



Kent Academic Repository

Gellé, Adrien, Nicoll, Malcolm A.C., Kettel, Esther F., Pernetta, Angelo P., Gath, Helen, Groombridge, Jim, Henshaw, Sion, Jones, Carl G., Ruhomaun, Kevin, Tatayah, Vikash and others (2026) *Demographic responses to population recovery illustrated by 30 years of monitoring a once critically endangered parrot*. *Journal of Applied Ecology*, 63 (8). ISSN 0021-8901.

Downloaded from

<https://kar.kent.ac.uk/115821/> The University of Kent's Academic Repository KAR

The version of record is available from

<https://doi.org/10.1111/1365-2664.70523>

This document version

Publisher pdf

DOI for this version

Licence for this version

CC BY (Attribution)

Additional information

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in **Title of Journal**, Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our [Take Down policy](https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies) (available from <https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies>).

RESEARCH ARTICLE

Demographic responses to population recovery illustrated by 30 years of monitoring a once critically endangered parrot

Adrien Gellé^{1,2}  | Malcolm A.C. Nicoll²  | Esther F. Kettel¹  | Angelo P. Pernetta¹  |
 Helen Gath² | Jim Groombridge³  | Sion Henshaw⁴ |
 Carl G. Jones^{4,5} | Kevin Ruhomaun⁶ | Vikash Tatayah⁴  | Ken Norris⁷  |
 Simon Tollington^{1,5} 

¹School of Animal, Rural and Environmental Sciences, Nottingham Trent University, Southwell, UK; ²Institute of Zoology, Zoological Society of London, London, UK; ³School of Natural Sciences, Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, UK; ⁴Mauritian Wildlife Foundation, Vacoas, Mauritius; ⁵Durrell Wildlife Conservation Trust, Trinity, Jersey; ⁶National Parks and Conservation Service, Government of Mauritius, Reduit, Mauritius and ⁷Natural History Museum, London, UK

Correspondence

Adrien Gellé

Email: adrien.gelle2023@my.ntu.ac.uk**Funding information**

Nottingham Trent University; Research England; Research England's Expanding Excellence in England (E3) Fund; UK Research and Innovation

Handling Editor: Don A Driscoll**Abstract**

1. Understanding how demographic rates change during population recovery is critical for evaluating conservation success and determining when populations become self-sustaining. However, documenting such transitions requires long-term monitoring across substantial changes in population size— conditions that are rarely met.
2. We leverage a 29-year capture-mark-recapture dataset from the echo parakeet population (*Alexandrinus eques*), a vulnerable endemic parrot of Mauritius island that recovered from fewer than 20 individuals to over 500 during the study period. Using multistate capture-mark-recapture models, we analysed encounter histories of 2734 known-aged wild individuals to estimate age and state-specific survival probabilities while accounting for temporal variation, transitions between breeding states and controlling for unequal recapture probabilities.
3. Demographic rates changed substantially during population recovery. Recruitment into the breeding population declined across all age classes as the population approached carrying capacity. Survival showed contrasting patterns: juveniles (<2 years old) exhibited a declining temporal trend (from 0.68 in 1994 to 0.57 in 2020), whereas adult survival remained stable across years, with breeding adults showing consistently higher rates (0.96–0.97) than non-breeding individuals (0.76–0.90).
4. *Synthesis and applications.* These findings highlight the dynamic nature of demographic processes throughout population recovery and emphasise the value of continued monitoring beyond apparent recovery to detect density-dependent shifts in demographic rates of wildlife populations.

KEYWORDS

Alexandrinus eques, carrying capacity, mark-recapture, population demography, Psittaciformes, recruitment, survival probability, threatened species

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Population recovery is a primary goal of conservation management for endangered species, yet the demographic processes underlying recovery are rarely static. As populations grow from small founder sizes towards carrying capacity, demographic rates are expected to shift in response to changing density-dependent pressures (Newton, 1998). Understanding how survival and recruitment change across distinct phases of recovery, from low numbers through rapid growth to eventual regulation is critical for setting realistic population targets, evaluating conservation success and anticipating when intervention may still be required (Armstrong & Seddon, 2008; Ewen et al., 2012). However, few studies have the opportunity to track demographic parameters across the full recovery trajectory, from near extinction to carrying capacity, as this requires long-term monitoring programmes that are logistically challenging and difficult to maintain (Clutton-Brock & Sheldon, 2010).

A further challenge in demographic studies is that early-life stages and non-breeding individuals are often difficult to monitor. Juvenile survival and recruitment probability remain poorly understood in long-lived avian species with delayed maturity, because these individuals are frequently unobservable during the years between fledging and first breeding (Jenouvrier, 2013). In many long-lived species, pre-breeders and individuals that skip reproduction in a given year comprise a substantial proportion of the adult population (Votier et al., 2008), yet their survival rates remain poorly understood due to reduced detectability and tendency to range widely outside monitored breeding areas (Katzner et al., 2011; Pardo et al., 2013; Porter & Coulson, 1987). When non-breeders cannot be observed, multistate capture–recapture models with unobservable states can be applied, but these require constraining survival to be equal between states (Kendall & Nichols, 2002). This demographic blind spot has important implications; if survival differs between breeding and non-breeding individuals, population projections based solely on breeding adults may be upwardly biased (Fletcher et al., 2012; Lee et al., 2017). Where both breeding and non-breeding individuals can be reliably monitored, multistate models with fully observable states allow this constraint to be relaxed, enabling direct estimation of state-specific survival (Barbraud & Weimerskirch, 2005; Cam et al., 1998) and several studies have revealed that survival can differ substantially between breeding states in long-lived species including mammals (Oosthuizen et al., 2019) and seabirds (Pardo et al., 2013; Wood et al., 2021), suggesting this pattern may be widespread across other long-lived taxa and highlighting the potential for bias when equal survival is assumed.

Here, we analyse a three-decade resightings dataset of a vulnerable parrot species endemic to Mauritius, the echo parakeet (*Alexandrinus eques*), that has been intensively monitored since 1993 and is the subject of one of the most successful conservation recovery programmes globally (Jones & Merton, 2012). While this long-term monitoring has advanced understanding of disease dynamics (Fogell et al., 2021), genetics (Raisin et al., 2012) and their effects on productivity (Fogell et al., 2019; Louch, 2025; Tollington et al., 2019),

survival rates across the recovery trajectory have yet to be examined. This uninterrupted monitoring generated encounter histories of known-aged wild individuals resighted across different breeding states over three decades, enabling multistate age-structured modelling with fully observable states. The resulting dataset presents an opportunity to assess age- and state-dependent apparent survival patterns and examine how demographic rates fluctuate across distinct phases of population recovery.

In this paper, we wanted to address three objectives: (1) quantify how recruitment and age-specific apparent survival change across three phases of population recovery (recovery, growth, regulation); (2) estimate state-specific survival probabilities to test whether survival differs between breeding and non-breeding individuals and (3) assess how survival estimates may be biased in studies where only breeding individuals can be monitored, necessitating the assumption that breeders and non-breeders share equal survival. By answering these questions, we aim to provide insights relevant both to the understanding of population dynamics of long-lived species and to the management of recovering populations.

2 | MATERIALS AND METHODS

2.1 | Study species and population recovery

The echo parakeet is an endemic medium-sized parrot of Mauritius and the only surviving native parrot species of the Mascarene Islands (Jones, 1987). They are generally monogamous and produce one clutch of eggs per year (Tollington et al., 2015) in tree cavities formed in native hardwood trees or artificial nest boxes (Tatayah et al., 2007). Individuals reach sexual maturity at 2 years but typically breed for the first time at 3–4 years, key life-history traits that inform our age constraints for breeding state transitions. Crucially, 95% of breeding attempts occur in monitored artificial nests (Henshaw et al., 2025), creating inherent detection heterogeneity for the modelling approach—breeding individuals are systematically encountered at nest sites, while non-breeders are detected opportunistically. The population declined to fewer than 20 individuals by the early 1990s (Jones & Duffy, 1993) primarily due to habitat loss and fragmentation (Cheke & Hume, 2008; Safford, 1997; Vaughan & Wiehe, 1937) and the introduction of invasive alien species (Lorence & Sussman, 1986), but has recovered to over 500 individuals in 2025 (Henshaw et al., 2025) through intensive conservation management such as predator control, nest manipulation, nest box provisioning, supplementary feeding and habitat protection (Thorsen & Jones, 1998), leading to downlisting from critically endangered (Collar et al., 1994) to vulnerable on the IUCN Red List (BirdLife International, 2019). The population recovery can be divided into three distinct phases: an initial recovery phase (1997–2003) characterised by slow growth with the population fluctuating between 11 and 23 breeding pairs, a sustained growth phase (2004–2015) during which the population increased rapidly to over 120 pairs and an apparent regulation

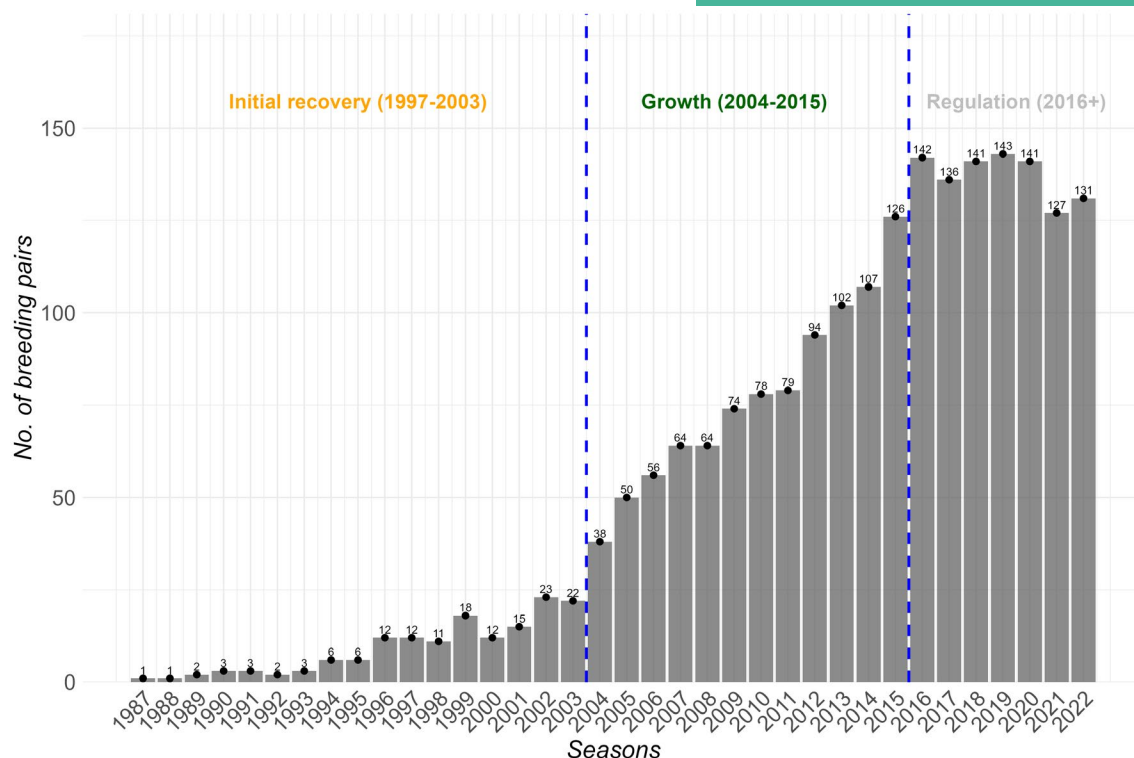


FIGURE 1 Number of wild echo parakeet breeding pairs monitored between 1987 and 2022 in the Black River Gorges National Park (Mauritius).

phase from 2016 onwards as the population approached carrying capacity. This recovery trajectory (Figure 1) provides a unique opportunity to examine how demographic rates (i.e. recruitment, survival) change throughout different phases of population growth.

