EMU AUSTRAL ORNITHOLOGY

Emu - Austral Ornithology

ISSN: 0158-4197 (Print) 1448-5540 (Online) Journal homepage: https://www.tandfonline.com/loi/temu20

Effect of nest cavity morphology on reproductive success of a critically endangered bird

Dejan Stojanovic, Laura Rayner, Matthew Webb & Robert Heinsohn

To cite this article: Dejan Stojanovic, Laura Rayner, Matthew Webb & Robert Heinsohn (2017) Effect of nest cavity morphology on reproductive success of a critically endangered bird, Emu - Austral Ornithology, 117:3, 247-253, DOI: 10.1080/01584197.2017.1311221

To link to this article: https://doi.org/10.1080/01584197.2017.1311221

EMU - AUSTRAL ORNITHOLOGY, 2017
VOL. 117, NO. 3, 247–253
https://doi.org/10.1080/01584197.2017.1311221

Effect of nest cavity morphology on reproductive success of a critically endangered bird

Dejan Stojanovic, Laura Rayner, Matthew Webb and Robert Heinsohn

Fenner School of Environment and Society, Australian National University, Canberra, Australia

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 considered the relative importance of cavity morphology in limiting the breeding success of a critically endangered secondary cavity nesting bird that is severely affected at broad scales by nest predation. Swift Parrots (*Lathamus discolor*) select 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 by physically preventing access to the nest chamber; only one introduced nest predator is able to overcome this passive nest defence. Introduced Sugar Gliders (*Petaurus breviceps*) could prey on Swift Parrot nests irrespective of nest cavity morphology. 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 in excluding native Tasmanian predators.

ARTICLE HISTORY
Received 30 January 2017
Accepted 20 March 2017

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 spatial 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 specific preferences may be unable to nest, or be forced to occupy sub-optimal cavities, in places where preferred cavities are limiting (Gibbons and Lindenmayer 2002). In landscapes where cavities are uncommon, determining whether breeding success varies with cavity morphology is fundamental to conservation of secondary cavity nesters, particularly if sub-optimal nests reduce nest survival. 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 breeding success because collecting the necessary data can be logistically challenging and requires specialist field techniques (Heinsohn 2008; Davis *et al.* 2013; Cockle *et al.* 2015).

Consequently, studies reporting effects of cavity morphology on breeding success typically use data collected at nest boxes (Møller *et al.* 2014; Olah *et al.* 2014). However, nest boxes have been shown to differ from natural cavities in both morphological variability (i.e. boxes vary less) and in lower predation risk (Libois *et al.* 2012). Furthermore, morphological variation in cavities selected for nesting will be species-specific (i.e. generalists may tolerate a wider range of cavity

CONTACT Dejan Stojanovic dejan.stojanovic@anu.edu.au

morphologies than specialists), which may 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 number of eggs, fledglings, and predation vary with different cavity morphologies. This question has recently been identified as a key knowledge gap for some cavity nesting birds (Renton *et al.* 2015).

Here we consider the critically endangered secondary cavity nesting Swift Parrot (*Lathamus discolor*) (Heinsohn *et al.* 2015) where population effects of broad-scale ecological processes have been described, but the relative impact of cavity morphology on breeding success is unknown. They are nomadic migrants (Stojanovic *et al.* 2015) that select cavities with small entrances and deep chambers (Stojanovic *et al.* 2012) which usually occur in old trees (Webb *et al.* 2012). Swift Parrots exploit rich patches of flowering trees to breed (Webb *et al.* 2014) which may release them from food limitation during nesting (Stojanovic *et al.* 2015). 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 1851). Whether nest cavity characteristics affect Swift Parrot reproductive investment (clutch size) and success (fledglings reared) has not been studied. Likewise, it is not known whether Sugar Glider predation is dependent on the morphology of Swift Parrot nest cavities. We present data collected over a 6-year monitoring program across the entire breeding range of Swift Parrots to: (1) describe patterns of selection by Swift Parrots on nest cavity morphology, (2) determine whether the number of eggs laid and fledglings reared varies with nest cavity morphology, and (3) determine whether glider predation varies with cavity morphology.

