



High nest survival, but variable reproductive output in the Superb Parrot (*Polytelis swainsonii*)

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ABSTRACT

Quantifying the reproductive output of species is fundamental in understanding population dynamics, life history, and in conservation management. The use of multiple metrics to quantify reproductive variation allows for a clear interpretation of the species' breeding biology and is often needed for robust models of population trajectory. Using measures of nest survival, clutch size, brood size, and nestling body condition we quantified reproductive output and annual variation of the Superb Parrot *Polytelis swainsonii* over 5 years in Canberra, Australia. We found consistent nest survival probability, maintained at over 89% throughout the nesting period in all years of study, but variation in all other metrics. Clutch sizes of Superb Parrots varied annually, and we found seasonal declines in both clutch and brood sizes. Furthermore, nestling body condition also varied annually and by order in which hatching occurred. The annual breeding performance of this bird has implications for conservation assessment and provides critical baseline data. Continuing to address critical knowledge gaps in Superb Parrot ecology and biology should be prioritised to better inform management and resolve the uncertainty that remains in the species' conservation status.

ARTICLE HISTORY

Received 4 November 2021
Accepted 23 November 2022

KEYWORDS

Productivity; body condition; threatened species; conservation; Australian bird


Introduction

Quantifying demographic variation requires good-quality baseline data on the life histories of animal populations. These data are essential for modelling population growth and conservation management for threatened species (Beissinger and Westphal 1998; Heinsohn *et al.* 2015). Robust modelling of extinction risk relies on the collection of spatially and temporally representative demographic parameters and their response to environmental conditions and land-use (Morrison *et al.* 2016), yet the availability of adequate data for threatened species is often poor (Norris 2004; Scheele *et al.* 2018). This is because rarity can hinder the collection of statistically rigorous data as individuals are uncommon and hard to find (Crates *et al.* 2019). Demographic models, such as population viability analysis, are sensitive to the veracity of life history data (Chaudhary and Oli 2020), so it is important that wherever possible these be founded in statistically robust data collected from wild populations. Identifying and rectifying data deficiencies can empower effective monitoring and management of threatened species (Legge *et al.* 2018; Scheele *et al.* 2018).

Information about reproductive rates is one of the most basic types of data needed to understand

demographic variation. There are several ways to measure reproductive success in animal populations, and it may be necessary to use multiple metrics to avoid overlooking important details of life history (Murray 2000). For example, nest survival – the probability that at least one offspring is successfully fledged from a nest – is commonly used in studies of birds (Mayfield 1975; Dinsmore *et al.* 2002; Rotella *et al.* 2004) and provides a straightforward way to quantify how different factors (e.g. predation and poor weather) affect reproductive success. However, in populations with high mean nest survival, other more subtle processes may affect fecundity. For example, brood reduction (i.e. the loss of one or more nestlings before fledging – Mock and Parker 1986; Mock and Forbes 1994) may be overlooked if breeding success is measured only using nest survival. Thus, nest survival should be considered too coarse to reflect true reproductive success (Thompson *et al.* 2001; Streby *et al.* 2014). Collecting additional information on reproductive output of species may provide the detail required to observe more subtle variation. Clutch and brood sizes are limited by interacting intrinsic (e.g. parent quality) and extrinsic (e.g. resource availability) factors (Jetz *et al.* 2008). Understanding why some nests produce more or better quality offspring than others can

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 Supplemental data for this article can be accessed at <https://doi.org/10.1080/01584197.2022.2153257>

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be important for understanding a species' ecology. For example, mothers may lay eggs of different sizes that vary in their hatching rates and subsequent nestling survival (Smith and Bruun 1998; Saino *et al.* 2018; Song *et al.* 2020). Likewise, siblings can vary in their early life body condition which may carry over and cause differences in fitness post-fledging (Magrath 1991; Sedinger *et al.* 1995; Song *et al.* 2018). To fully understand variation in reproductive success, detailed data on individual breeding attempts must be collected in addition to nest survival.