2.2 | Study area

Historically, the echo parakeet inhabited the native tropical forests present across Mauritius and Reunion Island (Cheke & Hume, 2008; Jansen & Cheke, 2021; Jones, 1987), but severe habitat degradation and the introduction of invasive alien species have left the species largely confined to a limited area of 41 km² within the Black River Gorges National Park in the South West of Mauritius (Figure 2), where remnants of the native forest remain (Safford, 1997). This study uses resighting data from two populations of echo parakeet (The Gorges 'North'; -20.398, 57.441 & Bel Ombre 'South'; -20.460, 57.429) that, based on previous evidence, are spatially separated and exhibit little to no natural gene flow (Raisin et al., 2012; Tollington et al., 2013).

2.3 | Data collection and encounter histories

Since 1993, both populations have been intensively monitored every year during the austral summer breeding season (September to March), which defines our annual encounter occasions. Field

biologists from the Mauritian Wildlife Foundation systematically check all known nest boxes and natural cavities to identify breeding pairs and record their reproductive success. While ringing records began in 1991, the first chicks to successfully fledge were marked in 1994, establishing this cohort as the starting point for our capture-recapture analysis. Individuals are ringed in the nest before fledging, enabling long-term tracking and identification of birds within the population. As nearly all individuals are ringed (>95%) in the population (Henshaw et al., 2025), this unique recovery programme has generated comprehensive individual encounter histories through systematic monitoring, with resightings comprising both breeding (41%) and non-breeding (59%) individuals. This balanced representation of both breeding and non-breeding individuals provides a robust dataset for demographic analysis. All data were collected by trained field staff at the Mauritian Wildlife Foundation (MWF) and the Government of Mauritius' National Parks and Conservation Service (NPCS) as part of routine monitoring. The project received a favourable ethical opinion from the Animal, Rural and Environmental Sciences Ethical Review Panel at Nottingham Trent University.

A total of 3011 echo parakeets were individually marked with unique coloured ring combinations between 1994 and 2022, representing 28 cohorts (488 males, 558 females and 1965 of unknown sex). As sex can only be determined in echo parakeets from age 2 onwards and was known for 37% of individuals, we pooled the sexes for all analyses. These marked individuals generated 12,906 sightings throughout the study period (1994–2022). Individual encounter histories were compiled using various sighting sources (field

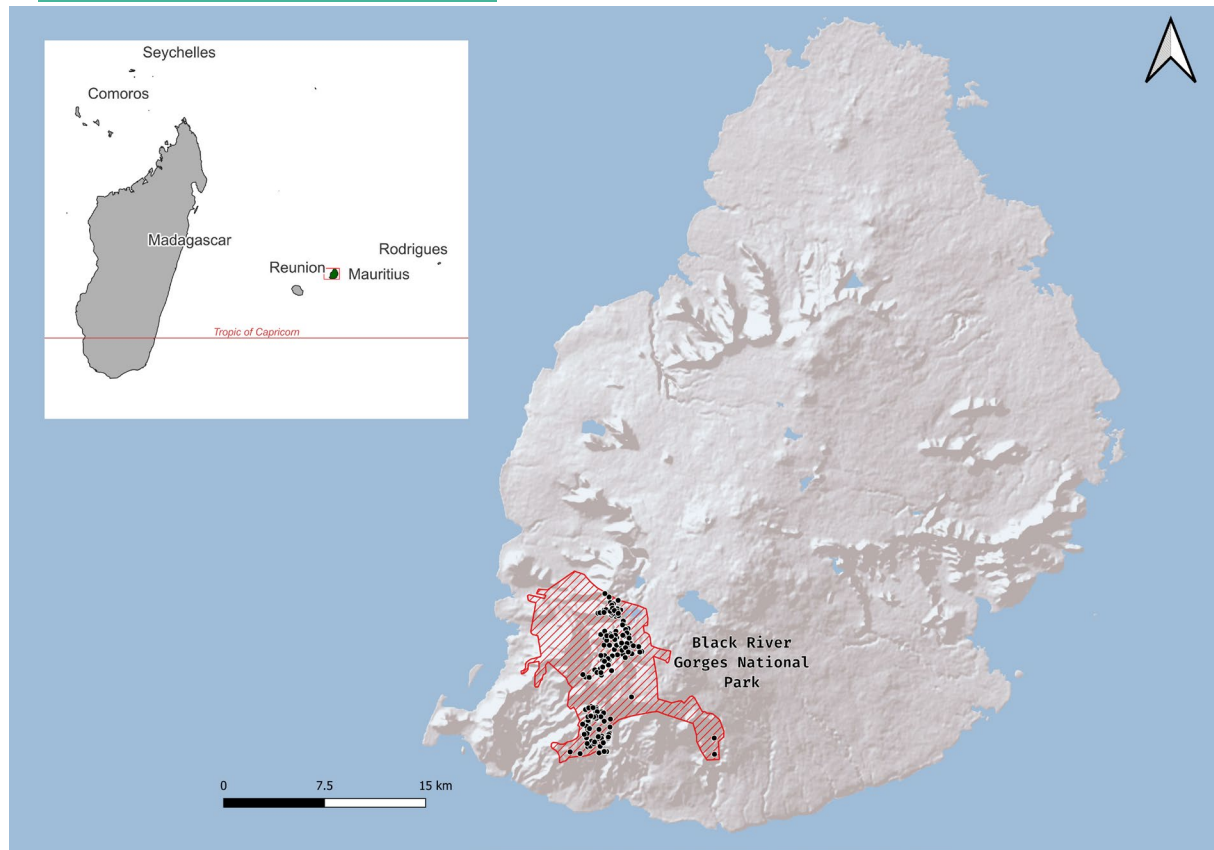


FIGURE 2 The Black River Gorges National Park (south-west of Mauritius) and the echo parakeet natural and artificial nest locations (black dots).

observations, feeding observations, ringing data, breeding data), and bird IDs were cross-referenced with the studbook to confirm their origin and age. From the master dataset of resighting histories, some individuals were excluded from the analysis if we believed they could bias survival estimates due to their atypical life history or conservation management actions: individuals may have been ringed as adults (unknown age), never successfully fledged (died in the nest), translocated ($N=151$), taken into captivity ($N=4$) or known to have bred prematurely <2 years ($N=2$). The last cohort was removed ($N=120$) due to no recapture events after 2022. This filtering process resulted in a final dataset of 2734 known-age individuals, of which 997 (36.4%) were resighted in at least one subsequent breeding season following their initial ringing event.

Encounters at supplementary feeding stations were excluded to maintain the assumption of equal-resighting probability among individuals (Pollock et al., 1990) that could potentially bias demographic parameter estimates if violated. Birds nesting closer to feeding stations aggregate around them (Fogell et al., 2019), creating spatial heterogeneity in detection probabilities.

2.4 | Breeding state attribution

Accurate state assignment is critical for multistate models (Conn & Cooch, 2009). In our study, individuals were classified as breeders

only when positively identified as parents at a monitored nest and actively participating in reproduction (where a breeding attempt is characterised by at least one egg being laid); all other resighted individuals were classified as non-breeding (pre-breeders if never recorded breeding, non-breeders if previously recorded breeding but not in the current season).

Several factors support the reliability of this classification. First, the scarcity of natural cavities means that the majority of breeding attempts occur in monitored nest boxes, which were visited multiple times by field biologists each breeding season to confirm parent identities through unique colour ring combinations. Second, echo parakeets exhibit high nest site fidelity and low divorce rates, allowing cross-validation with records from previous years. Third, continuous surveys across the species' limited range ($\sim 41 \text{ km}^2$) throughout the breeding season minimised the probability of undetected breeding attempts. Fourth, natural cavities outside monitored areas are unlikely to support successful breeding due to lack of maintenance during the non-breeding season and competition from invasive species for cavity access. Thus, we expect breeder resightings probabilities to be very close to 1. Moreover, the low number of unringed individuals encountered throughout the study period (S. Henshaw *in litt.* 2026) provides indirect validation of the monitoring coverage: if substantial unrecorded breeding were occurring, we would expect higher resighting rates of unringed birds, which was not observed.

2.5 | Statistical methods

2.5.1 | Goodness-of-fit

Individual heterogeneity in survival and resighting probabilities can bias parameter estimates (Lebreton & Pradel, 1998; Pradel et al., 1997). To determine the optimal age structure for survival (ϕ) and detection (p) probabilities, we used a sequential approach in the Cormack–Jolly–Seber (CJS) framework where ϕ and p were manipulated until the best model was found without time effect. We started with a model containing the maximum biologically meaningful number of age classes (six age classes for both ϕ and p) with constant time. After establishing the optimal age structure for each parameter, we incorporated time-dependence to create our 'global model' (Table S1, model 1).

To evaluate the homogeneity assumptions, we applied the median $\hat{c}$ approach implemented in Program MARK (White & Burnham, 1999) to our most parameterised CJS single-state model ($[\phi(0-4t), p(1-6t)]$) accounting for age structure which included time-varying survival for age classes 0 through 4+ and time-varying detection probabilities for age 1 (set equal to 0) and 2–6+. This represents the most complex biologically relevant parameterisation for our study population accounting for expected heterogeneity in survival and detection among age classes. The median $\hat{c}$ procedure estimates overdispersion by simulating datasets from the fitted model and finding the $\hat{c}$ value at which the observed deviance falls at the median of the simulated deviance distribution (for more details, see Cooch & White, 2025). A $\hat{c}$ value of 1.0 indicates no overdispersion, while values up to 3.0 are considered acceptable for reliable survival modelling (Lebreton et al., 1992). Following Brown (2003), datasets satisfying single-state assumptions should also adequately fit multistate models, making this approach appropriate for our subsequent multistate analyses. We therefore used quasi-AICc (QAICc) (White & Burnham, 1999) for model selection incorporating the variance inflation factor ($\hat{c}$) to adjust for overdispersion, reducing the risk of selecting overly complex models and emphasising parsimony (Lebreton et al., 2003). This approach has been successfully implemented across various capture–recapture studies in the literature (Converse et al., 2009; Horswill et al., 2014; Wood et al., 2018) and provides reliable assessment for multistate models incorporating age-dependent transition probabilities (Cooch & White, 2025).

2.5.2 | Modelling framework

We used multistate capture–recapture models (Brownie et al., 1993; Lebreton et al., 2009) to simultaneously estimate survival probability (ϕ), transition probability (ψ) between breeding states and detection probability (p). Capture occasions corresponded to annual breeding seasons with intervals between occasions (t to $t+1$) representing 1 year. These models estimate three key parameters: the probability of being resighted at time t in state r given survival and presence; the probability of transitioning from state r at time t to state s at

time $t+1$ conditional on survival; and apparent survival from time t to $t+1$ (Nichols et al., 1994). In these models, survival estimates represent 'apparent survival', which cannot distinguish mortality from permanent emigration. However, several factors suggest emigration is minimal in this system: (1) echo parakeets are restricted to native forest habitat within Black River Gorges National Park, (2) extensive annual surveys throughout the park rarely encounter previously undetected individuals, (3) natural cavity availability is limited outside monitored areas and (4) no echo parakeets have been recorded outside native forest boundaries (S. Henshaw *in litt.* 2026). These factors suggest that survival estimates from the study are more likely to be closer to true survival than apparent survival.

