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1 **Effects of nest cavity morphology on reproductive success of a critically endangered**
2 **bird.**

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6

7 **Abstract**

8 Population limitation is the outcome of cumulative and synergistic processes that act on
9 species over multiple spatial scales. Tree cavity dependent animals are good case studies for
10 exploring processes that potentially limit populations across multiple scales. Fine scale cavity
11 characteristics have important consequences for predator exclusion and fecundity, while
12 broad scale processes (food or habitat availability) can determine population viability. We
13 consider the relative importance of cavity morphology in limiting the vital rates of a critically
14 endangered secondary cavity nesting severely affected at broad-scales by nest predation. We
15 show that Swift Parrots *Lathamus discolor* prefer nest cavities where the minimum entrance
16 diameter is positively associated with cavity depth, floor diameter and maximum entrance
17 diameter. These cavity characteristics are adaptive because they exclude native predators;
18 only one introduced nest predator is able to breach these defences. We found no effect of
19 cavity morphology on the number of eggs laid or fledglings reared by Swift Parrots. This
20 suggests that fine scale nest cavity characteristics do not influence the nest success of Swift
21 Parrots beyond their effectiveness for excluding native predators. Nest boxes may be used to
22 address cavity limitation where introduced nest predators are absent. Our results suggest
23 boxes could vary within the full range of active nest dimensions with little consequence for
24 nest productivity. We show that isolating the impacts of processes that act at different scales

25 is helpful for understanding factors that limit populations and, in turn, informing conservation
26 approaches.

27 **Keywords**

28 *forest ecology, habitat selection, population limitation, Swift Parrot *Lathamus discolor*, tree*
29 *hollow*

30

31 **Introduction**

32 Identifying the individual and cumulative impacts of ecological processes acting on species at
33 different spatial scales is fundamental to understanding how populations are limited (Szabo et
34 al. 2012). Such information is crucial for developing management interventions to conserve
35 species and interpreting outcomes of those interventions. Tree cavity nesting animals are
36 affected by diverse factors operating over multiple scales. Secondary cavity nesters—species
37 that do not excavate their own tree cavities—are of global conservation concern
38 (Lindenmayer et al. 2013) and are highly vulnerable to anthropogenic and stochastic
39 processes that reduce the availability of cavity-bearing trees (Lindenmayer et al. 2012). The
40 sensitivity of secondary cavity nesters to forest cover may be exacerbated by their strong
41 preferences for cavities with particular morphology (Martin et al. 2004), and the availability
42 of suitable nesting cavities may limit their populations (Newton 1994).

43 Cavity-dependent species with very specific preferences may be unable to nest, or be forced
44 to occupy suboptimal cavities, in places where this resource is limiting (Gibbons and
45 Lindenmayer 2002). In landscapes where cavities are uncommon, determining whether
46 population vital rates vary with cavity morphology is fundamental to conservation of
47 secondary cavity nesters, particularly if suboptimal nests reduce fitness. This may occur when
48 cumulative anthropogenic changes act simultaneously on threatened populations of secondary
49 cavity nesters (Heinsohn et al. 2015). However, few studies have considered how fine scale
50 cavity characteristics impact vital rates because collecting the necessary data can be
51 logistically challenging and requires specialist field techniques (Heinsohn 2008; Cockle et al.
52 2015; Davis et al. 2013).

53 Consequently, studies reporting effects of cavity morphology on vital rates typically use data
54 collected at nest boxes (Møller et al. 2014; Olah et al. 2014). But nest boxes have been shown

55 to differ from natural cavities in both morphological variability and predation risk (Libois et
56 al. 2012). Further, morphological variation in cavities selected for nesting will be species-
57 specific (i.e. generalists may tolerate a wider range of cavity morphologies than specialists),
58 which can have flow on effects for nest fate (Martin et al. 2004).

59 Data on fitness effects of natural cavity morphology are scarce and sometimes contradictory.
60 For example, cavities with larger floor areas may increase clutch size (Rendell and Robertson
61 1989), but not always (Lambrechts et al. 2016). Height above ground (Vanderwerf 2012) and
62 entrance diameter (Czeszczewik et al. 2008) are often related to predation risk, which reflects
63 the results of some nest box studies (Le Roux et al. 2016). In cases where nest predators are
64 introduced to naïve ecosystems, cavity characteristics may offer little or no protection
65 (Moorhouse et al. 2003) but parental behaviour (McIntyre et al. 2014) and local nest predator
66 guild composition (introduced/native) may be important in determining nest fate (Blackburn
67 et al. 2004). To understand whether cavity characteristics affect reproductive success, it is
68 necessary to establish how vital rates (e.g. number of eggs, fledglings, predation) vary over
69 different cavity morphologies. This question has recently been identified as a key gap in
70 knowledge for some cavity nesting birds (Renton et al. 2015).