We studied the breeding biology of the Superb Parrot (*Polytelis swainsonii*) to quantify variation in their reproductive success. The species is listed as vulnerable (Commonwealth of Australia 2021) but there are conflicting views of this status and population trends (Garnett and Baker 2021). Superb Parrots are long-lived (up to 25 years), mobile, philopatric, dependent on tree hollows for nesting, and are known to produce clutches of four to six eggs (Webster 1988; Higgins 1999; Manning *et al.* 2004). Their range in south-eastern mainland Australia varies considerably in resource richness over time (Manning *et al.* 2007), and it follows that a species breeding in such an environment should also exhibit major variation in reproductive success. However, to date there has been no detailed study of the species' breeding biology.

We address these knowledge gaps using 5 years of data from a breeding population in Canberra, Australia. We first used nest survival analysis to calculate the overall rate at which breeding Superb Parrots produced at least one fledgling. We then examined finer resolution variation in clutch and brood sizes over time. Finally, we evaluated factors that might explain variation in the body condition of nestlings. We predicted, given the variable environmental conditions of our study area, the traits we measured should vary between years. We also expected that coarse metrics (nest survival) would vary less than the more detailed metrics (clutch/brood sizes, nestling body condition). We provide an important first step in developing an understanding of Superb Parrot breeding biology and population dynamics.

Methods

Study species and area

Superb Parrots are endemic to south-eastern Australia, restricted to south-eastern New South Wales and parts of northern Victoria and the Australian Capital Territory (Webster 1988; Webster and Ahern 1992; Higgins 1999). The species is considered to inhabit two key breeding areas within these regions: riparian

River Red Gum (*Eucalyptus camaldulensis*) forest or woodland, and scattered Box-Gum woodland (Webster 1988; Webster and Ahern 1992). Superb Parrots are threatened by the effects of deforestation and climate change and large areas of their range have been heavily modified by agriculture (Manning *et al.* 2005, 2013; Manning and Lindenmayer 2009). They may undertake regular seasonal movements between breeding and non-breeding areas, but the spatial ecology of Superb Parrots is poorly studied (Higgins 1999; Manning *et al.* 2007). Breeding adults depend on cavities in mature trees for nesting and will often nest in groups where habitat is available (Webster 1988; Higgins 1999). Breeding pairs produce one clutch per year, incubated by the female, during which the male will undertake all provisioning. Hatching typically occurs at day 22 after which both parents will attend the nest to feed the nestlings until fledging 40 days (approximately) after hatching (Higgins 1999).

We studied two nesting aggregations (locations withheld) approximately 15 km apart in the Australian Capital Territory. Our study period spanned the spring breeding seasons (September to December) between 2017 and 2021, when rainfall ranged from 373 to 1102 mm (mean 693 mm) per year (Table S1). Both sites occur in Yellow Box, Blakely's Red Gum (*Eucalyptus melliodora*, *Eucalyptus blakelyi*) grassy woodlands in peri-urban Canberra (Webster 1988; Webster and Ahern 1992; Stojanovic *et al.* 2021), and there is evidence to suggest that breeding pairs forage in urban Canberra during the breeding season (Rayner *et al.* 2015). Whether or not foraging in urban areas buffers against variation in environmental conditions is not known.

Data collection

We monitored nests between September and December each year. Nest trees were identified following Manning *et al.* (2004), and we climbed trees using single rope techniques. We confirmed an active nest with visual inspection (i.e. presence of eggs or nestlings) and recorded clutch and brood sizes. We installed motion-activated cameras to monitor activity at each nest cavity entrance. Where possible, we temporarily extracted nestlings to record their wing chord (mm) and body mass (g) to derive a measure of nestling body condition. Active nests were usually inspected twice to confirm contents and accessed once to measure nestlings. We estimated lay date and hatch date if nests were found during the egg or nestling stage based on approximate nestling age and average incubation period (22 days).