We developed biologically informed hypotheses about factors affecting these parameters based on the species' life history and prior research, which guided our construction of candidate models. Parrots typically follow patterns where juveniles experience substantially lower survival rates compared to adults (Saunders, 1982; Saunders et al., 2024), and previous research suggests that echo parakeets exhibit similar age-structured survival patterns, with notable differences even among adult age classes (Gath, 2018).

- (i) Survival (ϕ): We defined three age groups for survival modelling: juveniles (ages 0 and 1, comprising fledglings in their first year and yearlings in their second year), young adults (ages 2 and 3) and adults (ages 4 and above). We tested models ranging from complex age-state interactions to simpler structures, guided by three primary hypotheses: (1) juvenile survival would show temporal variation due to sensitivity to environmental factors such as density-dependent processes and climatic variation; (2) adult survival would differ between breeding states; and (3) young adults (ages 2–3) might exhibit different state-specific survival patterns compared to older adults (ages 4+). We tested both fully age-stratified models ($\phi(0, 1, 2, 3, 4+)$) and models with pooled age classes ($\phi(0:1, 2:3, 4+)$) to reduce the number of estimated parameters and increase statistical power for estimating early-life survival while maintaining biologically meaningful age distinctions.
- (ii) Transitions (ψ): We tested whether transitions between breeding states varied by age, time or both. Specifically, we evaluated models with: (1) four or five age classes, with temporal effects modelled as either additive or interactive with age; (2) full annual temporal variation versus pooling into three broader time periods corresponding to distinct phases of population recovery (initial recovery 1994–2003, growth 2004–2015, regulation 2016–2022; Figure 1); and (3) age effects only, without temporal variation. We simplified from four to three age classes to reduce the number of estimated parameters while retaining biologically meaningful transitions. Unlike survival, transition parameters could not be pooled by age in the same way because of biological constraints: the breeding state is not reachable before age 2 (sexual maturity), so age-specific transitions were only estimable from age 1 onwards. Interactive effects between age and full time-dependence

were initially considered but proved overparameterised, resulting in inestimable parameters for certain age-specific transitions, leading us to adopt the more parsimonious additive model structure in this case.

- (i) Detection (p): We hypothesised that detection probability would be driven primarily by breeding state rather than age, because field monitoring actively targets breeding sites while encounters with non-breeders or pre-breeders are much more opportunistic, resulting in lower detection probability for individuals in these states. The higher detection rates observed in older birds in the CJS framework may therefore reflect their higher probability of being breeders rather than an independent age effect. We tested models where detection probability varied by state, age and time (due to changes in overall density, monitoring teams and management intensity). Detection probability for pre-breeders was both age- and time-dependent, distinguishing yearlings (age 1) from older pre-breeders (age 2+) to account for potential differences in site prospecting behaviour, whereas detection for adult breeders and non-breeders was time-dependent only (Table 1). We evaluated three temporal structures: (1) full time-dependence, with state interaction ($p(1t, 2t^*s)$), where yearlings varied by time independently and adults varied by state and time; (2) state-time interaction without age distinction ($p(s^*t)$) assuming no differences in detection between yearlings and adults; and (3) simplified temporal structures where time effects were pooled into recovery periods (Figure 1) or management intensity (Gath, 2018). We also tested models with state and age effects only with no temporal variation (more details in Table S2).

Parameters were fixed to zero when transitions were biologically impossible, based on species life history and the delayed maturity (Clobert et al., 1994). These constraints reflected two key biological realities: (1) sexual maturity occurs at age 2 (confirmed by our data showing no breeding before this age), and (2) individuals must progress sequentially through breeding states (Table 2 and Figure 3).

Following Lebreton et al. (1992) methodology and notation, these hypotheses were translated into a set of candidate models ($n=177$) representing different combinations of age, time and state effects on demographic parameters (Table S2). The most

parsimonious models were determined using Akaike's Information Criterion (Burnham & Anderson, 2002). Analyses were conducted in R version 4.4.0 (Team, R Core, 2024), using the 'RMark' package version 3.0.0 (Laake & Rexstad, 2022) as an alternative interface to MARK's GUI to build models that were fitted to the data in Program MARK version 10.1 (White & Burnham, 1999).

Additionally, to evaluate the validity of assumptions underlying multistate models with unobservable state commonly used when non-breeding individuals cannot be monitored, we fitted UMS models where pre-breeder and non-breeder states were designated as unobservable ($p=0$) with survival constrained to equal that of breeders.

3 | RESULTS

3.1 | Goodness-of-fit

Goodness-of-fit testing using the median $\hat{c}$ procedure revealed slight overdispersion ($\hat{c}=1.27$, bounds: 1.0–3.0, 1000 simulations), well within acceptable limits ($\hat{c}<3.0$) recommended for reliable survival modelling (Lebreton et al., 1992).

3.2 | Model selection

Two strongly supported models ($\Delta AICc < 2$; Burnham & Anderson, 2002) together accounted for approximately 70% of the total model weight. These top models shared similar structures for detection probability and state transitions, while differing slightly in their survival parameterisation. The second-ranked (Model 214,

TABLE 2 Transition matrix (Ψ) for movements between breeding states from time t (rows) to $t+1$ (columns), conditional on survival.

State at t	To: Pre-breeder	To: Breeder	To: Non-breeder
Pre-breeder (1)	$1 - \psi_{12}$	ψ_{12}	0
Breeder (2)	0	$1 - \psi_{23}$	ψ_{23}
Non-breeder (3)	0	ψ_{32}	$1 - \psi_{32}$

Note: Zeros indicate biologically impossible transitions. States are defined as: Pre-breeder (state 1), breeder (state 2) and non-breeder (state 3).

TABLE 1 Detection probability (p) matrix for the echo parakeet multistate model.

State at t	Not detected	Pre-breeder (1)	Breeder (2)	Non-breeder (3)
Pre-breeder (1)	$1 - p_1^{(a,t)}$	$p_1^{(a,t)}$	0	0
Breeder (2)	$1 - p_2^{(t)}$	0	$p_2^{(t)}$	0
Non-breeder (3)	$1 - p_3^{(t)}$	0	0	$p_3^{(t)}$

Note: The matrix describes the probability of each observation event (columns) conditional on the individual's true state (rows). Detection probabilities vary across different states with time (t) and age (a) variation: $p_1^{(a,t)}$ for pre-breeders (age and time-dependent), $p_2^{(t)}$ for breeders and $p_3^{(t)}$ for non-breeders. Zeros indicate no state misclassification.

$\Delta AICc=0.67$, weight=0.29) included time-dependent juvenile (i.e. first 2 years post-fledging) survival and state-dependent adult survival with distinct parameters for ages 2, 3 and 4+. The top model (Model 165, weight=0.41) simplified the adult age structure by grouping young adults (ages 2–3) while maintaining separate estimates for older adults (4+). Model 165 was selected as the most parsimonious (Table 3).

3.3 | Apparent survival estimates

The most parsimonious model (Model 165, Table 3) revealed substantial state-dependent variation in echo parakeet apparent survival (Figure 4). Juvenile survival (age 0–1 and 1–2) was best described with full time-dependence, showing a declining trend since 2003 (Figures 5 and 6). In contrast, adult survival remained constant across years with significantly higher rates for breeding

adults (0.96–0.97) than non-breeding adults (0.76–0.9). For older adults (age 4+), breeding individuals exhibited the highest survival probability at 0.96 (CI=0.94–0.97), which was 0.13 higher than pre-breeders at 0.83 (CI=0.79–0.86) and substantially higher than non-breeders at 0.76 (CI=0.70–0.81). A similar pattern was observed in younger adults (ages 2–3), where breeders showed 0.07 higher survival probability at 0.97 (CI=0.94–0.99) compared to pre-breeders at 0.90 (CI=0.86–0.93). These consistent differences across age classes suggest that breeding state is a significant determinant of survival probability that is independent of age effects.

3.4 | Bias from equal-survival assumptions

For comparison, multistate models with unobservable state (UMS) estimated young adult survival at 0.93 (CI=0.89–0.95) and 0.91

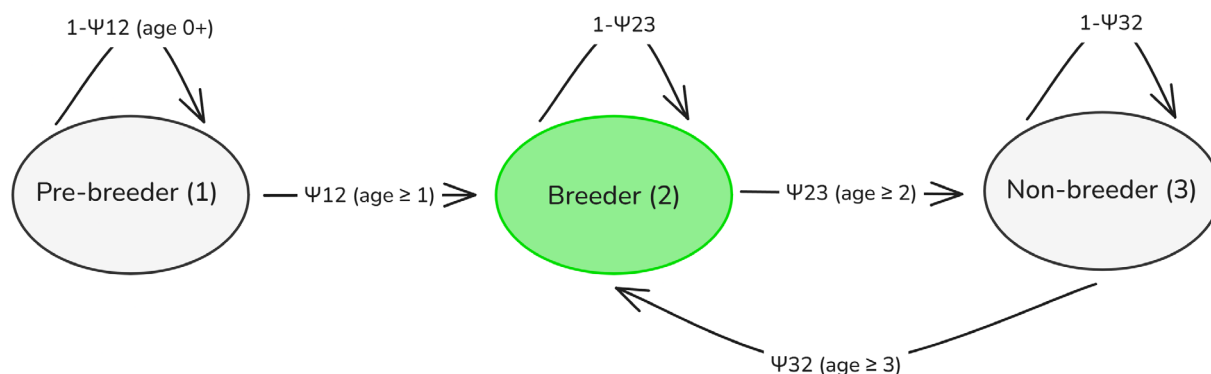


FIGURE 3 Breeding states transitions diagram of echo parakeet (*Alexandrinus eques*). Pre-breeding individuals (state 1, age 0+), active breeders (state 2, age ≥ 2) and non-breeders (state 3, age ≥ 3). Transitions 1 to 1, 2 to 2 and 3 to 3 (remaining in the same state) are computed by subtraction.

TABLE 3 Top 10 candidate models evaluating factors affecting survival (Φ), state transition (ψ) and detection (p) probabilities.

Model	Model structure	Num. par.	AICc	$\Delta AICc$	Weight	Deviance
165	$\Phi(0:1t, 2:3s, 4s), \psi(0-3^*period), p(1t, 2t^*s)$	160	15156.60	0.00	0.41	5963.53
214	$\Phi(0:1t, 2s, 3s, 4s), \psi(0-3^*period), p(1t, 2t^*s)$	162	15157.26	0.67	0.29	5960.00
18	$\Phi(0:1t, 2s), \psi(0-3^*period), p(1t, 2t^*s)$	157	15159.21	2.61	0.11	5972.43
217	$\Phi(0:1t, 2s, 3s, 4s), \psi(0-4^*period), p(1t, 2t^*s)$	171	15159.59	2.99	0.09	5943.41
168	$\Phi(0:1t, 2:3s, 4s), \psi(0-4^*period), p(1t, 2t^*s)$	169	15160.07	3.47	0.07	5948.10
21	$\Phi(0:1t, 2s), \psi(0-4^*period), p(1t, 2t^*s)$	166	15161.94	5.34	0.03	5956.28
186	$\Phi(0:1t, 2:3s, 4s), \psi(0-3^*period), p(s^*t)$	134	15170.90	14.31	<0.01	6032.16
235	$\Phi(0:1t, 2s, 3s, 4-s), \psi(0-3^*period), p(s^*t)$	136	15171.82	15.23	<0.01	6028.91
39	$\Phi(0:1t, 2s), \psi(0-3^*period), p(s^*t)$	131	15173.24	16.64	<0.01	6040.73
238	$\Phi(0:1t, 2s, 3s, 4s), \psi(0-4^*period), p(s^*t)$	145	15174.01	17.41	<0.01	6012.33

Note: Notation: Numbers (0, 1, 2, 3, 4) represent age classes; ':' indicates grouped age classes (e.g. 0:1 = ages 0 and 1 grouped); 't' = full time-dependent; 's' = state-dependent (pre-breeder, breeder, non-breeder); '*' = interaction between effects; 'period' = temporal variation in broader three time periods (representing population growth stages) rather than annually (t). Models are ranked by Akaike's information criterion (AICc). The best model is in bold and highlighted.