71 Here we consider a critically endangered secondary cavity nesting bird (Heinsohn et al. 2015)
72 where population effects of broad-scale ecological processes have been described, but the
73 relative impact of cavity morphology on vital rates is unknown. Swift Parrots *Lathamus*
74 *discolor* are nomadic migrants (Stojanovic et al. 2015) that prefer cavities with small
75 entrances and deep chambers (Stojanovic et al. 2012) which usually occur in old trees (Webb
76 et al. 2012). Swift Parrots undertake nomadic movements to exploit rich patches of tree
77 flowering to breed (Webb et al. 2014) which may release them from food limitation during
78 nesting (Stojanovic et al. 2015). Nest fate largely depends on local occurrence of an
79 introduced nest predator (Stojanovic et al. 2014b). Whether nest cavity characteristics affect

80 Swift Parrot reproductive investment (clutch size) and success (fledglings reared) has not
81 been studied. We present data collected over a six-year monitoring program across the entire
82 breeding range of Swift Parrots to: (1) describe Swift Parrot nest cavity morphology and
83 relationships between different cavity characteristics, (2) determine whether the number of
84 eggs laid and fledglings reared varies with cavity morphology and (3) determine whether nest
85 predation varies with cavity morphology. We show that Swift Parrots exhibit strong selection
86 for fine scale cavity characteristics, but we find no relationship between these traits and
87 measured vital rates. We show that vital rates of Swift Parrots are not influenced directly by
88 cavity morphology, but the species exhibits strong preferences for particular cavity
89 characteristics which are adaptive in excluding native nest predators. We discuss our results
90 in context of conservation management of secondary cavity nesting species, and evaluate the
91 evidence for population limitation of Swift Parrots at broader spatial scales.

92 **Methods**

93 *Study area and species*

94 Swift Parrots are small (70 g) and breed in Tasmania, Australia during the Austral summer
95 (Higgins 1999). Swift Parrot breeding settlement patterns vary annually with flowering
96 patterns of their preferred food trees (Webb et al. 2014). We monitored Swift Parrot breeding
97 settlement patterns across their entire breeding range for six seasons (2010 - 2015, Figure 1:
98 Webb et al. 2014). The study area is dominated by *Eucalyptus* forest fragmented by
99 deforestation predominantly for agriculture and logging. Swift Parrots prefer cavities with
100 small entrances, deep chambers and wide floors, but such cavities are rare in Tasmania
101 (Stojanovic et al. 2012; Stojanovic et al. 2014a). Swift Parrots are critically endangered by
102 severe nest predation by Sugar Gliders *Petaurus breviceps* (Heinsohn et al. 2015), a small
103 (100 - 140 g) secondary cavity nesting, volant marsupial introduced to Tasmania (Gunn

104 1851). Sugar Gliders have not been introduced to offshore islands (Fig. 1, region 6) where
105 Swift Parrots sometimes breed (Stojanovic et al. 2014b).

106 *Nest monitoring*

107 We found nests during systematic and unstructured searches at seven Swift Parrot breeding
108 regions (Fig 1). We repeatedly climbed trees using single rope techniques to monitor nests
109 visually and using motion-activated cameras (Reconyx HC600™, Holmen, WI, USA). At
110 each Swift Parrot nesting attempt, we recorded: (1) number of eggs laid, (2) number of
111 fledglings reared, and (3) Sugar Glider predation (yes/no). At each Swift Parrot nest, we also
112 measured: (1) tree species, (2) tree diameter at breast height (DBH), (3) minimum entrance
113 diameter (cm) of the nest cavity, (4) maximum entrance diameter (cm) of the nest cavity, (5)
114 depth (cm) of the nest cavity, measured from the bottom lip of the entrance to the floor, (6)
115 floor diameter (cm) of the nest cavity, and (7) whether the cavity occurred on an island or the
116 Tasmanian mainland.