Analytical approach

Nest survival – We collected survival data by manually checking nests and using motion-activated cameras to identify the date of fledging or the cause and date of nest failure. All analyses were completed in R v4.0.0 (R Development Core Team 2020). We modelled daily nest survival rate (DSR) of Superb Parrot nests using the package *RMark* (Laake *et al.* 2019), an R-interface for the program ‘MARK’ (White and Burnham 1999). We grouped nests by study site and year to evaluate possible spatial and temporal variation in survival, and modelled the effect of nest age (i.e. number of days since the first egg was laid) and time (i.e. the timing of the nest within each breeding season) on nest survival. We compared models (Table 2) based on AICc (Burnham and Anderson 2002) and calculated DSR based on the preferred model.

Reproductive output – We fitted linear mixed models using the package *lme4* (Bates *et al.* 2012). We fitted clutch and brood size as response variables each in turn to consider the effects of conditions on reproductive investment and productivity, respectively. We examined spatial and temporal variation in these traits by using study site and year as fixed effects. Additionally, we included lay date (ordinal date) to examine possible variation due to the timing of nest initiation within each year. We note that other unmeasured environmental variation may have affected Superb Parrots in our study area, but at this small spatial scale these factors are confounded with space and time, so we kept our analysis simple.

Nestling quality – We developed an index of body condition for nestling Superb Parrots using our measures of wing chord and body mass. Older (larger) nestlings are heavier than their younger (smaller) siblings, so we corrected for this by correcting body mass for size (wing chord). We first used linear regression to model body mass and wing chord (Newbrey and Reed 2009; Vitz and Rodewald 2011; Labocha and Hayes 2012), but the straight line fitted poorly ($r^2 = 0.18$) so we opted for a quadratic function that fit better ($r^2 = 0.41$, $P < 0.0001$, Figure S1). The quadratic relationship we observed suggests Superb Parrots undergo weight recession prior to fledging (Ricklefs 1968; Renton 2002; Wright *et al.* 2006). We used the residual values of individual nestlings from this quadratic relationship as the body condition index. Positive residual values indicate above average body condition, whereas negative residuals indicate below average condition. We explored factors that might influence the body condition of Superb Parrot nestlings by fitting linear mixed models, using our body condition index as the response variable. We

included study site, year, hatch order, brood size and lay date as fixed effects. To assign hatch order (first, middle, last), we used wing chord such that longest wing = first hatched, and shortest wing = last hatched (Stojanovic *et al.* 2020). We included brood ID as a random effect to control for non-independence between siblings within a given brood.

Results

We monitored 105 nests and measured 209 nestlings (Table 1). Two nests were excluded from our nest survival models due to camera failure and three nests were excluded from our models of clutch and brood size due to lack of visibility in the nesting hollow. While it was not possible to identify individuals within this study, it is possible that nesting attempts examined over the study period included nests of the same pair (or individual) across years. In total, 86/103 nests successfully produced a fledgling (83%). Of the 17 nests that failed, 15 (88%) failed during the 22-day incubation period. Our preferred nest survival model (Table 2) included only a positive effect of nest age on daily survival rates (Figure 1). Daily survival rates rose from 0.974 ± 0.011 (SE) when the first egg was laid to 0.996 ± 0.001 (SE) by the end of incubation, and to 0.999 ± 0.0001 (SE) by the time the eldest chick fledged. Overall, this corresponded to a nest survival probability of 0.915 (95% CI 0.850–0.953) for nests at the end of incubation, and 0.994 (95% CI 0.943–0.999) for nests at the fledging stage. The 17 nest failures were attributable to nest abandonment ($n = 11$), flooding ($n = 2$), unidentified predators ($n = 3$), and usurped hollow by common Brushtail Possum *Trichosurus vulpecula* ($n = 1$). Nest survival was independent of study site and year.

