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1 **Spatial bias in implementation of recovery actions has not improved survival of Orange-**
2 **bellied Parrots *Neophema chrysogaster***

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15 **Running Head:** Survival of Orange-bellied Parrots

16 **Abstract**

17 Not all conservation interventions are successful at correcting threatening processes and
18 the odds of failure increase with uncertainty concerning the true threats to a population.

19 Failure of conservation actions to improve demographic rates might be evidence of their
20 ineffectiveness, or that other unaddressed threats nullify the potential benefits of

21 interventions. Knowledge of key threatening processes that afflict Orange-bellied Parrots

22 *Neophema chrysogaster* is lacking, but population modelling predicts that actions in the

23 breeding range are unlikely to correct decline unless mortality during migration/wintering is
24 addressed. Despite this, there has been a spatial bias in recovery effort towards the
25 breeding range in recent decades. We model annual survival data spanning 1995 – 2017 for
26 the last known wild population to evaluate whether the predictions about the efficacy of
27 recovery efforts are accurate. Based on our best-supported model, probability of adult
28 survival was constant at 0.58, but juvenile survival declined from 0.51 to 0.20. Survival did
29 not improve when we considered the effects of recovery actions in the breeding grounds
30 (which only aimed to correct local scale threats anyway). This result supports predictions
31 that conservation interventions in the breeding ground alone are not sufficient to recover
32 this species. We conclude that although interventions in the breeding ground may have
33 corrected local threats, birds succumbed to other threats during migration/winter. It is
34 crucial that new targeted interventions be identified and implemented to reduce mortality
35 of Orange-bellied Parrots in their migration/winter habitats to prevent extinction.

36 **Key Words**

37 Survival, mark recapture, Cormack Jolly Seber models, conservation, threatened species,
38 population viability model

39 **Introduction**

40 Effective conservation relies on detailed understanding of species biology and clear
41 diagnosis of threats (Caughley 1994). Gathering this information is not always
42 straightforward, and knowledge gaps are a major hindrance for effective management of
43 many species (Scheele *et al.* 2018). As a result, when knowledge of threats is incomplete,
44 conservation managers may implement actions that they presume will be effective (Wintle
45 *et al.* 2010). Such ‘educated guesses’ may pay off when managers can make reasonable

46 assumptions about the types of threats a species faces (e.g. protecting nesting birds from
47 predation is likely to prove beneficial on rat-infested islands). However, interventions often
48 fail (Scheele *et al.* 2018), and the odds of failure increase with uncertainty concerning the
49 true threats to a population (Caughley 1994; Doherty and Ritchie 2017). It is not always
50 possible to diagnose threats confidently, and this is further complicated if the original
51 causes of population decline are superseded by new threats that arise at small population
52 sizes (e.g. Allee effects – inverse density dependence) (Crates *et al.* 2017). In such scenarios,
53 conservation managers could use adaptive management to trial different actions that might
54 improve metrics of population health. However, this requires careful evaluation of how
55 population vital rates respond to the intervention (Gerber and Kendall 2018). Furthermore,
56 it is important to evaluate conservation actions in the context of life history. For example,
57 targeted action at one time/place may mitigate a local threatening process (Crates *et al.*
58 2018b), but this benefit may not support population recovery if individuals succumb to
59 different threats at other times/places (Crates *et al.* 2018a; Crates *et al.* 2019). Thus, the
60 failure of conservation actions to improve demographic rates might be evidence of their
61 ineffectiveness, or that other unaddressed threats nullify their potential benefits.