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 the flowering patterns of their preferred food trees (Webb *et al.* 2014, 2017). 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 are known to select cavities with small entrances, deep chambers and wide floors, but such cavities are rare in Tasmania (Stojanovic *et al.* 2012; Stojanovic *et al.* 2014a). Sugar Gliders have not been introduced to offshore islands (Figure 1, region 6) where Swift Parrots sometimes breed with high nesting success (Stojanovic *et al.* 2014b).

Nest monitoring

We found nests during systematic and unstructured searches at seven Swift Parrot breeding regions (Figure 1). We repeatedly climbed trees using single rope techniques to monitor nests visually and using

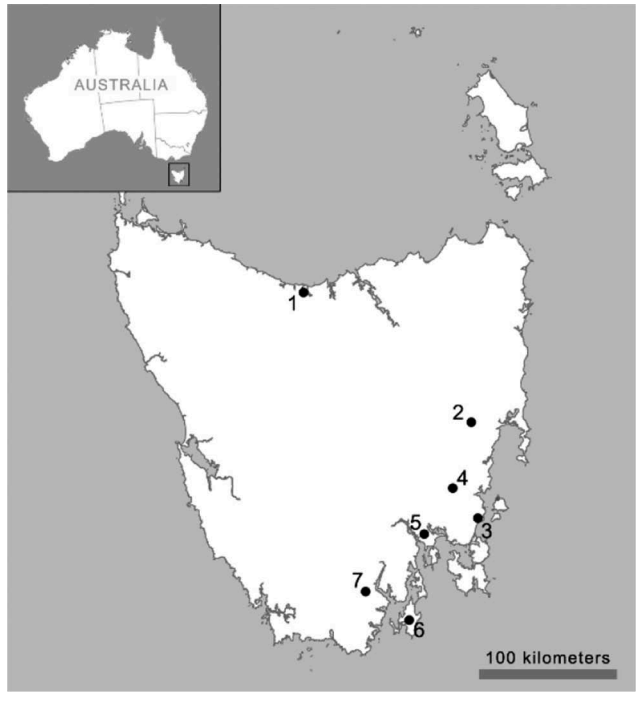

Figure 1. Regions where Swift Parrots were monitored for breeding activity: (1) Devonport, (2) Eastern Tiers, (3) Wielangta, (4) Buckland, (5) Meehan Range, (6) Bruny Island, and (7) Southern Forests.

motion-activated cameras (Reconyx HC600^{TM}, 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 determined by reviewing cameras or by presence of depredated parrots/eggs). 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 2008) 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.* 2013) to assess the effect of cavity morphology on number of eggs, number of fledglings and 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 (Figure 1) as a random term to account for spatial autocorrelation in breeding data. To examine the effect of cavity morphology on breeding success 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 GLMMs to determine whether 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 nests. We located nest cavities in seven tree species (*Eucalyptus 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 standard deviation – hereinafter all data in parentheses are standard deviation). Cavity characteristics varied among Swift Parrot nests, with cavity depth being the most variable (Figure 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) the mean number of eggs laid was 3.3 (±1.1), and the mean number of fledglings reared was 2.1 (±1.6). We did not find any relationship between the number of eggs ($0.559 < p < 0.961$), fledglings ($0.377 < p < 0.881$) or fledglings/eggs ($0.202 < p < 0.865$) 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 fledglings/eggs ($0.097 < p < 0.633$).