117 *Analytical approach*

118 We fitted generalised linear models in R (R Core Development Team 2016) to identify
119 patterns in cavity selection by Swift Parrots, using all combinations of our cavity
120 characteristics as response and predictor variables. We additionally included tree species,
121 DBH, and island/mainland as predictor variables in these models. We used forward selection
122 (implemented using MASS; Venables and Ripley 2002) to identify significant relationships
123 among cavity dimensions

124 We fitted generalised linear mixed models (GLMM implemented using nlme4; Bates et al.
125 2015) to assess the effect of cavity morphology on vital rates, using number of eggs, number
126 of fledglings and breeding success (fledglings/eggs) as response variables. We fitted all nest
127 cavity and nest tree characteristics as predictor variables. To account for repeated use of some

128 cavities in our sample, we included a unique nest identifier as a random term. We also
129 included nesting region (Fig. 1) as a random term to account for spatial autocorrelation in
130 breeding data. To examine the effect of cavity morphology on vital rates in the absence of
131 predation, we repeated the modelling process using data from cavities where Sugar Glider
132 predation was not a factor in nest fate.

133 We used GLMM to determine if cavity morphology influenced predation rates, using Sugar
134 Glider predation as the response variable, and all cavity measurements as predictor variables.
135 As above, we included nest and nesting region as random terms in these models.

136 **Results**

137 *Cavity morphology*

138 We report data from 105 Swift Parrot nest cavities for which data on cavity characteristics,
139 reproductive parameters and nest fate were available. We located nest cavities in seven tree
140 species (*E. obliqua* n = 33, *E. globulus* n = 22, *E. dalrympleana* n = 21, *E. pulchella* n = 10,
141 *E. amygdylina* n = 7, *E. viminalis* n = 7, *E. delegatensis* n = 5) of 107.9 cm mean DBH (\pm
142 38.5 SD). Cavity characteristics varied among Swift Parrot nests, with cavity depth being the
143 most variable dimension (Fig. 2). We found positive associations among entrance diameters
144 (minimum and maximum) and cavity depth (Table 1), whereas floor diameter decreased with
145 increasing cavity depth. We found no significant effect of tree species, DBH or
146 island/mainland on cavity morphology.

147 *Reproductive Success*

148 Of our total sample of nests (including 27 nests that failed due to Sugar Glider predation, one
149 that failed due to usurpation of the cavity by *Apis mellifera* and another that failed due to
150 cavity collapse) mean number of eggs laid was 3.3 (\pm 1.1 SD), and mean number of
151 fledglings reared was 2.1 (\pm 1.6 SD). We did not find any relationship between the number of

152 eggs ($0.559 < p < 0.961$), fledglings ($0.377 < p < 0.881$) or breeding success ($0.202 < p <$
153 0.865) and any characteristic of nest cavities. When we excluded the effect of Sugar Glider
154 predation, we still found no effect of cavity characteristics on number of eggs ($0.45 < p <$
155 0.936), fledglings ($0.175 < p < 0.636$) or breeding success ($0.097 < p < 0.633$).

156 *Predation*

157 At nests unaffected by Sugar Gliders, mean number of eggs laid was $3.5 (\pm 0.9 \text{ SD})$ and mean
158 number of fledglings reared was $2.9 (\pm 1.2 \text{ SD})$. Sugar Glider depredated nests produced
159 mean $2.6 (\pm 1.2 \text{ SD})$ eggs and 0 fledglings. Seven cavities of our sample of mainland
160 Tasmanian nests were used in more than one year (maximum three years) by Swift Parrots
161 and Sugar Gliders caused nest failure of successive nesting attempts at three of these cavities.
162 Fewer eggs in Sugar Glider affected nests was likely attributable to predation of incomplete
163 clutches, resulting in nest abandonment or death of the female Swift Parrot. We found no
164 relationship between cavity characteristics and Sugar Glider predation ($0.176 < p < 0.987$).

165 **Discussion**

166 We use multi-year data collected across the entire Swift Parrot breeding range to provide new
167 evidence that Swift Parrot breeding success and nest fate are not correlated with fine scale
168 nest cavity characteristics. Our study reveals that Swift Parrots select nest cavities where
169 minimum entrance diameter, maximum entrance diameter and depth are positively correlated.
170 These specific nest selection patterns may be explained by predation risk from native
171 Tasmanian nest predators. Unlike Sugar Gliders, native Tasmanian nest predators are larger
172 than Swift Parrots or are hesitant to enter deep cavities (Stojanovic et al. 2014b). The two
173 most common potential native predators observed at Swift Parrot nests are Grey Shrike
174 Thrushes *Colluricincla harmonica* and Black Currawongs *Strepera fuliginosa* (D.S.
175 unpublished data and Stojanovic et al. 2014b). Morphological relationships described here
176 may be adaptive for Swift Parrots because (1) shallow nest cavities have small entrances that

177 exclude large predators (e.g. Black Currawongs), and (2) cavities with larger entrances are
178 deeper, which excludes both small predators (e.g. Grey shrike Thrushes) that do not fully
179 enter cavities and large predators that cannot reach the nest contents. Our data support the
180 notion that selection for these cavity traits is adaptive because Swift Parrots that nest on
181 offshore islands (where the nest predator guild comprises only native species) have very high
182 nesting success (Heinsohn et al. 2015; Stojanovic et al. 2014b). We found no difference
183 between nest cavities on islands and those on the Tasmanian mainland. Unlike native nest
184 predators, introduced Sugar Gliders can breach Swift Parrot nest cavities on the mainland and
185 are a serious conservation problem (Heinsohn et al. 2015).