62 The Orange-bellied Parrot *Neophema chrysogaster* may be the rarest parrot in the world
63 and now breeds only at Melaleuca in southwestern Tasmania, Australia (Lat: 43°25' S, Long:
64 146° 9' E) (Department of Environment, Land, Water and Planning 2016; Stojanovic *et al.*
65 2018). In 2016/17 the wild population declined to only two breeding females and 12 males
66 (Stojanovic *et al.* 2018). Unusually for a parrot, the species is an obligate migrant, wintering
67 in coastal habitats along southeastern mainland Australia (Loyn *et al.* 1986). Their key
68 threatening processes are not clearly diagnosed, but habitat loss and degradation, disease
69 and small population size have been implicated in their decline (Department of

70 Environment, Land, Water and Planning 2016). This uncertainty hinders the species
71 management because recovery strategies that directly target the most important threats
72 are difficult to develop and prioritize (Department of Environment, Land, Water and
73 Planning 2016). Most direct management of Orange-bellied Parrots is implemented at
74 Melaleuca, and includes provision of nest boxes, supplementary food, predator control and
75 release of captive-born birds to increase the number of breeding pairs, correct adult sex
76 ratio bias and maximize reproductive success (Troy and Hehn 2019). In contrast, during
77 migration/winter the species can occur at multiple locations along about 1200 km of coast,
78 and conservation efforts are mostly indirect. The main conservation actions in the
79 migration/winter range involve studies of habitat use (Loyn *et al.* 1986), ecological modeling
80 (White *et al.* 2017), population (Starks *et al.* 1992) and habitat monitoring (Tolsma *et al.*
81 2014), plus reservation and removal of livestock from habitat, rehabilitation of hydrological
82 processes, control of predators, weeds and human access (Department of Environment,
83 Land, Water and Planning 2016). Aggregation of the entire parrot population at Melaleuca
84 makes management of threats to the breeding population feasible (Troy and Hehn 2019),
85 which partially explains the spatial bias in recovery actions.

86 Previous studies have suggested that conservation actions at the breeding grounds are likely
87 to be ineffective at reducing mortality over migration and winter (Drechsler *et al.* 1998),
88 which is a severe threat to the species (Department of Environment, Land, Water and
89 Planning 2016). Given the spatial bias in recovery efforts for this species, we evaluate the
90 predictions of Drechsler *et al.* (1998) by modeling annual survival. Survival is a useful
91 demographic trait to study because it is the outcome of multiple, cumulative, discrete
92 threats over the full annual cycle. If the predictions of Drechsler *et al.* (1998) are correct, we
93 would expect that survival of Orange-bellied Parrots has not improved over two decades,

94 despite an increase in conservation attention and effort directed at their protection in
95 breeding habitat.

96 **Methods**

97 *Study context*

98 A citizen science monitoring program has been implemented by the Tasmanian Government
99 at Melaleuca since 1979 (Department of Environment, Land, Water and Planning 2016).
100 Monitoring consists of observation of individually colour banded birds at feed tables during
101 the summer breeding season by volunteers (Department of Environment, Land, Water and
102 Planning 2016; Troy and Hehn 2019). We collated survival data from the monitoring
103 program between 1995 and 2017 for this study. The Tasmanian Government implemented
104 most recovery actions annually, including provision of nest boxes, supplementary feeding,
105 predator and competitor control, and health management, so these activities were
106 generally consistent over time. In 2010, due to a steep decline in the population size of
107 Orange-bellied Parrots, 21 juveniles were collected from the wild as new founders for the
108 captive population (Martin *et al.* 2012). Orange-bellied Parrots may be unusually vulnerable
109 to Allee effects (Crates *et al.* 2017), and after 2010, the collection of juveniles for captive
110 breeding reduced the wild population size. Later recovery actions including release of
111 captive-bred parrots (Troy and Hehn 2019) further altered wild population size. Hence, we
112 subset our data into two time periods (i) 1995 – 2010, i.e. natural demographic rates, and
113 (ii) 2011 – 2017 i.e. demographic rates potentially influenced by recent management
114 actions.