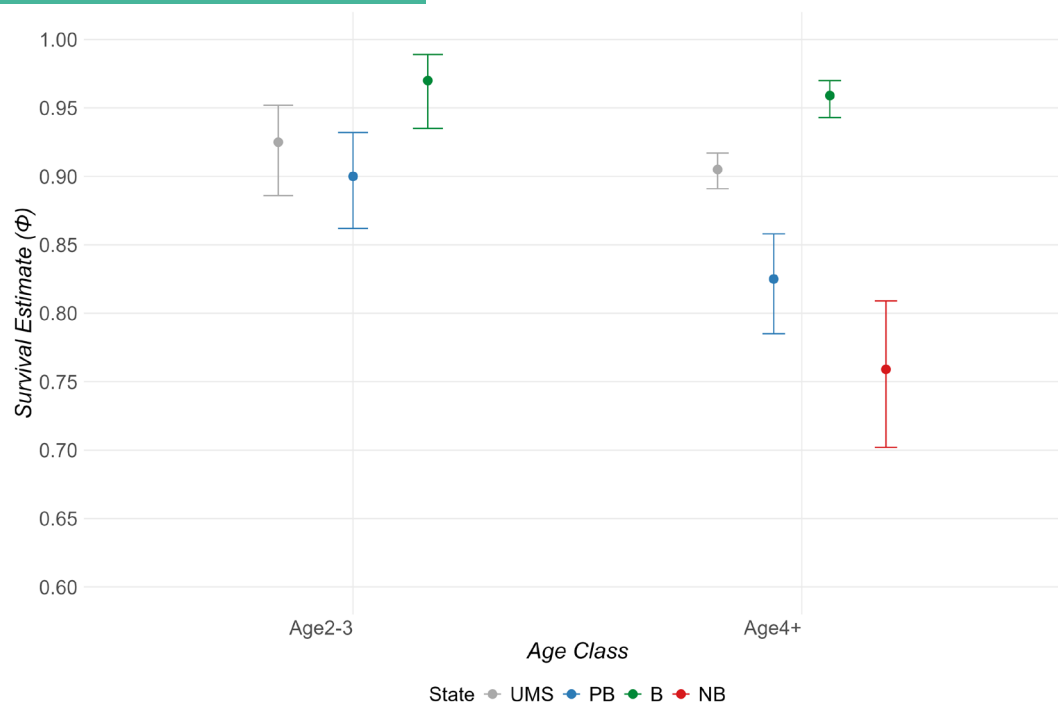


FIGURE 4 Differences in adult apparent survival estimates between age classes and states (estimates derived from the best-supported model (model 165, Table 3). Green = breeders, blue = pre-breeders, red = non-breeders and grey = estimations from multistate model with unobservable state (UMS).

(CI=0.89–0.92) for age 4+, underestimating breeders' survival by 0.04–0.05 and overestimating survival of non-breeding individuals by 0.03–0.15 (Figure 4).

3.5 | Transition probabilities

Transition probabilities were found to be age-dependent and time-dependent (population growth periods) with breeders having higher probabilities of retaining their status as breeders (Table 4). In the multistate parameterisation we adopted, survival precedes transition within each occasion; consequently, the 'age 1' transition probabilities reported here represent the probability that a bird surviving its second year of life transitions into the breeder state—and is therefore first recorded as a breeder at age 2 (consistent with the known minimum age of first breeding reported throughout this study). State transitions revealed declining recruitment probabilities for all age classes, with the probability of breeding for the first time dropping by 0.1 for age 1, 0.25 for 2-year-olds and 0.07 for 3-year-olds and older between the early recovery period (1996–2003) and recent years (2016–2021) (Figure 7). Details about the differences between periods can be found in Table S4.

3.6 | Resighting probabilities

Across all competitive models (Table 3, $\Delta AIC_c < 7$), detection probability was best modelled with two age classes (yearlings and adults)

and state-specific full-time variation, with yearlings' detection varying independently from adults (see Table S3). When constrained to state-only variation, adult breeders showed near-perfect detection ($p=1.000$), consistent with intensive nest box monitoring, while yearlings ($p=0.32$), adult pre-breeders ($p=0.29$) and adult non-breeders ($p=0.21$) showed substantially lower detection, reflecting the opportunistic nature of encounters outside monitored breeding sites.

4 | DISCUSSION

4.1 | Apparent survival estimates

4.1.1 | General findings

Building on previous demographic analyses (Gath, 2018), this study provides the first estimates of survival and recruitment for the echo parakeet across three decades of population recovery. By tracking demographic rates from near-extinction to apparent carrying capacity, we reveal complex patterns of age-, state- and time-dependent survival with important implications for conservation management. While demographic studies exist for other threatened parrots such as the Puerto Rican parrot (*Amazona vittata*) (Beissinger et al., 2008), kakapo (*Strigops habroptilus*) (Elliott et al., 2001), orange-bellied parrot (*Neophema chrysogaster*) (Holdsworth et al., 2011; Stojanovic et al., 2020) and green-rumped parrotlet (*Forpus passerinus*) (Beissinger, 2008; Sandercock et al., 2000), our study offers a unique

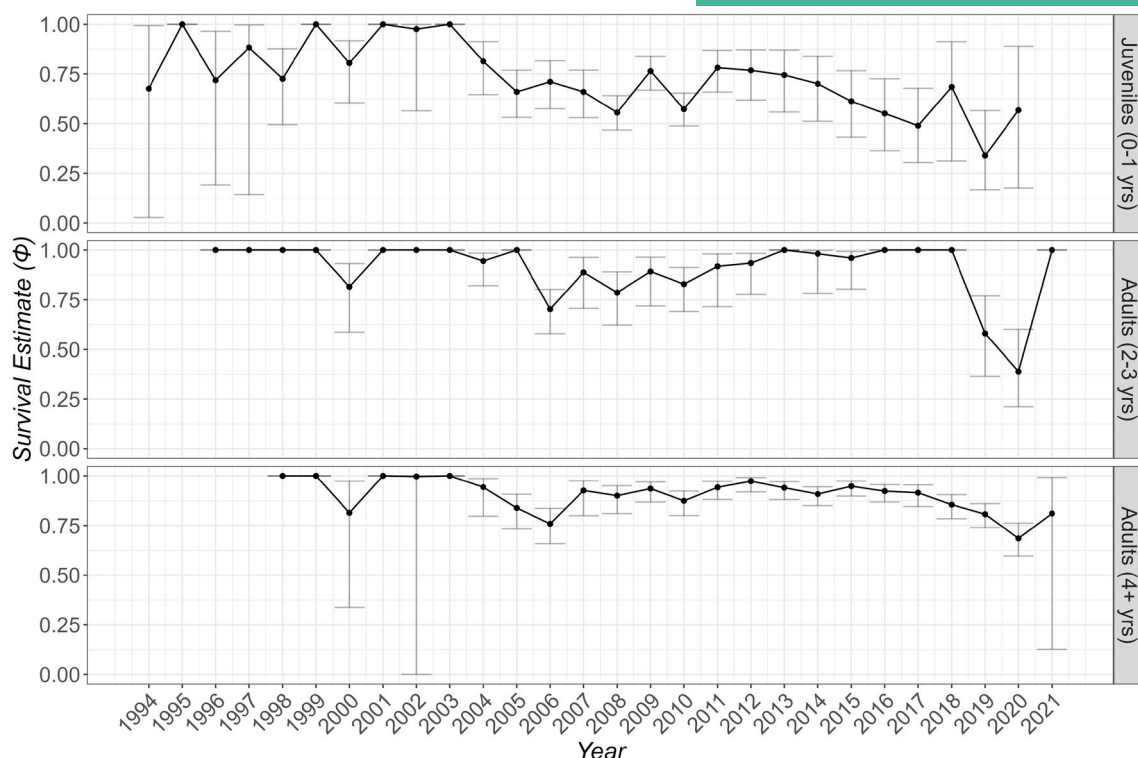


FIGURE 5 Apparent survival estimates from 1994 to 2021 across age classes in the multistate framework (Error bars represent 95% confidence intervals). Juvenile estimates derived from the best-supported model (model 165: $\Phi(0:1t, 2:3s, 4s)$), with adult survival estimated from a time-parameterised variant (Table S2; model 239: $\Phi(0:1t, 2:3t, 4t)$).

perspective on demographic change during population recovery. In long-lived avian populations, density-dependent effects on recruitment have rarely been demonstrated across time within a single population (e.g. Fay et al., 2017; Sandercock et al., 2000; Tavecchia et al., 2007) due to the long-term data requirements. This 29-year dataset, spanning the echo parakeet's recovery from near-extinction (<20 individuals) to apparent carrying capacity (>500 individuals), provides a rare opportunity to examine how breeding probabilities and age-specific survival rates shift across distinct phases of population recovery.

4.1.2 | State-dependent survival patterns

Our multistate approach revealed pronounced state-dependent variation in survival across all age classes, with breeding individuals consistently showing higher survival probabilities than non-breeding birds. The magnitude of this difference increased with age, culminating in a 0.2 survival advantage for breeders in the oldest age group (4+).

This pattern of higher survival in breeding individuals has been documented in other long-lived species and contrasts with the 'prudent-parent' hypothesis (Drent & Daan, 1980), which predicts that reproduction should impose survival costs. Wood et al. (2021) found that Skomer Island's Manx shearwaters (*Puffinus puffinus*) that successfully raised a chick showed 10% higher survival compared to non-breeders, and similar patterns have been observed in other long-lived species including parrots (Lescroël et al., 2009;

Sandercock et al., 2000; Weladji et al., 2008). However, this pattern is not universal among avian populations. Studies have also documented the opposite relationship, where breeding individuals show reduced body condition and/or survival compared to non-breeders, supporting the expected costs of reproduction. For example, Cruz-Flores et al. (2021) demonstrated that reproductive effort negatively affected survival in Bulwer's petrel (*Bulweria bulwerii*) females, and similar breeding costs have been reported in other bird studies (Sanz-Aguilar et al., 2012; Williams, 2005), reptiles (Madsen & Shine, 1994; Reading, 2024), amphibians (Reading & Jofré, 2021) and mammals (Clutton-Brock et al., 1989, 1996; Tavecchia et al., 2005). These conflicting results indicate substantial variation in how breeding status affects survival among different species and populations, making the widespread assumption of equal-survival between breeding and non-breeding individuals in multistate models problematic.