186

187 Within our sample of active nests, fine-scale morphological patterns emerged but we found
188 no significant effect of any individual cavity characteristic on the number of eggs laid or
189 fledglings reared by Swift Parrots. This confirms the results of some studies (Alatalo et al.
190 1988; Wiebe and Swift 2001) but contrasts with others (Møller et al. 2014). We interpret
191 these results with caution, emphasising that morphological variation examined here (i.e.
192 within active nests) does not reflect morphological variation across the broader cavity
193 resource. Previous research demonstrates that Swift Parrots are highly selective in their nest
194 cavity choice (Stojanovic et al. 2012) and shortages of suitable cavities may still be an
195 important limitation on the Swift Parrot population. Importantly, it is not currently known
196 whether cavity limitation prevents some Swift Parrots from attempting to nest in locations
197 where suitable cavities are scarce. Cavity limitation has profound effects on cavity nesting
198 species (Heinsohn and Legge 2003; Cockle et al. 2010) and deforestation reduces cavity
199 abundance (Manning et al. 2013). Swift Parrot breeding habitat is subject to ongoing and
200 contentious deforestation (Allchin et al. 2013). Even in extant Tasmanian mature forest, only
201 5 % of available cavities may be suitable as nesting sites for Swift Parrots (Stojanovic et al.

202 2012). Furthermore, stochastic events severely affect tree cavity availability (Stojanovic et al.
203 2016) and the cumulative effects of these factors are recognised as key factors driving Swift
204 Parrot population decline (Saunders and Tzaros 2011). In addition, Swift Parrots move
205 between disparate locations annually to breed (Webb et al. 2014) and so may be particularly
206 vulnerable to anthropogenic changes to habitat (Runge et al. 2014). Our results support the
207 conservation significance of suitable tree cavities, but highlight a gap in our understanding of
208 cavity limitation and its effects on the Swift Parrot population. We suggest that conservation
209 managers should aim to maximise availability of suitable cavities at broad scales to ensure
210 Swift Parrot breeding participation is not curtailed by cavity limitation.

211

212 This study has important implications for the conservation management of Swift Parrots.
213 First, we confirm that Swift Parrot nests on the Tasmanian mainland have a high likelihood of
214 predation (Heinsohn et al. 2015) irrespective of internal nest cavity characteristics. Mitigating
215 nest predation is possible using predator control (Moorhouse et al. 2003) or mechanical
216 exclusion from nests (Mitchell et al. 1999) and these management approaches may be
217 applicable to our study system because Swift Parrot nests lack natural defenses against Sugar
218 Gliders. Second, the non-significant relationships between cavity characteristics and Swift
219 Parrot vital rates provide valuable information for conservation action involving nest boxes.
220 Whereas fecundity of some species may be curtailed or enhanced with different nest box
221 designs (Møller et al. 2014), our study suggests that Swift Parrots could tolerate variable box
222 shapes and breed successfully, provided that box dimensions fall within the range of
223 preferred nest characteristics. Finally, deployment of nesting boxes in Sugar Glider free
224 habitats may be a useful conservation tool for Swift Parrots to address potential cavity
225 limitation in disturbed forest. However, we caution that nest boxes are only one of a range of
226 management strategies for conserving secondary cavity nesting fauna (Lindenmayer et al.

227 2006) and can provide habitat for non-target species and create new management problems
228 (Le Roux et al. 2016). We argue that nest boxes should form only part of a broader approach
229 that addresses deforestation (Lindenmayer et al. 2012) and predation risk by Sugar Gliders
230 (Stojanovic et al. 2014b).