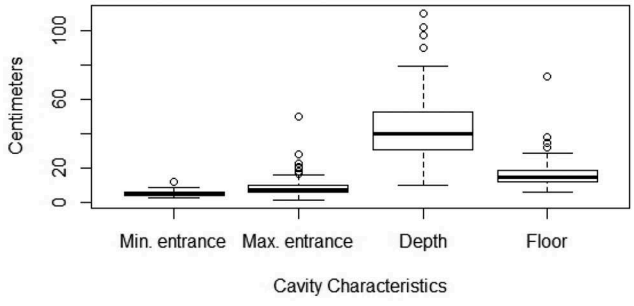

Figure 2. Cavity characteristics measured at active Swift Parrot nests (n = 105). Values for 'entrance' and 'floor' are diameter measurements. 'Min.' = minimum, 'Max.' = maximum.

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

Response (range)	Predictor	Est.	SE	*P*
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	Min. entrance	5.88	1.05	<0.0001
	Floor	−0.53	0.22	0.0185
Floor	Depth	−0.14	0.04	0.0001

Predation

At nests unaffected by Sugar Gliders, the mean number of eggs laid was 3.5 (±0.9) and the mean number of fledglings reared was 2.9 (±1.2). Sugar Glider depredated nests produced mean 2.6 (±1.2) eggs and 0 fledglings. Seven cavities of our sample of mainland Tasmanian nests were used in more than 1 year (maximum 3 years) by Swift Parrots. Sugar Gliders caused nest failure of each successive nesting attempt at three of these cavities. Fewer eggs in Sugar Glider affected nests was attributable to predation of incomplete clutches, resulting in nest abandonment or death of the adult 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 affected by variation in cavity characteristics within our sample of nests. Stojanovic *et al.* (2012) found that, compared to random cavities, nest cavities were strongly selected for particular morphological traits. We build on this result by (1) quantifying patterns in variation of Swift Parrot nest cavity morphologies, and (2) demonstrating that variation in cavity morphology is independent of the reproductive parameters we measured. Swift Parrots selected nest cavities where minimum entrance diameter, maximum entrance diameter and depth were positively correlated. These specific nest selection patterns may be explained by predation risk from native Tasmanian nest predators (Stojanovic *et al.* 2014b). 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 between cavity characteristics 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 enter deep 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 (Stojanovic *et al.* 2014b ; Heinsohn *et al.* 2015). We found no morphological 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 in our sample. 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 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 (Webb *et al.* 2017). 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.* 2012). Furthermore, stochastic events severely affect tree cavity availability (Stojanovic *et al.* 2016). The cumulative effects of these processes are recognised as key drivers of 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 is not curtailed by cavity limitation.

This study has important implications for the conservation management of Swift Parrots. Firstly, we confirmed that Swift Parrot nests on the Tasmanian mainland have a high likelihood of predation

(Heinsohn *et al.* 2015) irrespective of nest cavity morphology. 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 valuable because Swift Parrot nests lack natural defences against Sugar Gliders. Secondly, the non-significant relationships between cavity characteristics and Swift Parrot breeding success 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 otherwise suitable habitat. However, we caution that nest boxes are only one of a range of management strategies for conserving secondary cavity nesting fauna (Lindenmayer *et al.* 2006) 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.

Acknowledgements

Weetapoona Aboriginal Corporation, the Indigenous Land Council (Lynne and Bruce Michaels), Gill Fowler, Rick Murray, Joanne Naylor, Chris Brearley and Tony McLain provided land access. Thanks also to Fernanda Alves, Allegra Biggs-Dale, Adrian Dale, Fred and Mercedes Duncan, Henry Cook, Mathew Eyles, Mark Holdsworth, Fiona Hume, Inala Nature Tours, Dave James, Eric Lira, Cecilia Phu, Sue Robinson and Allan Wiltshire.

Funding

Funding was provided by a Commonwealth Government research environmental offset (paid by Cumnock Management Pty Ltd), the Australian Research Council, the Australian Government National Environmental Science Programme and the Loro Parque Fundacion. The work was conducted with a Tasmanian Government Scientific Permit (TFA14232) and ANU Animal Ethics Committee approval (A2014/26). The paper was conceived by D.S. and M.W. The data were collected by D.S. and analysed by D.S. and L.R. D. S., L.R., M.W. and R.H. wrote the paper.