Several non-mutually exclusive mechanisms likely contribute to this state-dependent survival pattern. First, individual heterogeneity creates a selection effect whereby individuals in better condition are more likely to both secure breeding opportunities and survive longer (Aubry et al., 2011; Barbraud & Weimerskirch, 2005; Cam et al., 1998; Robert et al., 2012; Sanz-Aguilar et al., 2011). This quality-based sorting means that we might expect the breeding population to inherently represent a subset of higher quality individuals (those with superior competitive ability, disease resistance or better body condition) within each age class. Second, in accordance with life-history theory (Roff, 1993; Stearns, 1992), breeding

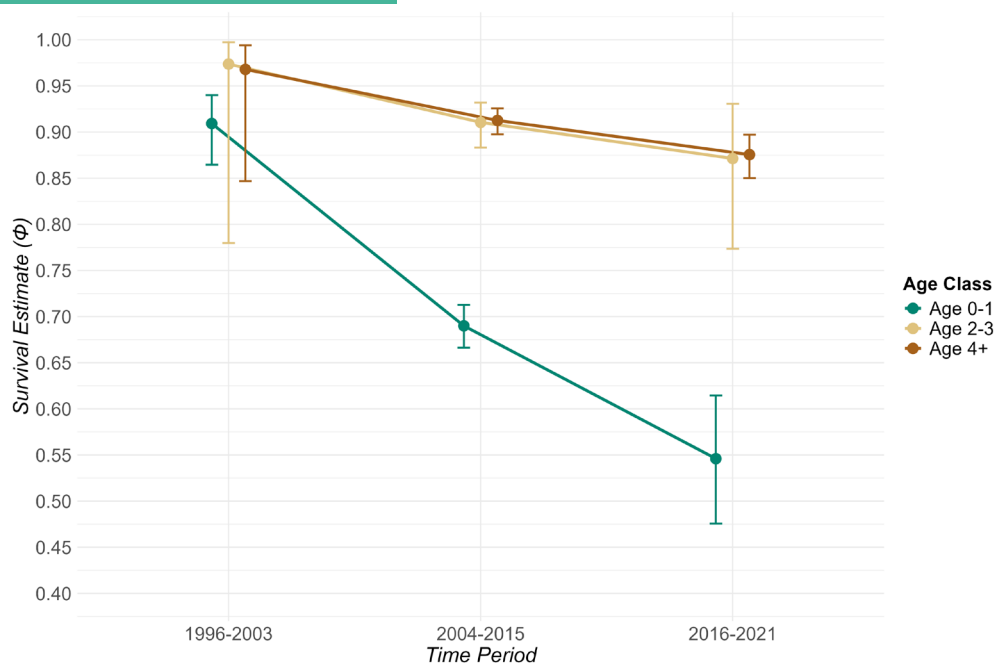


FIGURE 6 Age-specific apparent survival estimates (Φ) across three phases of population recovery (initial recovery 1996–2003, growth 2004–2015, regulation 2016–2021) (Error bars represent 95% confidence intervals). Estimates derived from model with time-period constraints replacing full-time parameterisation (Table S2; model 240).

TABLE 4 Transition rates by age class throughout the study ('PB'=pre-breeding/'B'=breeding/'NB'=non-breeding).

Transition	Age class	ψ	SE	LCI	HCI
PB-B	Age 0	0	0	0	0
PB-B	Age 1	0.11	0.01	0.09	0.13
PB-B	Age 2	0.21	0.02	0.18	0.25
PB-B	Age 3+	0.18	0.01	0.16	0.21
B-NB	Age 2	0.15	0.04	0.09	0.24
B-NB	Age 3+	0.11	0.01	0.09	0.13
NB-B	Age 3+	0.43	0.03	0.37	0.49

Note: Survival precedes transition: Transition values for 'age 1' is their transition to breeding state after surviving their second year.

experience itself may confer survival advantages through improved foraging efficiency (Daunt et al., 2007; Pärt, 2001), better predator avoidance and enhanced responses to environmental variation (Forslund & Pärt, 1995; Nevoux et al., 2007).

4.1.3 | Age-specific patterns and population implications

Consistent with life-history theory predictions (Sæther & Bakke, 2000; Stearns, 1998), empirical findings across long-lived avian species (Ratcliffe et al., 2002; Tavecchia et al., 2001) and other psittacines (Senar et al., 2019), we found lower survival probabilities in juveniles (<2 years old) compared to adults. Our temporal analysis also revealed a declining trend among the younger age class; when

survival was modelled by recovery phase rather than year, juvenile survival declined from 0.91 (95% CI: 0.86–0.94) during initial recovery to 0.55 (95% CI: 0.48–0.61) during the regulation phase, while adult survival remained stable across all three periods (Figure 6). This pattern likely reflects density-dependent regulation (Newton, 1998) as the population approaches carrying capacity, with increased competition (e.g. food resources, nesting sites) disproportionately affecting younger, less competitive individuals (Armstrong et al., 2005; Nicoll et al., 2003; Wunderle, 1991). Age-specific survival patterns are well documented in a range of taxonomic groups, with distinct differences in survival estimates between short-lived and long-lived taxa (Gaillard et al., 1998; Loery et al., 1987; Mihoub et al., 2010; Sæther et al., 1996). Individual heterogeneity in survival tends to be more pronounced in short-lived species than in those with longer generation times (Péron et al., 2016). Additionally, survival rates of early life stages (juveniles and sub-adults) are often more sensitive to environmental factors than survival rates of older individuals, showing greater variability in response to climate and resource availability (Naef-Daenzer et al., 2001; Nicoll et al., 2017; Oro et al., 2010; Payo-Payo et al., 2016; Sæther et al., 1996). Future analyses should explicitly examine how environmental factors (e.g. density, cyclonic events) and individual-level covariates (e.g. supplementary feeding, disease, inbreeding) may influence these age-specific survival patterns.

4.2 | Recruitment rates

Transitions between breeding states depended on an individual's current state and age, not on chance alone (Markovian). While

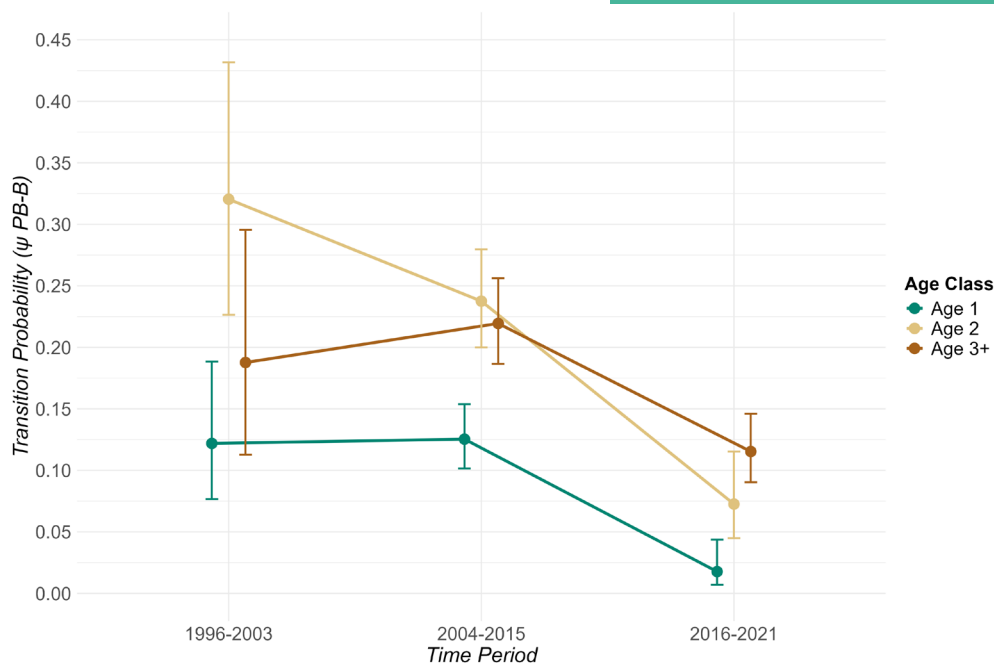


FIGURE 7 Estimates of echo parakeet recruitment rates (ψ) (pre-breeder to breeder state transition) across age classes from 1996 to 2021 (Error bars represent 95% confidence intervals). Estimates derived from the best-supported model (model 165: $\psi(0-3 \cdot \text{period})$).

breeders have high probabilities to breed again the following year, previous non-breeders were far less likely to return to breeding, and both rates shifted across the phases of recovery. Transition from pre-breeder to breeder state (recruitment) showed clear age-dependence, with initial recruitment probability for 2-year-olds ranging from 0.02 to 0.12 depending on the time periods. This relatively low probability of recruitment in the breeding population at the end of their second year suggests that many echo parakeets delay breeding beyond physiological maturity, likely due to competition for limited breeding resources or the need to reach optimal condition before attempting reproduction. Recruitment probabilities showed variation across the three time periods of population growth (1996–2003, 2004–2015, 2016–2020). Recruitment was overall highest during 1996–2003, coinciding with the recovery period and lowest during 2014–2021 when the population approached the regulation phase. The probability of returning from non-breeding to breeding declined in the final period (from 0.53 to 0.60 before 2016 to 0.28 in the last years), suggesting increasing difficulty in re-entering the breeding population. Taken together, the declines in first-time recruitment of pre-breeders and in re-entry by experienced non-breeders point to density-dependent effects on transitions into the breeding state, as documented in other bird populations (Crespin et al., 2006; Newton, 1998; Tavecchia et al., 2007), with increasing competition for space and food as the population grew. However, recruitment rates may also be influenced by other temporal and individual-level factors such as diseases (e.g. beak and feather disease virus). Further investigation is necessary to assess how these covariates affect transitions to breeding state.

4.3 | Resighting probabilities

Our analyses revealed complex patterns in detection probabilities that were better understood through multistate modelling. Breeding state was a fundamental driver of detection differences, with breeding individuals showing substantially higher detection rates than non-breeders regardless of age, likely due to their more consistent presence at monitored nest sites. In numerous long-lived species, breeding individuals exhibit strong territorial fidelity to breeding sites (Greenwood & Harvey, 1982), making them more consistently detectable than non-breeders. Moreover, immature individuals often show higher dispersal rates (Gaines & McClenaghan, 1980) than adults, reducing their detection probability. These biological patterns, combined with potential fluctuations in the monitoring effort, create sources of detection heterogeneity that have been accounted for in these multistate capture–recapture models to avoid biased demographic estimates.

5 | CONCLUSION AND CONSERVATION IMPLICATION

As conservation programmes increasingly recognise the importance of evidence-based management (Cook et al., 2010; Pullin & Knight, 2001; Sutherland et al., 2004), these findings have direct implications for the ongoing management of the echo parakeet and emphasise the importance of comprehensive monitoring programmes for understanding demographic processes in recovering populations.

First, the substantial decline in juvenile apparent survival and recruitment probability as the population approached carrying capacity underscores that continued demographic monitoring is essential to detect density-dependent shifts in vital rates. The transition from rapid growth to regulation represents a critical phase where management priorities may need to shift, from maximising population growth and abundance to maintaining demographic stability and genetic diversity (Raisin et al., 2012; Van Oosterhout et al., 2026).

Second, the declining probability of non-breeders that were known to previously breed re-entering the breeding population shows that a growing number of these experienced adults remained outside the breeding pool as densities increased. Where breeding is limited by nest-site availability, management that increases access to nest sites could allow more of these experienced individuals to resume breeding.

Third, the assumption of equal survival between breeding and non-breeding individuals, commonly used in demographic models, appears inappropriate for echo parakeets and likely many other species. Population projections based on this assumption may be overly optimistic, potentially misleading management goals and actions (Fletcher et al., 2012; Lee et al., 2017; Sanz-Aguilar et al., 2016). For conservation practitioners, we recommend prioritising monitoring programmes that capture demographic complexity across all life stages and reproductive states when feasible, as these observations have been proven to significantly improve the accuracy of demographic parameter estimation (Kendall, 2004; Oosthuizen et al., 2019; Pardo et al., 2013). We therefore strongly recommend the continuation of field surveys that systematically document non-breeding echo parakeets.