231

232 We confirm that habitat preferences of a critically endangered secondary cavity nesting bird
233 are strong and adaptive under natural conditions. However, introduced predators and
234 anthropogenic habitat change can severely impact the availability of habitat and fate of
235 nesting attempts. Secondary cavity nesters are a seriously threatened species guild (Gibbons
236 and Lindenmayer 2002) and understanding the processes that limit their populations requires
237 disentangling synergistic effects over multiple spatial scales. Our study demonstrates that
238 when suitable cavities are available and habitat quality is unaffected by these changes,
239 breeding success of secondary cavity nesters is high. However, conservation of secondary
240 cavity nesters must take into account heterogeneous availability of resources and threatening
241 processes over space and time to avoid misdirecting scarce conservation resources.

242

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254 wrote the paper.

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380 **Figure Captions**

381 Fig. 1. Regions where Swift Parrots were monitored for breeding activity: (1) Devonport, (2)
382 Eastern Tiers, (3) Wielangta, (4) Buckland, (5) Meehan Range, (6) Bruny Island and (7)
383 Southern Forests.

384 Fig. 2. Cavity characteristics measured at active Swift Parrot nests (n = 105). Values for
385 *entrance* and *floor* are diameter measurements. *Min.* = minimum, *Max.* = maximum..

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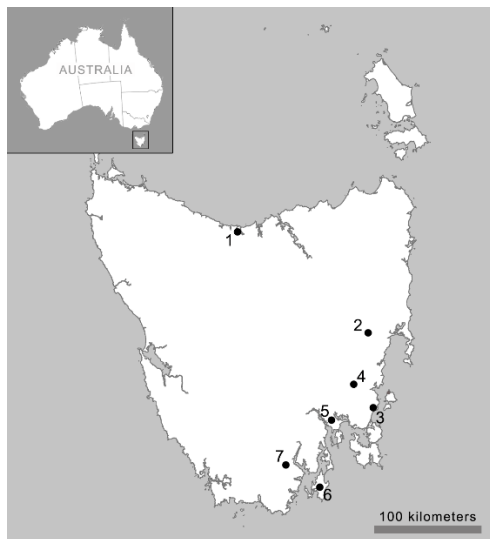
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400 **Figures**

401 Figure 1

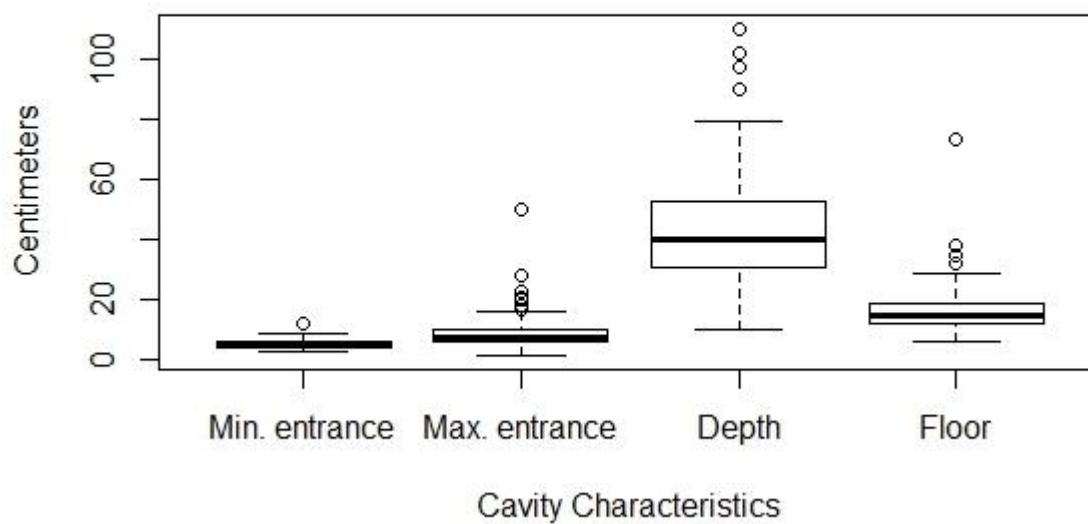


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405 Figure 2



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407 **Table 1.** Associations among cavity characteristics measured at active Swift Parrot nests (n =
 408 105). Values for *entrance* and *floor* are diameter measurements. *Min.* = minimum, *Max.* =
 409 maximum.

<u>Response (range)</u>	<u>Predictor</u>	<u>Est.</u>	<u>SE</u>	<u>P</u>
Min. entrance	Depth	0.04	0.01	< 0.0001
	Max. entrance	0.06	0.02	0.005
Max. entrance	Min. entrance	1.34	0.35	0.0002
	Depth	5.88	1.05	< 0.0001
Depth	Min. entrance	5.88	1.05	< 0.0001
	Floor	-0.53	0.22	0.0185
Floor	Depth	-0.14	0.04	0.0001

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