The average clutch size was 4.3 (± 1.24 SD) between the two sites across all years of study (range: 1–7), and average brood size was 3.3 (± 1.69 SD, range: 0–6). We observed only two cases of nestling mortality before fledging. Clutch and brood sizes were best explained by different fixed effects (Table 3). For clutch size, the preferred model included an additive effect of lay date and year, whereas the preferred model of brood size only included the effect of lay date (Table 3). The modelled estimates for both clutch and brood sizes in each year (with confidence intervals) are shown in Figure S2. While our preferred model of brood size did not include year, we show the effect size of this variable for reference. Lay date was negatively related to both clutch and brood sizes (Figure S3). Based on these models, nests of larger clutches were found in 2018 and 2019 than nests in 2017, 2020, and 2021. Nests that

Table 1. Summary of Superb Parrot (*Polytelis swainsonii*) nestlings and nests measured between 2017 and 2021 in Canberra, Australia (mean \pm SD).

	2017		2018		2019		2020		2021		Overall
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	
No. nests monitored	10	8	12	10	11	15	7	14	5	13	105
No. nestlings measured	8	13	27	34	19	49	16	35	2	6	209
Nestling weight	150 \pm 11.24	143 \pm 29.51	159 \pm 26.38	158.2 \pm 17.28	148.9 \pm 12.26	146 \pm 18	144.9 \pm 18.63	156.4 \pm 18.72	143.6 \pm 21.07	147.9 \pm 14.68	151.6 \pm 20.04
Clutch size	4.0 \pm 1.25	3.9 \pm 0.64	4.5 \pm 1.13	4.9 \pm 0.88	4.5 \pm 0.52	4.9 \pm 1.25	4.1 \pm 0.69	4.0 \pm 1.48	3.4 \pm 0.55	3.9 \pm 1.98	4.3 \pm 1.24
Brood size	2.8 \pm 1.81	3.0 \pm 1.20	3.6 \pm 1.63	4.1 \pm 1.45	3.7 \pm 0.79	3.7 \pm 1.75	2.9 \pm 2.12	3.4 \pm 1.51	3.2 \pm 0.84	1.9 \pm 2.18	3.3 \pm 1.69
Lay date (ordinal date)	281.1 \pm 3.41	284.1 \pm 5.82	287 \pm 7.10	282.3 \pm 3.37	282 \pm 4.31	282.4 \pm 5.25	290.9 \pm 13.04	277.2 \pm 8.82	288.4 \pm 7.67	294.5 \pm 16.66	284.6 \pm 9.76

Table 2. Nest survival models ranked by AIC_c for 103 Superb Parrot (*Polytelis swainsonii*) nests from 2017 to 2021. The preferred model (indicated by *) included an effect of nest age on daily survival rate. The constant model assumes that daily survival does not change among nests and over time.

Models	nPars	AIC _c	ΔAIC _c	W _i	Deviance
Nest age*	2	154.324	0	0.51	150.32
Nest age + Time	3	156.176	1.852	0.20	150.17
Nest age + Location	3	156.314	1.990	0.19	150.31
Nest age + Year	6	157.556	3.232	0.10	145.54
Time	2	166.351	12.027	0.00	162.35
Time + Year	6	172.864	18.540	0.00	160.84
Constant	1	173.379	19.055	0.00	171.38
Location	2	175.349	21.025	0.00	171.35
Year	5	178.629	24.305	0.00	168.61