Fourth, our results provide essential baseline parameters for future population viability analyses that would help inform management decisions (Beissinger & McCullough, 2002; Norris, 2004; Reed et al., 2002). Elasticity analyses would identify which vital rates have the greatest proportional influence on population growth rate λ (Caswell, 2001), but management should also consider the variance of demographic rates (Caswell, 2000; Koons et al., 2016), as a more variable rate such as juvenile survival can drive year-to-year fluctuations despite lower elasticity. Thus, reliable projections for the echo parakeet will need to incorporate the density-dependent effects documented here, including the declining proportion of individuals recruiting into the breeding population, the reduction in early-life survival at higher densities and the higher temporal variance in juvenile survival. Such analyses could help identify which vital rates offer the greatest potential for management intervention (Ewen et al., 2012), informing decisions about ongoing (V. Tatayah, S. Henshaw and C. Jones *in litt.* 2026) and future translocations to establish additional populations on the island.

AUTHOR CONTRIBUTIONS

Simon Tollington designed the study, conceived the original research questions and supervised the research; Adrien Gellé designed the study, conducted statistical analyses, interpreted results, designed

the figures and led manuscript writing; Angelo P. Pernetta, Esther F. Kettel, Malcolm Nicoll and Ken Norris supervised the research, contributed to the analytical framework, statistical guidance, data interpretation and manuscript revision; Jim Groombridge supervised the research and contributed to the manuscript revision; Helen Gath performed initial data formatting, collation (first 20 years), analyses and interpreted results; Sion Henshaw and Vikash Tatayah coordinated field data collection, managed the long-term monitoring database and provided ecological expertise on the echo parakeet project. Kevin Ruhomaun provided oversight of field data collection. Carl G. Jones established the original monitoring protocol and provided expertise on the project. All authors contributed to data interpretation, provided critical feedback on manuscript drafts and approved the final version for publication.

ACKNOWLEDGEMENTS

This research was made possible through the dedication of numerous staff and volunteers from the Mauritian Wildlife Foundation (MWF) and the National Parks and Conservation Service (NPCS), who collectively established and maintained a comprehensive ringing and recovery programme for the echo parakeet over the past three decades. The echo parakeet recovery programme receives support from the Durrell Wildlife Conservation Trust and a host of collaborating partners with in situ coordination by MWF. Malcolm Nicoll was supported by Research England. Jim Groombridge was supported by Research England's Expanding Excellence in England (E3) Fund, UK Research and Innovation. We extend special gratitude to Jeffrey L. Laake for his assistance with RMark modelling, which enhanced the reproducibility of this work.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data for this project was provided by the Mauritian Wildlife Foundation (MWF) and is part of the echo parakeet recovery project and long-term monitoring. Data available are from the Dryad Digital Repository <https://doi.org/10.5061/dryad.dz08kpsdk> (Gellé et al., 2026).

ORCID

Adrien Gellé  <https://orcid.org/0009-0006-5654-5335>

Malcolm A.C. Nicoll  <https://orcid.org/0000-0001-6212-4787>

Esther F. Kettel  <https://orcid.org/0000-0001-8555-6195>

Angelo P. Pernetta  <https://orcid.org/0000-0003-4492-2798>

Jim Groombridge  <https://orcid.org/0000-0002-6941-8187>

Vikash Tatayah  <https://orcid.org/0000-0003-0759-254X>

Ken Norris  <https://orcid.org/0000-0003-0894-245X>

Simon Tollington  <https://orcid.org/0000-0003-2450-7255>

REFERENCES

Armstrong, D. P., Davidson, R. S., Perrott, J. K., Roygard, J., & Buchanan, L. (2005). Density-dependent population growth in a reintroduced

- population of North Island saddlebacks. *Journal of Animal Ecology*, 74, 160–170. <https://doi.org/10.1111/j.1365-2656.2004.00908.x>
- Armstrong, D. P., & Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in Ecology & Evolution*, 23, 20–25. <https://doi.org/10.1016/j.tree.2007.10.003>
- Aubry, L. M., Cam, E., Koons, D. N., Monnat, J.-Y., & Pavard, S. (2011). Drivers of age-specific survival in a long-lived seabird: Contributions of observed and hidden sources of heterogeneity: Reproduction and survival trade-offs in the kittiwake. *Journal of Animal Ecology*, 80, 375–383. <https://doi.org/10.1111/j.1365-2656.2010.01784.x>
- Barbraud, C., & Weimerskirch, H. (2005). Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology*, 86, 682–692. <https://doi.org/10.1890/04-0075>
- Beissinger, S. (2008). Long-term studies of the green-rumped parrotlet (*Forpus passerinus*) in Venezuela: Hatching asynchrony, social system and population structure. *Ornitología Neotropical*, 19, 73–83.
- Beissinger, S. R., & McCullough, D. R. (2002). *Population viability analysis*. University of Chicago Press.
- Beissinger, S. R., Wunderle, J. M., Jr., Meyers, J. M., Sæther, B.-E., & Engen, S. (2008). Anatomy of a bottleneck: Diagnosing factors limiting population growth in the puerto rican parrot. *Ecological Monographs*, 78, 185–203. <https://doi.org/10.1890/07-0018.1>
- BirdLife International. (2019). *IUCN Red List of Threatened Species: Alexandrinus eques*. IUCN Red List of Threatened Species.
- Brown, C. R. (2003). Multistate estimates of survival and movement in relation to colony size in the sociable weaver. *Behavioral Ecology*, 14, 463–471. <https://doi.org/10.1093/beheco/arg034>
- Brownie, C., Hines, J. E., Nichols, J. D., Pollock, K. H., & Hestbeck, J. B. (1993). Capture-recapture studies for multiple strata including non-markovian transitions. *Biometrics*, 49, 1173–1187. <https://doi.org/10.2307/2532259>
- Burnham, K. P., & Anderson, D. R. (Eds.). (2002). *Model selection and multimodel inference*. Springer. <https://doi.org/10.1007/b97636>
- Cam, E., Hines, J. E., Monnat, J.-Y., Nichols, J. D., & Danchin, E. (1998). Are adult nonbreeders prudent parents? The kittiwake model. *Ecology*, 79, 2917–2930. [https://doi.org/10.1890/0012-9658\(1998\)079%255B2917:ANPPT%255D2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079%255B2917:ANPPT%255D2.0.CO;2)
- Caswell, H. (2000). Prospective and retrospective perturbation analyses: Their roles in conservation biology. *Ecology*, 81, 619–627. [https://doi.org/10.1890/0012-9658\(2000\)081%255B0619:PARPAT%255D2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081%255B0619:PARPAT%255D2.0.CO;2)
- Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation* (2nd ed.). Sinauer Associates.
- Cheke, A. S., & Hume, J. P. (2008). *Lost land of the dodo: An ecological history of Mauritius, Réunion & Rodrigues*. A&C Black.
- Clobert, J., Lebreton, J.-D., Allaine, D., & Gaillard, J. M. (1994). The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. *Biometrics*, 50, 375. <https://doi.org/10.2307/2533381>
- Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, 25, 562–573. <https://doi.org/10.1016/j.tree.2010.08.002>
- Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, 337, 260–262. <https://doi.org/10.1038/337260a0>
- Clutton-Brock, T. H., Stevenson, I. R., Marrow, P., MacColl, A. D., Houston, A. I., & McNamara, J. M. (1996). Population fluctuations, reproductive costs and life-history tactics in female soay sheep. *Journal of Animal Ecology*, 65, 675–689. <https://doi.org/10.2307/5667>
- Collar, N. J., Crosby, M. J., & Stattersfield, A. J. (1994). *Birds to watch 2: The world list of threatened birds: The official source for birds on the IUCN red list*, BirdLife conservation series. BirdLife International; Distributed in the Americas by Smithsonian Institution Press.
- Conn, P. B., & Cooch, E. G. (2009). Multistate capture-recapture analysis under imperfect state observation: An application to disease models. *Journal of Applied Ecology*, 46, 486–492. <https://doi.org/10.1111/j.1365-2664.2008.01597.x>
- Converse, S. J., Kendall, W. L., Doherty, P. F., Jr., & Ryan, P. G. (2009). Multistate models for estimation of survival and reproduction in the grey-headed albatross (*Thalassarche chrysostoma*). *The Auk*, 126, 77–88. <https://doi.org/10.1525/auk.2009.07189>
- Cooch, E. G., & White, G. C. (2025). Chapter 5: Goodness of fit testing..., in: Program MARK, "A Gentle Introduction".
- Cook, C. N., Hockings, M., & Carter, R. (Bill). (2010). Conservation in the dark? The information used to support management decisions. *Frontiers in Ecology and the Environment*, 8, 181–186. <https://doi.org/10.1890/090020>
- Crespin, L., Harris, M. P., Lebreton, J., Frederiksen, M., & Wanless, S. (2006). Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology*, 75, 228–238. <https://doi.org/10.1111/j.1365-2656.2006.01035.x>
- Cruz-Flores, M., Pradel, R., Bried, J., González-Solís, J., & Ramos, R. (2021). Sex-specific costs of reproduction on survival in a long-lived seabird. *Biology Letters*, 17, 20200804. <https://doi.org/10.1098/rsbl.2020.0804>
- Daunt, F., Wanless, S., Harris, M. P., Money, L., & Monaghan, P. (2007). Older and wiser: Improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology*, 21, 561–567. <https://doi.org/10.1111/j.1365-2435.2007.01260.x>
- Drent, R. H., & Daan, S. (1980). The prudent parent: Energetic adjustments in avian breeding. *Ardea*, 38–90, 225–252. <https://doi.org/10.5253/arde.v68.p225>
- Elliott, G. P., Merton, D. V., & Jansen, P. W. (2001). Intensive management of a critically endangered species: The kakapo. *Biological Conservation*, 99, 121–133. [https://doi.org/10.1016/S0006-3207\(00\)00191-9](https://doi.org/10.1016/S0006-3207(00)00191-9)
- Ewen, J. G., Armstrong, D. P., Parker, K. A., & Seddon, P. J. (2012). *Reintroduction biology: Integrating science and management*, Conservation science and practice series; no. 9. Wiley-Blackwell.
- Fay, R., Barbraud, C., Delord, K., & Weimerskirch, H. (2017). Contrasting effects of climate and population density over time and life stages in a long-lived seabird. *Functional Ecology*, 31, 1275–1284. <https://doi.org/10.1111/1365-2435.12831>
- Fletcher, D., Lebreton, J., Marescot, L., Schaub, M., Gimenez, O., Dawson, S., & Slooten, E. (2012). Bias in estimation of adult survival and asymptotic population growth rate caused by undetected capture heterogeneity. *Methods in Ecology and Evolution*, 3, 206–216. <https://doi.org/10.1111/j.2041-210X.2011.00137.x>
- Fogell, D. J., Groombridge, J. J., Tollington, S., Canessa, S., Henshaw, S., Zuel, N., Jones, C. G., Greenwood, A., & Ewen, J. G. (2019). Hygiene and biosecurity protocols reduce infection prevalence but do not improve fledging success in an endangered parrot. *Scientific Reports*, 9, 4779. <https://doi.org/10.1038/s41598-019-41323-w>
- Fogell, D. J., Tollington, S., Tatayah, V., Henshaw, S., Naujeer, H., Jones, C., Raisin, C., Greenwood, A., & Groombridge, J. J. (2021). Evolution of beak and feather disease virus across three decades of conservation intervention for population recovery of the Mauritius parakeet. *Diversity*, 13, 584. <https://doi.org/10.3390/d13110584>
- Forslund, P., & Pärt, T. (1995). Age and reproduction in birds—Hypotheses and tests. *Trends in Ecology & Evolution*, 10, 374–378. [https://doi.org/10.1016/S0169-5347\(00\)89141-7](https://doi.org/10.1016/S0169-5347(00)89141-7)
- Gaillard, J.-M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, 13, 58–63. [https://doi.org/10.1016/S0169-5347\(97\)01237-8](https://doi.org/10.1016/S0169-5347(97)01237-8)
- Gaines, M. S., & McClenaghan, L. R. (1980). Dispersal in small mammals. *Annual Review of Ecology and Systematics*, 11, 163–196.
- Gath, H. C. (2018). Conservation management of the endangered Mauritius parakeet, *Psittacula echo*.
- Gellé, A., Nicoll, M., Kettel, E., Pernetta, A. P., Gath, H., Groombridge, J., Henshaw, S., Jones, C., Ruhomaun, K., Tatayah, V., Norris, K.,

