et al.*, 2020). In Tasmania's southern forests, where one-third of forest has been logged in 20 years (Webb *et al.*, 2019), sugar glider occupancy was high overall and greater than 0.5 in areas where mature forest cover was less than 10% (Allen *et al.*, 2018).

Given that forest loss is continuing in Tasmania (Webb *et al.*, 2019), the ongoing deterioration of landscape forest integrity is likely to worsen and compound the effects of predation and removal of breeding and foraging habitat. Currently, only 29.4% of Tasmania's remaining forests are of high forest landscape integrity (Grantham *et al.*, 2020). However, we calculate that within Swift Parrot Important Breeding Areas (Commonwealth of Australia, 2019) only 4.2% of forest is of high integrity, 62.4% of medium integrity and 33.4% of low integrity. Recent efforts to protect swift parrots from predation are either very expensive (Stojanovic *et al.*, 2018a) or ineffective (Owens *et al.*, 2020; Stojanovic, Owens, & Heinsohn, 2020) and are not applicable at large spatial scales. We suggest that protecting areas of good quality breeding habitat from ongoing deforestation (Webb *et al.*, 2019) is likely to be the most cost-efficient means of conserving swift parrots in the short to medium term.

Our PVA models provide alternative trajectories to Heinsohn *et al.* (2015) using prior and contemporary population estimates. Regardless of the initial population size used in models, the swift parrot population collapsed. Model A (where all parameters bar starting population size were updated) predicted a population decline of 93.2% over three generations. Model B (fully updated – our preferred model) predicted a similar decline of 92.3% over three generations. Both models predict fewer than 200 birds surviving beyond 2026, which is 2 years earlier than the baseline model. This result confirms that the trends we report are independent of initial population size and are more sensitive to other model parameters (i.e. female mortality, proportion of females breeding, juvenile mortality). Updates to sensitive parameters (female mortality, fledging success without predation

pressure) were marginally more optimistic than previously estimated, however, mean fledging success (including predation pressure) was relatively unchanged. We updated lifespan to 11 years (up from 9 years) but also increased the background mortality by 12% (Bird *et al.*, 2020). The preferred model of Heinsohn *et al.* (2015) used an (uncertain) generation length of 5.4 years (Garnett, Szabo, & Dutson, 2011), but in line with Bird *et al.* (2020), we shortened this to 3.7 years. This reduced the three-generation timespan of our models from 16 to 11 years. Interestingly, earlier models (Heinsohn *et al.*, 2015) that included shorter generation lengths (totalling a 12-year timespan) comparatively projected a 79–81% decline, whereas our new model predicted a 92.3% decline despite being across a shorter timespan (11 years). Collectively, parameter changes could have affected the predicted population trajectory positively (longer lifespans) and negatively (female mortality remained high, higher background mortality). Overall, the impacts of these changes on projections were negative, but the precision of our population trajectory improved. We now estimate population decline is faster than that of Heinsohn *et al.* (2015), underscoring the urgent need to protect this species.

Our simulations included conservative assumptions that render our predictions optimistic. We ignore ongoing deforestation of breeding habitat and associated decline in breeding opportunities and thus recruitment. Functional habitat, that is hollow-bearing trees in proximity to adequate flowering food trees (Webb *et al.*, 2017), is likely to become less available with current forest management practices (Webb *et al.*, 2019). Worsening forest integrity and scarcity of hollow-bearing trees will likely contribute to higher rates of nest failure. Increased foraging effort of breeding swift parrots in landscapes where food is scarce (Stojanovic *et al.*, 2021), may further compound our predicted declines. We excluded the impacts of an increasing sex-ratio bias on shared paternity (e.g. male competition for mates, harassment of nesting females) and subsequent fitness (Heinsohn *et al.*, 2018). We also ignored climate change which is likely to affect flowering phenology, background mortality rates and breeding success due to severe weather and other environmental stressors. Allee effects likely exist in swift parrots and these are ignored in our models but are likely to exert a negative effect on population growth (Crates *et al.*, 2017). Further, we applied the most recent published population estimate in our contemporary model (Webb *et al.*, 2021), although ongoing genetic research suggests this value may be lower (Olah *et al.*, 2021). Finally, we ignore the effect of introduced nest competitors, such as starlings *Sturnus vulgaris*, which may reduce the carrying capacity of existing nesting areas (Stojanovic *et al.*, 2020a). Together, the cumulative impacts of these deliberately omitted threats point to a bleak future for the swift parrot.

PVAs are relatively underused tools for conservation assessments largely due to demographic uncertainties for many species. Regardless, the management of threatened species must proceed. PVAs can test for uncertainty in parameter estimates provided there are some reasonable demographic data available, and can identify both (1) risks

to populations and (2) sensitive parameters that must be prioritised in species recovery efforts. Given the trivial number of critically endangered species on the IUCN Red List for which demographic modelling has been undertaken (IUCN, 2021), these benefits are rarely realised. The lack of demographic models in conservation assessments may suggest that some species are listed too conservatively and thus may not obtain adequate conservation protection.

We show that PVAs based on even sparse or imperfect data are capable of predicting meaningful trends for threatened species. Although our updated nest survival models improved the precision of PVA projections, the existing conservation assessment for the species stands. This lends support to using PVAs in conservation assessments for species when there is at least enough information to reasonably estimate parameters and shows the importance of explicitly considering the impacts on models of uncertain parameters.

Acknowledgements

We thank Joanne Potts for insight into the analysis and the editors for feedback on the manuscript. Thanks to Catherine Young, Laura Bussolini, Adam Cisterne and James Cordwell for assistance in the field. We thank Weetapooona Aboriginal Corporation and small landholders for providing access to their land. Our work was supported by the Holsworth Wildlife Research Endowment and the Ecological Society of Australia and the Australian Research Council (DP140104202). This work was conducted with approval from the ANU Animal Experimentation Ethics Committee and Tasmanian Department of Primary Industries, Parks, Water and Environment. Open access publishing facilitated by Australian National University, as part of the Wiley - Australian National University agreement via the Council of Australian University Librarians.

Authors' contributions

GO, DS and RH conceived the ideas and designed methodology; GO and DS collected the data; GO, DS and RC analysed the data; RH and DS provided supervision; GO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

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

Table S1. Summary of the number of Critically Endangered IUCN Red List assessments that include Criteria A “Population reduction measured over the longer of three generation or 10 years,” by each criterion A1 to A4 (IUCN, 2021).

Table S2. Summary of the criteria categories included in Critically Endangered IUCN Red List assessments ($n = 8188$) (IUCN, 2021).

Table S3. Forest structural complexity metrics from LiDAR aerial laser scanning (ALS) within 50 m and 500 m radius of nest trees used in a swift parrot nest survival analysis.

Table S4. Top ranked nest-survival (S) models for a subset of swift parrot nests with LiDAR coverage ($n = 74$) on the Tasmanian mainland between 2010–2019.

Table S5. Top-ranked (AICc <2) overall nest success generalized additive models (GAMs) for 95 swift parrot nests on mainland Tasmania from 2010 to 2019.

Figure S1. Moran’s I test of spatial autocorrelation for swift parrot nest fate on the Tasmanian mainland across a range of distance values.

Methods S1. LiDAR data and survival analysis.

Methods S2. Spatial autocorrelation of nest success.

Methods S3. Parameter calculations.

Methods S4. Sensitivity Test - Swift Parrot.