115 *Survival data*

116 We accounted for potential misidentification errors in the Tasmanian Government's citizen
117 science sightings data set which could affect our models by filtering the data (Isaac *et al.*
118 2014). Parrots seen fewer than five times needed either to be (i) verified by >1 observer, or
119 (ii) seen by the same person >3 times to be considered alive (Troy and Kuechler 2018). We
120 assumed that if a parrot was incorrectly categorised as dead using our criteria, such
121 infrequently detected individuals were unlikely to have successfully bred, and thus did not
122 contribute to the population growth. Since the species now probably only breeds at
123 Melaleuca (Stojanovic *et al.* 2018) we assumed this was a closed population, and that loss of
124 individuals was due to death, not dispersal to other breeding locations. We constructed
125 capture histories from 1995 to 2017. During this period, banding nestlings in nest boxes was
126 the main way marked birds entered the population. The first occasion in capture histories
127 represented nestlings banded in boxes, and subsequent occasions represented observations
128 at feeders over successive breeding seasons. We classified individuals in the first time-step
129 of capture histories as juvenile, and all subsequent time-steps as adult. This approach does
130 not differentiate between mortality in the breeding season and mortality during
131 migration/winter, but based on recent evidence we assumed that most juveniles died
132 during migration/winter (DPIPWE. unpublished data).

133 We used Cormack Jolly Seber models to estimate annual survival rates of Orange-bellied
134 Parrots, and explored whether the survival component was constant (i.e., $\phi(\cdot)$), or varied
135 with age class (i.e., $\phi_j(\cdot)$ $\phi_a(\cdot)$, for juveniles and adults, respectively), year (as a linear trend,
136 i.e., $\phi(\text{Year})$) and time period (using a dummy variable corresponding to 1995 – 2010, and
137 2011 – 2017, i.e., $\phi(\text{Period})$). We did not fit year as a factor (i.e. to estimate annual survival)
138 because data were too sparse in some years and age classes. In addition to these main
139 effects, we also fitted two age class \times year interaction models, where adult survival was

140 either held constant (i.e., $\phi_j(\text{Year}) \phi_a(\cdot)$) or allowed to vary as a linear trend with year (i.e.,
141 $\phi_j(\text{Year}) \phi_a(\text{Year})$). We also fitted year \times time period (i.e., $\phi(\text{Year} \times \text{Period})$), age class \times time
142 period (i.e., $\phi_j(\text{Period}) \phi_a(\text{Period})$), and year \times age class \times time period (i.e., $\phi_j(\text{Year} \times$
143 $\text{Period}) \phi_a(\text{Year} \times \text{Period})$). Recapture probability (ρ) was held constant because of high
144 detection likelihood at feeders (Stojanovic *et al.* 2018) except in the global model. Survival
145 analyses were conducted using RMark (Laake 2013) in R version 3.6.3 (R Development Core
146 Team 2020) as an interface to Program MARK (White and Burnham 1999) and model
147 selection was based on $\Delta\text{QAICc} < 2$ (Buckland *et al.* 1997). All models were fitted in RMark,
148 but program MARK was used to calculate median \hat{c} for the global model. We corrected
149 corresponding model selection in RMark for the estimate of median \hat{c} . Code and data are
150 presented in supplementary materials.

151

152 **Results**

153 We present data for 797 Orange-bellied Parrots hatched between 1995 and 2017. Five
154 hundred and twenty-two birds (65 %) died in their first year of life and 275 (35 %) died in
155 their second year of life or later, corresponding to a mean lifespan of 1.76 years (range: 0 –
156 11).

157 Based on the unconstrained global model, we corrected model selection in RMark by the
158 median \hat{c} (4.77). We present a full list of survival models ranked by AICc in Table 1. We
159 found no evidence that annual survival rates varied between the two time-periods we
160 considered. The most parsimonious model (based on lowest AICc and fewest parameters)
161 included constant adult survival and a juvenile survival trend over time, with constant
162 recapture probability. The next best model was within two ΔAICc and included juvenile and

163 adult survival trends over time. The best-supported model showed that probability of adult
 164 survival was constant at 0.58 over time, but juvenile survival declined from 0.51 to 0.20 over
 165 the study. We report effect sizes and standard errors in Figure 1, and based on this model,
 166 recapture probability (p) was 0.94 ± 0.01 se.