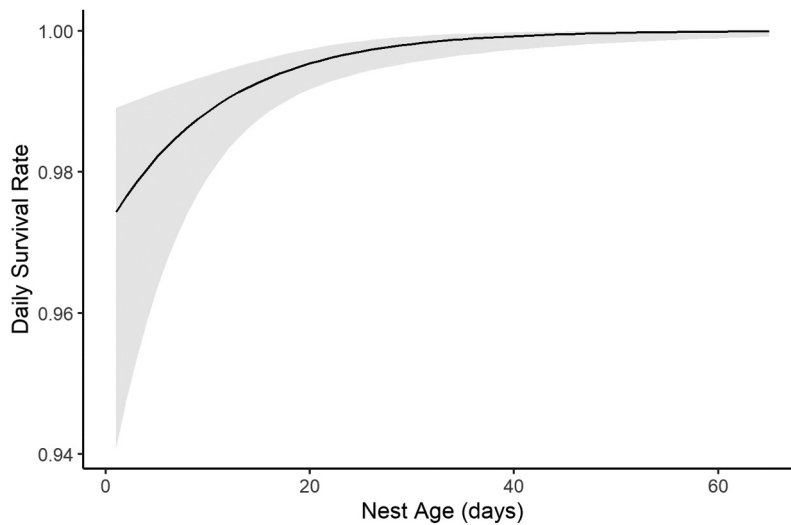


Figure 1. Effect of nest age (days) on daily survival rates (DSR) of Superb Parrot (*Polytelis swainsonii*) nests from 2017 to 2021 (the ribbon indicates 95% confidence intervals). DSR was lowest during the incubation period and increased with nest age. Hatching typically occurs at day 22 and fledging typically occurs at day 62.

Table 3. Superb Parrot (*Polytelis swainsonii*) clutch and brood size modelled as response variables and ranked by AIC. The preferred models (indicated by *) were selected based on AIC score ($\Delta AIC < 2$) with the fewest explanatory variables. Preferred models included the effect of lay date (ordinal date) on both response variables, with an additional additive effect of year on clutch size.

Effect	df	AIC	ΔAIC
<i>Clutch size</i>			
Year x Lay date	11	330.617	0
Year + Lay date*	7	331.547	0.930
Year	6	332.875	2.257
Lay date	3	332.989	2.372
Null	2	335.984	5.367
Location	3	337.659	7.042
<i>Brood size</i>			
Year x Lay date	11	375.752	0
Year + Lay date	7	376.677	0.925
Lay date*	3	377.297	1.544
Year	6	394.618	18.866
Null	2	399.116	23.363
Location	3	401.071	25.318

were initiated later in the breeding season had smaller clutch and brood sizes.

The most parsimonious model that predicted nestling body condition (Table 4) included additive effects of hatch order and year. Based on this model, nestling body condition declined with increasing hatch order, and was lowest in 2019 and 2021 compared with other years (Figure 2).

Discussion

We examined the breeding biology of the Superb Parrot using multiple metrics of differing resolution. We expected that the reproductive success of Superb Parrots would vary annually given the high variability of the species' breeding environment. We found evidence to support our expectations because we found

Table 4. Superb Parrot (*Polytelis swainsonii*) nestling body condition modelled as the response variable and ranked by AIC. The preferred model (indicated by *) was selected based on AIC score ($\Delta\text{AIC} < 2$). The preferred model included the effect of both hatch order (i.e. first, middle, or last hatched egg in each nest) and year.

Effect	df	AIC	ΔAIC
Hatch order + year*	9	1653.088	0
Hatch order	5	1659.775	6.687
Hatch order x year	17	1662.09	9.002
Brood size x year	26	1671.751	18.663
Year	7	1672.649	19.561
Brood size + year	12	1673.866	20.778
Null	3	1678.219	25.131
Brood size	8	1678.747	25.659
Lay date	4	1680.186	27.098
Location	4	1680.218	27.13