- & Tollington, S. (2026). Demographic responses to population recovery illustrated by 30-years of monitoring a once critically endangered parrot. [Dataset]. Dryad <https://doi.org/10.5061/dryad.dz08kpsdk>
- Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, 13, 1–21.
- Henshaw, S., Okwomi, I., Young, Z., Piang Nee, G., Haines, O., Tatayah, V., de Chazal, D., & Jones, C. (2025). *Mauritian Wildlife Foundation: Echo parakeet (Alexandrinus (Psittacula) eques) management report 2024/2025*. Mauritian Wildlife Foundation.
- Holdsworth, M., Dettmann, B., & Baker, G. B. (2011). Survival in the orange-bellied parrot (*Neophema chrysogaster*). *Emu - Austral Ornithology*, 111, 222–228. <https://doi.org/10.1071/MU09071>
- Horswill, C., Matthiopoulos, J., Green, J. A., Meredith, M. P., Forcada, J., Peat, H., Preston, M., Trathan, P. N., & Ratcliffe, N. (2014). Survival in macaroni penguins and the relative importance of different drivers: Individual traits, predation pressure and environmental variability. *Journal of Animal Ecology*, 83, 1057–1067. <https://doi.org/10.1111/1365-2656.12229>
- Jansen, J. J. F., & Cheke, A. S. (2021). Variation in echo parakeets (*Psittacula eques* (Boddaert, 1783) [Psittaculidae]) in relation to inter-island differences. *Zoosystema*, 43, 205–211. <https://doi.org/10.5252/zoosystema2021v43a12>
- Jenouvrier, S. (2013). Impacts of climate change on avian populations. *Global Change Biology*, 19, 2036–2057. <https://doi.org/10.1111/gcb.12195>
- Jones, C. G. (1987). The larger land-birds of Mauritius. In A. W. Diamond (Ed.), *Studies of Mascarene Island birds* (pp. 208–300). Cambridge University Press. <https://doi.org/10.1017/CBO9780511735769.007>
- Jones, C. G., & Duffy, K. (1993). Conservation management of the echo parakeet *Psittacula eques echo*. *Dodo*, 29, 126–148.
- Jones, C. G., & Merton, D. V. (2012). A tale of two islands: The rescue and recovery of endemic birds in New Zealand and Mauritius. In J. Ewen, D. Armstrong, K. A. Parker, & P. Seddon (Eds.), *Reintroduction biology: Integrating science and management* (pp. 33–72). Blackwell Publishing Ltd.
- Katzner, T. E., Ivy, J. A. r., Bragin, E. A., Milner-Gulland, E. j., & DeWoody, J. A. (2011). Conservation implications of inaccurate estimation of cryptic population size. *Animal Conservation*, 14, 328–332. <https://doi.org/10.1111/j.1469-1795.2011.00444.x>
- Kendall, W. L. (2004). Coping with unobservable and mis-classified states in capture-recapture studies. *Animal Biodiversity and Conservation*, 27, 97–107. <https://doi.org/10.32800/abc.2004.27.0097>
- Kendall, W. L., & Nichols, J. D. (2002). Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology*, 83, 3276–3284. [https://doi.org/10.1890/0012-9658\(2002\)083%255B3276:ESTPFU%255D2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083%255B3276:ESTPFU%255D2.0.CO;2)
- Koons, D. N., Iles, D. T., Schaub, M., & Caswell, H. (2016). A life-history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecology Letters*, 19, 1023–1031. <https://doi.org/10.1111/ele.12628>
- Laake, J., & Rexstad, E. (2022). RMark—An alternative approach to building linear models in MARK.
- Lebreton, J., Nichols, J. D., Barker, R. J., Pradel, R., & Spindelov, J. A. (2009). Chapter 3 modeling individual animal histories with multi-state capture-recapture models. In *Advances in ecological research* (pp. 87–173). Elsevier. [https://doi.org/10.1016/S0065-2504\(09\)00403-6](https://doi.org/10.1016/S0065-2504(09)00403-6)
- Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, 62, 67–118. <https://doi.org/10.2307/2937171>
- Lebreton, J. D., Hines, J. E., Pradel, R., Nichols, J. D., & Spindelov, J. A. (2003). Estimation by capture-recapture of recruitment and dispersal over several sites. *Oikos*, 101, 253–264. <https://doi.org/10.1034/j.1600-0706.2003.11848.x>
- Lebreton, J.-D., & Pradel, R. (1998). Re-evaluation of adult survival of black-headed gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *The Auk*, 115, 85–95. <https://doi.org/10.2307/4089114>
- Lee, A. M., Reid, J. M., & Beissinger, S. R. (2017). Modelling effects of nonbreeders on population growth estimates. *Journal of Animal Ecology*, 86, 75–87. <https://doi.org/10.1111/1365-2656.12592>
- Lescroël, A., Dugger, K. M., Ballard, G., & Ainley, D. G. (2009). Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology*, 78, 798–806.
- Loery, G., Pollock, K. H., Nichols, J. D., & Hines, J. E. (1987). Age-specificity of black-capped chickadee survival rates: Analysis of capture-recapture data. *Ecology*, 68, 1038–1044. <https://doi.org/10.2307/1938375>
- Lorence, D. H., & Sussman, R. W. (1986). Exotic species invasion into Mauritius wet forest remnants. *Journal of Tropical Ecology*, 2, 147–162. <https://doi.org/10.1017/S0266467400000742>
- Louch, R. (2025). *Understanding the effects of conservation management, inbreeding and diet on reproductive fitness in a threatened bird species*. University of Kent. <https://doi.org/10.22024/UNIKENT/01.02.111543>
- Madsen, T., & Shine, R. (1994). Costs of reproduction influence the evolution of sexual size dimorphism in snakes. *Evolution*, 48, 1389. <https://doi.org/10.2307/2410396>
- Mihoub, J.-B., Gimenez, O., Pilard, P., & Sarrazin, F. (2010). Challenging conservation of migratory species: Sahelian rainfalls drive first-year survival of the vulnerable lesser kestrel *Falco naumanni*. *Biological Conservation*, 143, 839–847. <https://doi.org/10.1016/j.biocon.2009.12.026>
- Naef-Daenzer, B., Widmer, F., & Nuber, M. (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology*, 70, 730–738. <https://doi.org/10.1046/j.0021-8790.2001.00533.x>
- Nevoux, M., Weimerskirch, H., & Barbraud, C. (2007). Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *Journal of Animal Ecology*, 76, 159–167. <https://doi.org/10.1111/j.1365-2656.2006.01191.x>
- Newton, I. (1998). *Population limitation in birds*. Elsevier. <https://doi.org/10.1016/B978-0-12-517365-0.X5000-5>
- Nichols, J. D., Hines, J. E., Pollock, K. H., Hinz, R. L., & Link, W. A. (1994). Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. *Ecology*, 75, 2052–2065. <https://doi.org/10.2307/1941610>
- Nicoll, M. A. C., Jones, C. G., & Norris, K. (2003). Declining survival rates in a reintroduced population of the Mauritius kestrel: Evidence for non-linear density dependence and environmental stochasticity. *Journal of Animal Ecology*, 72, 917–926.
- Nicoll, M. A. C., Nevoux, M., Jones, C. G., Ratcliffe, N., Ruhomaun, K., Tatayah, V., & Norris, K. (2017). Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology*, 23, 550–565. <https://doi.org/10.1111/gcb.13324>
- Norris, K. (2004). Managing threatened species: The ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology*, 41, 413–426. <https://doi.org/10.1111/j.0021-8901.2004.00910.x>
- Oosthuizen, W. C., Pradel, R., Bester, M. N., & De Bruyn, P. J. N. (2019). Making use of multiple surveys: Estimating breeding probability using a multievent-robust design capture-recapture model. *Ecology and Evolution*, 9, 836–848. <https://doi.org/10.1002/ece3.4828>
- Oro, D., Torres, R., Rodríguez, C., & Drummond, H. (2010). Climatic influence on demographic parameters of a tropical seabird varies with age and sex. *Ecology*, 91, 1205–1214. <https://doi.org/10.1890/09-0939.1>