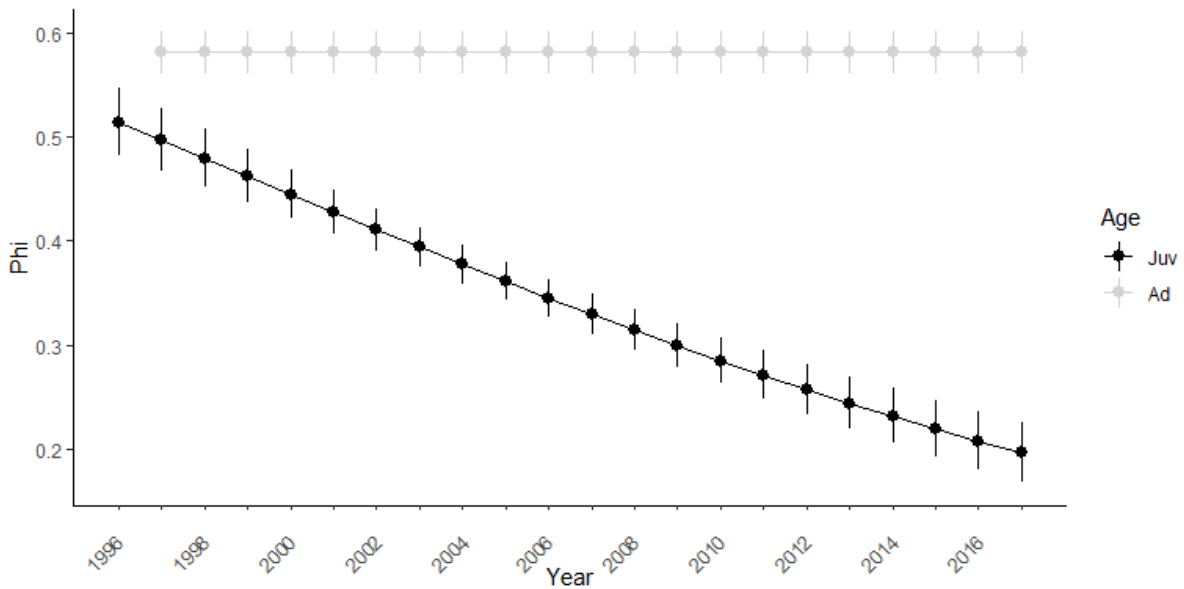
167

168 **Table 1.** List of nine models fitted to Orange-bellied Parrot survival data from the last known
 169 breeding ground between 1995 and 2017. Model notations are as follows: ‘.’ is a constant
 170 effect, ‘Year’ is a linear trend over year, ‘ ϕ_j ’ refers to juveniles and ‘ ϕ_a ’ is adults, ‘time
 171 period’ relates to 1995 – 2010 and 2011 – 2017 (before/after the time when the wild
 172 population size was reduced due to collection of 21 birds for captive breeding). * indicates
 173 the preferred models.

Model parameters	N.Par.	QAICc	Δ AICc	Weight	Qdeviance
$\phi_j(\text{Year}) \phi_a(\cdot)p(\cdot)^*$	4	419.29	0.00	0.50	67.91
$\phi_j(\text{Year}) \phi_a(\text{Year})p(\cdot)$	5	421.23	1.95	0.19	67.84
$\phi_j(\text{Year} \times \text{Time Period}) \phi_a(\text{Year} \times$ Period) $p(\cdot)$	6	422.30	3.02	0.11	66.89
$\phi_j(\text{Year} + \text{Time Period}) \phi_a(\text{Year} +$ Time Period) $p(\cdot)$	6	422.54	3.25	0.10	67.13
$\phi_j(\cdot) \phi_a(\cdot)p(\cdot)$	3	423.86	4.57	0.05	74.49
$\phi_j(\text{Time Period}) \phi_a(\text{Time}$ Period) $p(\cdot)$	5	424.03	4.74	0.05	70.64
$\phi(\text{Year})p(\cdot)$	3	433.15	13.87	0.00	83.78

