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

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Abstract

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

Keywords

forest ecology, habitat selection, population limitation, Swift Parrot Lathamus discolor, tree hollow
Introduction

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

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

Consequently, studies reporting effects of cavity morphology on vital rates typically use data collected at nest boxes (Møller et al. 2014; Olah et al. 2014). But nest boxes have been shown
to differ from natural cavities in both morphological variability and predation risk (Libois et al. 2012). Further, morphological variation in cavities selected for nesting will be species-specific (i.e. generalists may tolerate a wider range of cavity morphologies than specialists), which can have flow on effects for nest fate (Martin et al. 2004).

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

Here we consider a critically endangered secondary cavity nesting bird (Heinsohn et al. 2015) where population effects of broad-scale ecological processes have been described, but the relative impact of cavity morphology on vital rates is unknown. Swift Parrots Lathamus discolor are nomadic migrants (Stojanovic et al. 2015) that prefer cavities with small entrances and deep chambers (Stojanovic et al. 2012) which usually occur in old trees (Webb et al. 2012). Swift Parrots undertake nomadic movements to exploit rich patches of tree flowering to breed (Webb et al. 2014) which may release them from food limitation during nesting (Stojanovic et al. 2015). Nest fate largely depends on local occurrence of an introduced nest predator (Stojanovic et al. 2014b). Whether nest cavity characteristics affect
Swift Parrot reproductive investment (clutch size) and success (fledglings reared) has not been studied. We present data collected over a six-year monitoring program across the entire breeding range of Swift Parrots to: (1) describe Swift Parrot nest cavity morphology and relationships between different cavity characteristics, (2) determine whether the number of eggs laid and fledglings reared varies with cavity morphology and (3) determine whether nest predation varies with cavity morphology. We show that Swift Parrots exhibit strong selection for fine scale cavity characteristics, but we find no relationship between these traits and measured vital rates. We show that vital rates of Swift Parrots are not influenced directly by cavity morphology, but the species exhibits strong preferences for particular cavity characteristics which are adaptive in excluding native nest predators. We discuss our results in context of conservation management of secondary cavity nesting species, and evaluate the evidence for population limitation of Swift Parrots at broader spatial scales.

Methods

Study area and species

Swift Parrots are small (70 g) and breed in Tasmania, Australia during the Austral summer (Higgins 1999). Swift Parrot breeding settlement patterns vary annually with flowering patterns of their preferred food trees (Webb et al. 2014). We monitored Swift Parrot breeding settlement patterns across their entire breeding range for six seasons (2010 - 2015, Figure 1: Webb et al. 2014). The study area is dominated by Eucalyptus forest fragmented by deforestation predominantly for agriculture and logging. Swift Parrots prefer cavities with small entrances, deep chambers and wide floors, but such cavities are rare in Tasmania (Stojanovic et al. 2012; Stojanovic et al. 2014a). Swift Parrots are critically endangered by severe nest predation by Sugar Gliders Petaurus breviceps (Heinsohn et al. 2015), a small (100 - 140 g) secondary cavity nesting, volant marsupial introduced to Tasmania (Gunn...
Sugar Gliders have not been introduced to offshore islands (Fig. 1, region 6) where Swift Parrots sometimes breed (Stojanovic et al. 2014b).

**Nest monitoring**

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

**Analytical approach**

We fitted generalised linear models in R (R Core Development Team 2016) to identify patterns in cavity selection by Swift Parrots, using all combinations of our cavity characteristics as response and predictor variables. We additionally included tree species, DBH, and island/mainland as predictor variables in these models. We used forward selection (implemented using MASS; Venables and Ripley 2002) to identify significant relationships among cavity dimensions. We fitted generalised linear mixed models (GLMM implemented using nlme4; Bates et al. 2015) to assess the effect of cavity morphology on vital rates, using number of eggs, number of fledglings and breeding success (fledglings/eggs) as response variables. We fitted all nest cavity and nest tree characteristics as predictor variables. To account for repeated use of some
cavities in our sample, we included a unique nest identifier as a random term. We also included nesting region (Fig. 1) as a random term to account for spatial autocorrelation in breeding data. To examine the effect of cavity morphology on vital rates in the absence of predation, we repeated the modelling process using data from cavities where Sugar Glider predation was not a factor in nest fate.

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

Results

Cavity morphology

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

Reproductive Success

Of our total sample of nests (including 27 nests that failed due to Sugar Glider predation, one that failed due to usurpation of the cavity by Apis mellifera and another that failed due to cavity collapse) mean number of eggs laid was 3.3 (± 1.1 SD), and mean number of fledglings reared was 2.1 (± 1.6 SD). We did not find any relationship between the number of
eggs (0.559 < p < 0.961), fledgings (0.377 < p < 0.881) or breeding success (0.202 < p < 0.865) and any characteristic of nest cavities. When we excluded the effect of Sugar Glider predation, we still found no effect of cavity characteristics on number of eggs (0.45 < p < 0.936), fledglings (0.175 < p < 0.636) or breeding success (0.097 < p < 0.633).