- Pardo, D., Weimerskirch, H., & Barbraud, C. (2013). When celibacy matters: Incorporating non-breeders improves demographic parameter estimates. *PLoS One*, 8, e60389. <https://doi.org/10.1371/journal.pone.0060389>
- Pärt, T. (2001). Experimental evidence of environmental effects on age-specific reproductive success: The importance of resource quality. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268, 2267–2271. <https://doi.org/10.1098/rspb.2001.1803>
- Payo-Payo, A., Genovart, M., Bertolero, A., Pradel, R., & Oro, D. (2016). Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20153042. <https://doi.org/10.1098/rspb.2015.3042>
- Péron, G., Gaillard, J.-M., Barbraud, C., Bonenfant, C., Charmantier, A., Choquet, R., Coulson, T., Grosbois, V., Loison, A., Marzolin, G., Owen-Smith, N., Pardo, D., Plard, F., Pradel, R., Toigo, C., & Gimenez, O. (2016). Evidence of reduced individual heterogeneity in adult survival of long-lived species. *Evolution*, 70, 2909–2914. <https://doi.org/10.1111/evo.13098>
- Pollock, K. H., Nichols, J. D., Brownie, C., & Hines, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs*, 48, 3–97.
- Porter, J. M., & Coulson, J. C. (1987). Long-term changes in recruitment to the breeding group, and the quality of recruits at a kittiwake *Rissa tridactyla* colony. *The Journal of Animal Ecology*, 56, 675. <https://doi.org/10.2307/5076>
- Pradel, R., Hines, J. E., Lebreton, J.-D., & Nichols, J. D. (1997). Capture-recapture survival models taking account of transients. *Biometrics*, 53, 60. <https://doi.org/10.2307/2533097>
- Pullin, A. S., & Knight, T. M. (2001). Effectiveness in conservation practice: Pointers from medicine and public health. *Conservation Biology*, 15, 50–54. <https://doi.org/10.1111/j.1523-1739.2001.99499.x>
- R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Raisin, C., Frantz, A. C., Kundu, S., Greenwood, A. G., Jones, C. G., Zuel, N., & Groombridge, J. J. (2012). Genetic consequences of intensive conservation management for the Mauritius parakeet. *Conservation Genetics*, 13, 707–715. <https://doi.org/10.1007/s10592-012-0319-0>
- Ratcliffe, N., Catry, P., Hamer, K. C., Klomp, N. I., & Furness, R. W. (2002). The effect of age and year on the survival of breeding adult great skuas *Catharacta skua* in shetland. *Ibis*, 144, 384–392. <https://doi.org/10.1046/j.1474-919X.2002.00066.x>
- Reading, C. J. (2024). Differential longevity in free-living smooth snakes *Coronella austriaca*. *Herpetological Journal*, 34, 266–271. <https://doi.org/10.33256/34.4.266271>
- Reading, C. J., & Jofré, G. M. (2021). The cost of breeding for male common toads. *Biological Journal of the Linnean Society*, 134, 568–576. <https://doi.org/10.1093/biolinnean/blab040>
- Reed, J. M., Mills, L. S., Dunning, J. B., Menges, E. S., McKelvey, K. S., Frye, R., Beissinger, S. R., Anstett, M., & Miller, P. (2002). Emerging issues in population viability analysis. *Conservation Biology*, 16, 7–19. <https://doi.org/10.1046/j.1523-1739.2002.99419.x>
- Robert, A., Paiva, V. H., Bolton, M., Jiguet, F., & Bried, J. (2012). The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. *Ecology*, 93, 1944–1952. <https://doi.org/10.1890/11-1840.1>
- Roff, D. (1993). *Evolution of life histories: Theory and analysis*. Springer Science & Business Media.
- Sæther, B.-E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, 81, 642–653. [https://doi.org/10.1890/0012-9658\(2000\)081%255B0642:ALHVAC%255D2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081%255B0642:ALHVAC%255D2.0.CO;2)
- Sæther, B.-E., Ringsby, T. H., & Røskaft, E. (1996). Life history variation, population processes and priorities in species conservation: Towards a Reunion of research paradigms. *Oikos*, 77, 217–226. <https://doi.org/10.2307/3546060>
- Safford, R. J. (1997). A survey of the occurrence of native vegetation remnants on Mauritius in 1993. *Biological Conservation*, 80, 181–188. [https://doi.org/10.1016/S0006-3207\(96\)00048-1](https://doi.org/10.1016/S0006-3207(96)00048-1)
- Sandercock, B. K., Beissinger, S. R., Stoleson, S. H., Melland, R. R., & Hughes, C. R. (2000). Survival rates of a neotropical parrot: Implications for latitudinal comparisons of avian demography. *Ecology*, 81, 1351–1370. [https://doi.org/10.1890/0012-9658\(2000\)081%255B1351:SROANP%255D2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081%255B1351:SROANP%255D2.0.CO;2)
- Sanz-Aguilar, A., Igual, J. M., Oro, D., Genovart, M., & Tavecchia, G. (2016). Estimating recruitment and survival in partially monitored populations. *Journal of Applied Ecology*, 53, 73–82. <https://doi.org/10.1111/1365-2664.12580>
- Sanz-Aguilar, A., Mínguez, E., & Oro, D. (2012). Is laying a large egg expensive? Female-biased cost of first reproduction in a petrel. *Auk*, 129, 510–516. <https://doi.org/10.1525/auk.2012.12011>
- Sanz-Aguilar, A., Tavecchia, G., Genovart, M., Igual, J. M., Oro, D., Rouan, L., & Pradel, R. (2011). Studying the reproductive skipping behavior in long-lived birds by adding nest inspection to individual-based data. *Ecological Applications*, 21, 555–564. <https://doi.org/10.1890/09-2339.1>
- Saunders, D. A. (1982). The breeding behaviour and biology of the short-billed form of the white-tailed black cockatoo *Calyptorhynchus funereus*. *Ibis*, 124, 422–455. <https://doi.org/10.1111/j.1474-919X.1982.tb03790.x>
- Saunders, D. A., Mawson, P. R., Dawson, R., & Pickup, G. (2024). A challenging future for carnaby's cockatoo (*Zanda latirostris*) under a changing climate. *Pacific Conservation Biology*, 30, PC24065. <https://doi.org/10.1071/PC24065>
- Senar, J. C., Arroyo, L., Ortega-Segalerva, A., Carrillo, J. G., Tomás, X., Montalvo, T., & Sanz-Aguilar, A. (2019). Estimating age-dependent survival when juveniles resemble females: Invasive ring-necked parakeets as an example. *Ecology and Evolution*, 9, 891–898. <https://doi.org/10.1002/ece3.4366>
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press. <https://doi.org/10.1093/oso/9780198577416.001.0001>
- Stearns, S. C. (1998). Demography: Age and stage structure. In S. C. Stearns (Ed.), *The evolution of life histories*. Oxford University Press. <https://doi.org/10.1093/oso/9780198577416.003.0003>
- Stojanovic, D., Potts, J., Troy, S., Menkhurst, P., Loyn, R., & Heinsohn, R. (2020). Spatial bias in implementation of recovery actions has not improved survival of orange-bellied parrots *Neophema chrysogaster*. *Emu - Austral Ornithology*, 120, 263–268. <https://doi.org/10.1080/01584197.2020.1799411>
- Sutherland, W. J., Pullin, A. S., Dolman, P. M., & Knight, T. M. (2004). The need for evidence-based conservation. *Trends in Ecology & Evolution*, 19, 305–308. <https://doi.org/10.1016/j.tree.2004.03.018>
- Tatayah, R. V. V., Malham, J., Haverson, P., Reuleaux, A., & Van de Wetering, J. (2007). Design and provision of nest boxes for echo parakeets *Psittacula eques* in Black River Gorges National Park, Mauritius. *Conservation Evidence*, 4, 16–19.
- Tavecchia, G., Coulson, T., Morgan, B. J. T., Pemberton, J. M., Pilkington, J. C., Gulland, F. M. D., & Clutton-Brock, T. H. (2005). Predictors of reproductive cost in female soay sheep. *Journal of Animal Ecology*, 74, 201–213.
- Tavecchia, G., Pradel, R., Boy, V., Johnson, A. R., & Cézilly, F. (2001). Sex- and age-related variation in survival and cost of first reproduction in greater flamingos. *Ecology*, 82, 165–174. [https://doi.org/10.1890/0012-9658\(2001\)082%255B0165:SAARV%255D2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082%255B0165:SAARV%255D2.0.CO;2)
- Tavecchia, G., Pradel, R., Genovart, M., & Oro, D. (2007). Density-dependent parameters and demographic equilibrium in open populations. *Oikos*, 116, 1481–1492. <https://doi.org/10.1111/j.0030-1299.2007.15791.x>

- Thorsen, M., & Jones, C. G. (1998). The conservation status of echo parakeet, *Psittacula eques*, of Mauritius. *Bulletin of the African Bird Club*, 5, 122–126. <https://doi.org/10.5962/p.309556>
- Tollington, S., Ewen, J. G., Newton, J., McGill, R. A. R., Smith, D., Henshaw, A., Fogell, D. J., Tatayah, V., Greenwood, A., Jones, C. G., & Groombridge, J. J. (2019). Individual consumption of supplemental food as a predictor of reproductive performance and viral infection intensity. *Journal of Applied Ecology*, 56, 594–603. <https://doi.org/10.1111/1365-2664.13303>
- Tollington, S., Greenwood, A., Jones, C. G., Hoeck, P., Chowrimootoo, A., Smith, D., Richards, H., Tatayah, V., & Groombridge, J. J. (2015). Detailed monitoring of a small but recovering population reveals sublethal effects of disease and unexpected interactions with supplemental feeding. *Journal of Animal Ecology*, 84, 969–977. <https://doi.org/10.1111/1365-2656.12348>
- Tollington, S., Jones, C. G., Greenwood, A., Tatayah, V., Raisin, C., Burke, T., Dawson, D. A., & Groombridge, J. J. (2013). Long-term, fine-scale temporal patterns of genetic diversity in the restored Mauritius parakeet reveal genetic impacts of management and associated demographic effects on reintroduction programmes. *Biological Conservation*, 161, 28–38. <https://doi.org/10.1016/j.biocon.2013.02.013>
- Van Oosterhout, C., Speak, S. A., Birley, T., Hitchings, L. W. G., Bortoluzzi, C., Percival-Alwyn, L., Urban, L., Groombridge, J. J., Segelbacher, G., & Morales, H. E. (2026). Genomic erosion in the assessment of species' extinction risk and recovery potential. *Journal of Heredity*, esag011. <https://doi.org/10.1093/jhered/esag011>
- Vaughan, R. E., & Wiehe, P. O. (1937). Studies on the vegetation of Mauritius: I. A preliminary survey of the plant communities. *Journal of Ecology*, 25, 289–343. <https://doi.org/10.2307/2256197>
- Votier, S. C., Birkhead, T. R., Oro, D., Trinder, M., Grantham, M. J., Clark, J. A., McCleery, R. H., & Hatchwell, B. J. (2008). Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *Journal of Animal Ecology*, 77, 974–983. <https://doi.org/10.1111/j.1365-2656.2008.01421.x>
- Weladji, R. B., Loison, A., Gaillard, J.-M., Holand, Ø., Mysterud, A., Yoccoz, N. G., Nieminen, M., & Stenseth, N. C. (2008). Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia*, 156, 237–247. <https://doi.org/10.1007/s00442-008-0961-x>
- White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, 46, S120–S139. <https://doi.org/10.1080/00063659909477239>
- Williams, T. D. (2005). Mechanisms underlying the costs of egg production. *Bioscience*, 55, 39. [https://doi.org/10.1641/0006-3568\(2005\)055%255B0039:MUTCOE%25D2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055%255B0039:MUTCOE%25D2.0.CO;2)
- Wood, K. A., Nuijten, R. J. M., Newth, J. L., Haitjema, T., Vangeluwe, D., Ioannidis, P., Harrison, A. L., Mackenzie, C., Hilton, G. M., Nolet, B. A., & Rees, E. C. (2018). Apparent survival of an Arctic-breeding migratory bird over 44 years of fluctuating population size. *Ibis*, 160, 413–430. <https://doi.org/10.1111/ibi.12521>
- Wood, M. J., Canonne, C., Besnard, A., Lachish, S., Fairhurst, S. M., Liedvogel, M., Boyle, D., Patrick, S. C., Josey, S., Kirk, H., Dean, B., Guilford, T., McCleery, R. M., Perrins, C. M., & Horswill, C. (2021). Demographic profiles and environmental drivers of variation relate

to individual breeding state in a long-lived trans-oceanic migratory seabird, the manx shearwater. *PLoS One*, 16, e0260812. <https://doi.org/10.1371/journal.pone.0260812>

Wunderle, J. (1991). Age-specific foraging proficiency in birds. *Current Ornithology*, 8, 273–324.

SUPPORTING INFORMATION

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

Table S1. Set of candidate Cormack–Jolly–Seber (CJS) models evaluating age structure for survival (Φ) and detection (p) probabilities. Notation: numbers (0 to 7) represent age classes; 't' = full time-dependent; '.' = constant with age effect only. Models are ranked by quasi-Akaike's Information Criterion (QAICc).

Table S2. Set of candidate models evaluating factors affecting survival (Φ), detection (p) and state transition (ψ) probabilities. Notation: numbers (0, 1, 2, 3, 4) represent age classes; '.' indicates grouped age classes (e.g. 0:1 = ages 0 and 1 grouped); 't' = full time-dependent; 's' = state-dependent (pre-breeder, breeder, non-breeder); '*' = interaction between effects; 'period' = temporal variation in broader three time periods (representing population growth stages) rather than annually (t); 'management' = two periods of low and high management intensity; '.' = constant with age effect only. Models are ranked by Akaike's Information Criterion (AICc).

Table S3. Detection probabilities derived from the best supported model (Model 165, Table 3). SE = standard error; LCI/HCI = lower and upper bounds of the 95% confidence interval.

Table S4. Transition probabilities derived from the best supported model (Model 165, Table 3). Transitions shown: pre-breeder to breeder (PB-B), breeder to non-breeder (B-NB) and non-breeder to breeder (NB-B). Transition probabilities for age 0 to breeding state were fixed to 0, as individuals can only become breeders after surviving their second year. SE = standard error; LCI/HCI = lower and upper bounds of the 95% confidence interval.

How to cite this article: Gellé, A., Nicoll, M. A., Kettel, E. F., Pernetta, A. P., Gath, H., Groombridge, J., Henshaw, S., Jones, C. G., Ruhomaun, K., Tatayah, V., Norris, K., & Tollington, S. (2026). Demographic responses to population recovery illustrated by 30 years of monitoring a once critically endangered parrot. *Journal of Applied Ecology*, 63, e70523. <https://doi.org/10.1111/1365-2664.70523>