$\phi(\cdot)p(\cdot)$	2	434.24	14.96	0.00	86.89
$\phi(\text{Time Period})p(\cdot)$	3	435.18	15.89	0.00	85.81
$\phi(\text{Year} \times \text{Time Period})p(\cdot)$	5	435.82	16.53	0.00	82.42

174



175

176 **Figure 1.** Modeled estimates of survival probabilities ($\Phi(\phi)$ mean \pm se) of Orange-bellied
 177 Parrots at their last known breeding ground in Tasmania, Australia. Over the entire study,
 178 conservation interventions were implemented at the breeding ground, but these actions did
 179 not improve the declining survival of juveniles.

180 **Discussion**

181 Survival was age-related in Orange-bellied Parrots, and juvenile survival more than halved
 182 over the study period. We found no support for the models that included effects of different
 183 survival probabilities in the period before/after collection of juveniles for captive breeding in
 184 2010 artificially reduced wild population size. Instead, the best-supported models only
 185 contained effects of age and time. These results reveal a chronic decline of annual survival
 186 rates for juveniles, despite intensive conservation efforts at the breeding ground, and

187 suggest that targeted efforts to protect Orange-bellied Parrots in their migration/winter
188 habitats are needed. Our results also contrast with those of an earlier study that found no
189 temporal trend in juvenile survival of this species (Holdsworth *et al.* 2011). Our study
190 supports the prediction of Drechsler *et al.* (1998) that interventions in the breeding ground
191 alone are not enough to recover this species unless threats during migration/winter are
192 concurrently addressed.

193 There are two possible explanations for our results: (i) the interventions undertaken in
194 Tasmania do not address the primary threats in the breeding ground, or (ii) the
195 interventions do mitigate threats in the breeding ground, but mortality during
196 migration/winter nullifies the benefits. We consider the first explanation less likely given
197 that the aims of the Tasmanian interventions are not intended to improve inter-annual
198 survival but instead focus on local threats to survival and reproductive success within the
199 breeding season (Troy and Hehn 2019). For example, releasing captive-born female parrots
200 has corrected male-biased adult sex ratios and increased reproductive output at Melaleuca
201 (Troy and Hehn 2019), meaning that more nests are initiated and more juveniles enter the
202 population than would have occurred without intervention (which may be evidence that
203 these interventions mitigate the local threats they target). However, survival during
204 migration and winter are likely to be at least partly or entirely independent of interventions
205 in breeding habitat. If the potential second explanation is true, then our results provide
206 empirical support for modeled predictions that ongoing recovery actions in the breeding
207 ground will not improve the conservation status of Orange-bellied Parrots without
208 addressing mortality during migration/winter (Drechsler *et al.* 1998). Testing these
209 hypotheses is crucial because this information will clarify the aspects of life history
210 (breeding, migration, wintering) that should be targeted with new interventions.

211 Unfortunately, the initial causes of population decline in Orange-bellied Parrots may have
212 been usurped as the principal threats to the species by multiple component Allee effects
213 (Crates *et al.* 2017). For example, a migration component Allee effect may have major
214 implications for a juvenile's first full migration if they rely on flocking for safety in numbers
215 or for the experience afforded by uncommon adults to survive and maintain population-
216 level migration culture (Codling *et al.* 2007). Juveniles may also select poor-quality winter
217 habitat (Crates *et al.* 2017) if they depend on the few remaining adults for habitat selection
218 (Couzin *et al.* 2005; Schmidt *et al.* 2015). Given the low contemporary population size of the
219 species and the sparse but extensive geographic area of their contemporary
220 migration/winter distribution (Department of Environment, Land, Water and Planning
221 2016), it is unlikely that the survival impacts of historical threats (e.g. deteriorating habitat
222 quality) can be disentangled from the potential recent emergence of Allee effects. Recent
223 activities like releasing captive born parrots in areas of high quality wintering habitat may be
224 effective at overcoming some habitat selection Allee effects in winter, but the survival
225 impacts of these efforts are currently unclear. Other threats like genetic component Allee
226 effects, which may be signaled by low contemporary hatching success and heightened
227 disease vulnerability (Morrison *et al.* 2020; Stojanovic *et al.* 2018), are common in small
228 populations (Heber and Briskie 2010; Whiteman *et al.* 2006) and can affect juvenile survival
229 (Keller *et al.* 2007; Olson *et al.* 2011; Purwandana *et al.* 2015). We suggest that in context of
230 our results and uncertainty about important threats and intervention options (Drechsler
231 2000; Drechsler *et al.* 1998), increased focus on reducing mortality during migration and in
232 winter should be a conservation priority. However, given that translocation of captive birds
233 to the wild population has demonstrably mitigated some localized threatening processes at