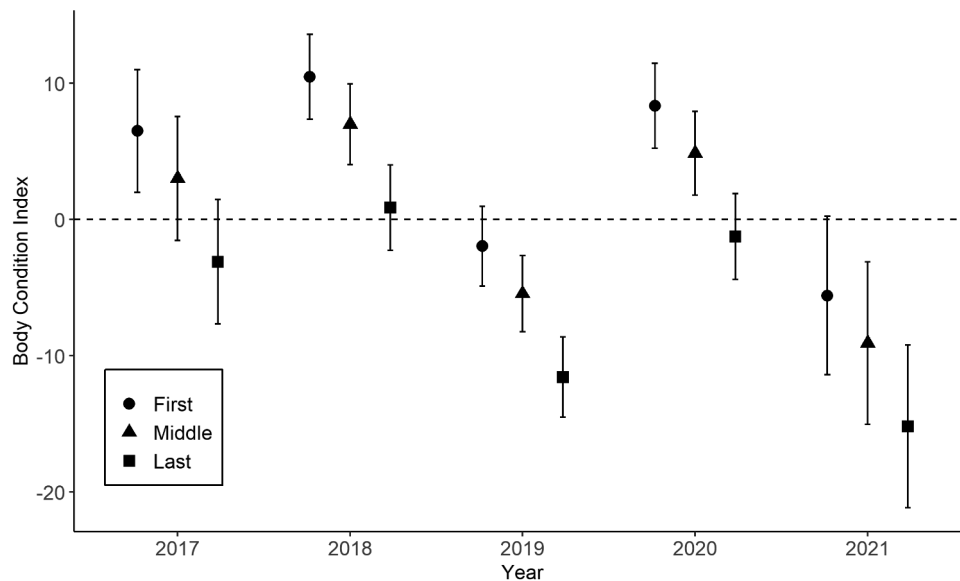


Figure 2. Superb Parrot (*Polytelis swainsonii*) mean nestling body condition for each year and hatch position (i.e. whether a nestling was the first, middle, or last hatched egg in each nest). Estimated means and confidence intervals were generated using the parameters from the preferred model.

annual variation in several reproductive metrics. Superb Parrots had consistently high nest survival over the study. Nest survival probabilities were lowest during incubation, but by the time nests reached fledging age their probability of success approached 100%. However, nest survival may be too coarse to fully describe individual fitness and breeding success (Streby *et al.* 2014). We found inter-annual and seasonal variation in clutch and brood sizes in Superb Parrots. For example, the smallest clutch size in 2021 was one egg, compared to a minimum of three in 2018. This variation may be evidence of plasticity in Superb Parrot reproductive strategies. This might be explained by annual variations in the condition of the breeding environment (or other unmeasured factors). Adaptive plasticity in clutch size is a widely employed strategy that allows high nest survival

to be maintained despite changes in resource availability (Clifford and Anderson 2001; Pettifor *et al.* 2001). Surprisingly, we found that clutch sizes were highest in the years of lowest rainfall (2018 and 2019). Additionally, we observed seasonal declines in both clutch and brood sizes across all years of study; this is a common pattern in other birds (Klomp 1970), including parrots (Saunders 1982; Krebs 1998; Ortiz-Catedral and Brunton 2009). This pattern has been attributed to various mechanisms, including food availability (Clifford and Anderson 2001), nesting female body condition (Gladbach *et al.* 2010) and predation (Decker *et al.* 2012).

While the number of offspring declined within seasons, this effect did not extend to nestling body condition or nest survival. The best explanation for the body

condition of Superb Parrot nestlings was their hatch year and hatch order. First-hatched nestlings had better body condition than later hatched siblings. In other birds this superior condition during early life can carry over into better fitness in later life (Magrath *et al.* 2003). Although in other species the size of broods has consequences for offspring quality (Reid *et al.* 2000; Uzun *et al.* 2010; Song *et al.* 2020), nestling body condition of Superb Parrots was independent of brood size. Our results raise several new questions about the breeding biology of Superb Parrots, and understanding the drivers of inter-annual variation observed in clutch size requires further investigation. Ideally, future research should be undertaken at more locations and over more years to overcome the confounding of environmental variability in our current sample with time and space.