References

Alatalo, R. V., Carlson, A., and Lundberg, A. (1988). Nest cavity size and clutch size of pied flycatchers ficedula hypoleuca breeding in natural tree-holes. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* **19**, 317–319. doi:10.2307/3676729

Allchin, R., Kirkpatrick, J., and Kriwoken, L. (2013). On not protecting the parrot: Impact of conservation and planning legislation on an endangered species in Tasmania. *Journal of International Wildlife Law & Policy* **16**, 81–104. doi:10.1080/13880292.2013.764777

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2013). lme4: Linear mixed-effects models using Eigen and S4.R package version 1.0-4. Available at http://CRAN.R-project.org/package=lme4.

Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L., and Gaston, K. J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955–1958. doi:10.1126/science.1101617

Cockle, K. L., Bodrati, A., Lammertink, M., and Martin, K. (2015). Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest. *Biological Conservation* **184**, 193–200. doi:10.1016/j.biocon.2015.01.026

Cockle, K. L., Martin, K., and Drever, M. C. (2010). Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation* **143**, 2851–2857. doi:10.1016/j.biocon.2010.08.002

Czeszczewik, D., Walankiewicz, W., and Sta≈Ñska, M. (2008). Small mammals in nests of cavity-nesting birds: Why should ornithologists study rodents? *Canadian Journal of Zoology* **86**, 286–293. doi:10.1139/Z07-139

Davis, A., Major, R. E., and Taylor, C. E. (2013). Housing shortages in urban regions: Aggressive interactions at tree hollows in forest remnants. *Plos One* **8**, e59332. doi:10.1371/journal.pone.0059332

Gibbons, P., and Lindenmayer, D. B. (2002). 'Tree Hollows and Wildlife Conservation in Australia.' (CSIRO Publishing: Melbourne.)

Gunn, R. C. (1851). On the introduction and naturalization of *Petaurus sciureus* in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **1**, 253–255.

Heinsohn, R. (2008). The ecological basis of unusual sex roles in reverse-dichromatic eclectus parrots. *Animal Behaviour* **76**, 97–103. doi:10.1016/j.anbehav.2008.01.013

Heinsohn, R., and Legge, S. (2003). Breeding biology of the reverse-dichromatic, co-operative parrot Eclectus roratus. *Journal of Zoology* **259**, 197–208. doi:10.1017/S0952836902003138

Heinsohn, R., Webb, M. H., Lacy, R., Terauds, A., Alderman, R., and Stojanovic, D. (2015). A severe predator-induced decline predicted for endangered, migratory swift parrots (*Lathamus discolor*). *Biological Conservation* **186**, 75–82. doi:10.1016/j.biocon.2015.03.006

Higgins, P. J. Ed. (1999). 'Handbook of Australian, New Zealand and Antarctic Birds.' (Oxford University Press: Melbourne.)

Lambrechts, M. M., Marrot, P., Fargevieille, A., Giovannini, P., Lucas, A., Demeyrier, V., Midamegbe, A., Perret, P., Grégoire, A., Charmantier, A., and Doutrelant, C. (2016). Nest size is not closely related to breeding success in Blue Tits: A long-Term nest-box study in a Mediterranean oak habitat. *Auk* **133**, 198–204. doi:10.1642/AUK-15-214.1

Le Roux, D. S., Ikin, K., Lindenmayer, D. B., Bistricer, G., Manning, A. D., and Gibbons, P. (2016). Effects of entrance size, tree size and landscape context on nest box occupancy: Considerations for management and biodiversity offsets. *Forest Ecology and Management* **366**, 135–142. doi:10.1016/j.foreco.2016.02.017

Libois, E., Gimenez, O., Oro, D., Mínguez, E., Pradel, R., and Sanz-Aguilar, A. (2012). Nest boxes: A successful management tool for the conservation of an endangered seabird. *Biological Conservation* **155**, 39–43. doi:10.1016/j.biocon.2012.05.020