**Predation**

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

**Discussion**

We use multi-year data collected across the entire Swift Parrot breeding range to provide new evidence that Swift Parrot breeding success and nest fate are not correlated with fine scale nest cavity characteristics. Our study reveals that Swift Parrots select nest cavities where minimum entrance diameter, maximum entrance diameter and depth are positively correlated. These specific nest selection patterns may be explained by predation risk from native Tasmanian nest predators. Unlike Sugar Gliders, native Tasmanian nest predators are larger than Swift Parrots or are hesitant to enter deep cavities (Stojanovic et al. 2014b). The two most common potential native predators observed at Swift Parrot nests are Grey Shrike Thrushes *Colluricincla harmonica* and Black Currawongs *Strepera fuliginosa* (D.S. unpublished data and Stojanovic et al. 2014b). Morphological relationships described here may be adaptive for Swift Parrots because (1) shallow nest cavities have small entrances that
exclude large predators (e.g. Black Currawongs), and (2) cavities with larger entrances are deeper, which excludes both small predators (e.g. Grey shrike Thrushes) that do not fully enter cavities and large predators that cannot reach the nest contents. Our data support the notion that selection for these cavity traits is adaptive because Swift Parrots that nest on offshore islands (where the nest predator guild comprises only native species) have very high nesting success (Heinsohn et al. 2015; Stojanovic et al. 2014b). We found no difference between nest cavities on islands and those on the Tasmanian mainland. Unlike native nest predators, introduced Sugar Gliders can breach Swift Parrot nest cavities on the mainland and are a serious conservation problem (Heinsohn et al. 2015).

Within our sample of active nests, fine-scale morphological patterns emerged but we found no significant effect of any individual cavity characteristic on the number of eggs laid or fledglings reared by Swift Parrots. This confirms the results of some studies (Alatalo et al. 1988; Wiebe and Swift 2001) but contrasts with others (Møller et al. 2014). We interpret these results with caution, emphasising that morphological variation examined here (i.e. within active nests) does not reflect morphological variation across the broader cavity resource. Previous research demonstrates that Swift Parrots are highly selective in their nest cavity choice (Stojanovic et al. 2012) and shortages of suitable cavities may still be an important limitation on the Swift Parrot population. Importantly, it is not currently known whether cavity limitation prevents some Swift Parrots from attempting to nest in locations where suitable cavities are scarce. Cavity limitation has profound effects on cavity nesting species (Heinsohn and Legge 2003; Cockle et al. 2010) and deforestation reduces cavity abundance (Manning et al. 2013). Swift Parrot breeding habitat is subject to ongoing and contentious deforestation (Allchin et al. 2013). Even in extant Tasmanian mature forest, only 5% of available cavities may be suitable as nesting sites for Swift Parrots (Stojanovic et al.
Furthermore, stochastic events severely affect tree cavity availability (Stojanovic et al. 2016) and the cumulative effects of these factors are recognised as key factors driving Swift Parrot population decline (Saunders and Tzaros 2011). In addition, Swift Parrots move between disparate locations annually to breed (Webb et al. 2014) and so may be particularly vulnerable to anthropogenic changes to habitat (Runge et al. 2014). Our results support the conservation significance of suitable tree cavities, but highlight a gap in our understanding of cavity limitation and its effects on the Swift Parrot population. We suggest that conservation managers should aim to maximise availability of suitable cavities at broad scales to ensure Swift Parrot breeding participation is not curtailed by cavity limitation.

This study has important implications for the conservation management of Swift Parrots. First, we confirm that Swift Parrot nests on the Tasmanian mainland have a high likelihood of predation (Heinsohn et al. 2015) irrespective of internal nest cavity characteristics. Mitigating nest predation is possible using predator control (Moorhouse et al. 2003) or mechanical exclusion from nests (Mitchell et al. 1999) and these management approaches may be applicable to our study system because Swift Parrot nests lack natural defenses against Sugar Gliders. Second, the non-significant relationships between cavity characteristics and Swift Parrot vital rates provide valuable information for conservation action involving nest boxes. Whereas fecundity of some species may be curtailed or enhanced with different nest box designs (Møller et al. 2014), our study suggests that Swift Parrots could tolerate variable box shapes and breed successfully, provided that box dimensions fall within the range of preferred nest characteristics. Finally, deployment of nesting boxes in Sugar Glider free habitats may be a useful conservation tool for Swift Parrots to address potential cavity limitation in disturbed forest. However, we caution that nest boxes are only one of a range of management strategies for conserving secondary cavity nesting fauna (Lindenmayer et al. 2012).
and can provide habitat for non-target species and create new management problems (Le Roux et al. 2016). We argue that nest boxes should form only part of a broader approach that addresses deforestation (Lindenmayer et al. 2012) and predation risk by Sugar Gliders (Stojanovic et al. 2014b).

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

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ANU Animal Ethics Committee approval (A2014/26). The paper was conceived by DS and MW. The data were collected by DS and analysed by DS and LR. DS, LR, MW and RH wrote the paper.

**Literature Cited**


R Foundation for Statistical Computing, Vienna, Austria.


**Figure Captions**

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

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

Figure 1

![Map of Australia with Western Tasmania highlighted.](image)

Figure 2

![Box plots showing cavity characteristics.](image)
Table 1. Associations among cavity characteristics measured at active Swift Parrot nests (n = 105). Values for *entrance* and *floor* are diameter measurements. *Min.* = minimum, *Max.* = maximum.

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