Depending on the metrics used, reproductive success may be interpreted differently (Murray 2000). Our findings support other studies that show that presenting only one metric may be misleading and skew interpretation (Streby *et al.* 2014). Oversimplification of the high nest survival of Superb Parrots might positively skew population growth in demographic models (Chaudhary and Oli 2020). However, the variation in clutch/brood sizes and nestling body condition between years suggests that reproductive success in this species may not be as clear-cut. Although Superb Parrots produced on average 4–5 eggs, and 3–4 chicks per nest, there was considerable finer variation in nest-level productivity. By describing this variability, our results provide a strong starting point for future conservation assessments and demographic studies. In addition to the metrics of reproductive success used in this study, the rates of post-fledging survival and recruitment remain as significant knowledge gaps in Superb Parrot population dynamics, and should be a focus of future study. These rates may be a limitation to population growth where nestlings may not survive to reproduce or are unable to do so due to poor resource availability (e.g. nesting hollows – Manning *et al.* 2013; Stojanovic *et al.* 2021). Further study of these critical demographic parameters would greatly improve estimates of population trajectory. The use of multiple metrics to examine Superb Parrot reproductive success in this study highlights the ways in which subtle variation (or lack thereof) in those metrics may be misinterpreted. In certain species or populations, using multiple metrics in conjunction with one another will not only allow for greater understanding, but also identify key threats that may apply to different levels (e.g. clutch or brood-level threats).

An important caveat to our results is the short duration and limited spatial replication of this study. These considerations limit interpretation of possible trends in

reproductive success to both the Canberra and broader population. The Canberra population may also be unusual in some ways because of the urban environment in which the parrots breed. Land use across most of the Superb Parrot breeding range is not urban, and it is not yet known if populations breeding in predominantly agricultural landscapes experience greater variation in their reproductive success. Therefore, future attempts to understand the demographic trends of the species would benefit from expansion of temporal and spatial replication of data on Superb Parrot breeding output and environmental variation. Examining seasonal variation in resource availability that Superb Parrots experience (e.g. food availability) may be more revealing if undertaken at a broader scale than attempted here to overcome confounding of data with space and time. For example, the spatial scale of our study was small enough that the entire population falls within a single city, meaning that broad scale environmental data like weather and greenness are not differentiable among sites. Given the mobility of the species (Webster 1988), all individuals potentially have access to the same foraging resources. Furthermore, the observed variation in clutch and brood size and nestling body condition may be associated with undetected intrinsic factors that might vary between subpopulations or individual Superb Parrots. For example, migration strategies may ameliorate the effects of environmental variability (Gillis *et al.* 2008). Given the movement patterns of Superb Parrots remain uncertain (Manning *et al.* 2007), expanding the number of populations sampled in future and marking individuals (e.g. colour banding) should better account for the potential variation in their life history strategies and reproductive success. Identifying and marking individuals will also allow for a detailed understanding of individual-level variation and an exploration into possible bet-hedging strategies.

The knowledge gap in demographic information for threatened species presents challenges that may impede management actions targeting their protection (Scheele *et al.* 2018; Crates *et al.* 2019). Our study shows that even relatively small datasets can reveal important aspects of a species' ecology and life history if data are collected in a rigorous way. The collection of these data is important because the use of poor or limited data in conservation assessments and population modelling can result in misleading conservation status and incorrect management strategies (Chaudhary and Oli 2020). We provide a starting point for future research into the Superb Parrot and highlight the intriguing variation in the species' life history strategies that requires further exploration. Specifically, we identify the following questions as high priorities for future research:

- (1) How do Superb Parrot subpopulations vary in reproductive output across the species' breeding range?
- (2) Is Superb Parrot reproductive output influenced by land use policy and practice?
- (3) What are the rates of Superb Parrot post-fledging survival and recruitment?

Answering these questions will provide a sound basis for confident demographic modelling of Superb Parrots, which will help address ongoing uncertainty in the species' conservation status and assessment.

Acknowledgements

The authors thank Chris Davey, Stuart Harris, Clare McInnes, Ingrid Stirnemann, Shoshana Rapley, and the Rangers of the ACT Parks and Conservation Service for their assistance during the project. We thank Mark and Meg Hartmann for their support and access to their property. Thanks to Jenny Newport for logistical and permit/ethics administrative support.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This research was funded by the ACT Parks and Conservation Service, CWP Renewables, and an Australian Government Research Training Program (AGRTP) scholarship. The work was undertaken with ANU Animal Ethics and Experimentation Committee approval [#A2018/54] and a scientific permit from the ACT Government [#LT201795].

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