234 Melaleuca, we suggest these actions should continue while more targeted interventions are
235 trialed in the migration/winter range.

236 Our study reaffirms that when faced with uncertainty about the factors driving the decline
237 of small populations, it is important to identify and implement management actions that can
238 improve vital demographic rates. Before translocations are implemented it is typically
239 necessary to ensure that the factors driving a species decline are identified and can be
240 corrected (IUCN/SSC 2013), but this has not been achieved for the Orange-bellied Parrot.

241 The migration/winter life history phases pose substantial logistic challenges and identifying
242 where and when to act is difficult. Locations where the species aggregates (e.g. key staging
243 sites for migration and recently used wintering areas) are good starting points for
244 management to maximize habitat availability (e.g. selective weed control and revegetation).
245 However, we caution that sites that are important for Orange-bellied Parrots today may not
246 reflect the utilization of historically important sites identified in earlier work (Loyn *et al.*
247 1986), both in terms of location and the food plants available/utilized. Prioritizing
248 interventions at places that achieve both short-term goals (e.g. food availability
249 immediately) and long-term habitat restoration goals may be a good starting point.

250 Furthermore, reducing mortality outside the breeding season may provide at least a
251 temporary reprieve from unidentified and unresolved threats during migration/winter.

252 ‘Head starting’ of wild juveniles (holding them in captivity for their first winter before
253 release at Melaleuca the following spring) and ‘ranching’ of captive-born mothers (by
254 releasing them to breed in spring/summer and recapturing them to winter in captivity) have
255 been implemented since 2017 (Troy and Hehn 2019). How these efforts have affected
256 demographic parameters (e.g. annual survival, per capita population growth) is not yet
257 clear.

258 Our study provides empirical support for the predictions of Drechsler *et al.* (1998) and
259 highlights the need for conservation managers to find new ways of overcoming the
260 challenges of working on small populations that disperse over large areas. Focusing
261 conservation effort where Orange-bellied Parrots aggregate to breed has corrected some
262 threats, but has not improved a key demographic rate. Unfortunately, important alternative
263 actions in migration/wintering habitats, including winter releases of captive-bred birds
264 aimed at attracting migrating individuals to high quality habitat, are still in the trial phase.
265 We hope that our study is a warning to other conservation practitioners to (i) model
266 demographic responses to management actions when uncertainty is high, (ii) act upon those
267 results early and (iii) regularly evaluate the impact of actions on population vital rates.

268 **Ethics**

269 The research utilised data collected by the Tasmanian Department of Primary Industries,
270 Parks, Water and Environment (DPIPWE) during their implementation of the Orange-bellied
271 Parrot Tasmanian Program.

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273 Survival data were collected by volunteers from DPIPWE and Wildcare Friends of the
274 Orange-bellied Parrot.

275 **Author contribution statement**

276 DS conceived the study, analysed the data and drafted the manuscript. JP analysed the data
277 and reviewed the manuscript. ST conceived the study and reviewed the manuscript. PM, RL
278 and RH reviewed the manuscript.

279 **Competing Interests**

280 The authors have no competing interests.

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286

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