Lindenmayer, D., Blanchard, W., McBurney, L., Blair, D., Banks, S., Likens, G., Franklin, J., Laurance, W., Stein, J. A., and Gibbons, P. (2012). Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. *Plos One* **7**, e41864. doi:10.1371/journal.pone.0041864

Lindenmayer, D. B., Franklin, J. F., and Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biologic Cons* **131**, 433–445. doi:10.1016/j.biocon.2006.02.019

Lindenmayer, D. B., Laurance, W. F., Franklin, J. F., Likens, G. E., Banks, S. C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A. D., and Stein, J. A. R. (2013). New policies for old trees: Averting a global crisis in a keystone ecological structure. *Conservation Letters* **7**, 61–69. doi:10.1111/conl.12013

Manning, A. D., Gibbons, P., Fischer, J., Oliver, D. L., and Lindenmayer, D. B. (2013). Hollow futures? Tree decline, lag effects and hollow-dependent species. *Animal Conservation* **16**, 395–403. doi:10.1111/acv.12006

Martin, K., Aitken, K. E. H., and Wiebe, K. L. (2004). Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. *Condor* **106**, 5–19. doi:10.1650/7482

McIntyre, E., Horn, A. G., and Leonard, M. L. (2014). Do nestling Tree Swallows (Tachycineta bicolor) respond to parental alarm calls? *Auk* **131**, 314–320. doi:10.1642/AUK-13-235.1

Mitchell, L. R., Carlile, L. D., and Chandler, C. R. (1999). Effects of Southern flying squirrels on nest success of red-cockaded woodpeckers. *The Journal of Wildlife Management* **63**, 538–545. doi:10.2307/3802640

Møller, A. P., Adriaensen, F., Artemyev, A., Bańbura, J., Barba, E., Biard, C., Blondel, J., Bouslama, Z., Bouvier, J.-C., Camprodon, J., Cecere, F., Charmantier, A., Charter, M., Cichoń, M., Cusimano, C., Czeszczewik, D., Demeyrier, V., Doligez, B., Doutrelant, C., Dubiec, A., Eens, M., Eeva, T., Faivre, B., Ferns, P. N., Forsman, J. T., García-Del-Rey, E., Goldshtein, A., Goodenough, A. E., Gosler, A. G., Góźdź, I., Grégoire, A., Gustafsson, L., Hartley, I. R., Heeb, P., Hinsley, S. A., Isenmann, P., Jacob, S., Järvinen, A., Juškaitis, R., Korpimäki, E., Krams, I., Laaksonen, T., Leclercq, B., Lehikoinen, E., Loukola, O., Lundberg, A., Mainwaring, M. C., Mänd, R., Massa, B., Mazgajski, T. D., Merino, S., Mitrus, C., Mönkkönen, M., Morales-Fernaz, J., Morin, X., Nager, R. G., Nilsson, J.-Å., Nilsson, S. G., Norte, A. C., Orell, M., Perret, P., Pimentel, C. S., Pinxten, R., Priedniece, I., Quidoz, M.-C., Remeš, V., Richner, H., Robles, H., Rytkönen, S., Senar, J. C., Seppänen, J. T., Da Silva, L. P., Slagsvold, T., Solonen, T., Sorace, A., Stenning, M. J., Török, J., Tryjanowski, P., Van Noordwijk, A. J., Von Numers, M., Walankiewicz, W., and Lambrechts, M. M. (2014). Variation in clutch size in relation to nest size in birds. *Ecology and Evolution* **4**, 3583–3595. doi:10.1002/ece3.2014.4.issue-18

Moorhouse, R., Greene, T., Dilks, P., Powlesland, R., Moran, L., Taylor, G., Jones, A., Knegtmans, J., Wills, D., Pryde, M., Fraser, I., August, A., and August, C. (2003). Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: Reversing the decline of a threatened New Zealand parrot. *Biological Conservation* **110**, 33–44. doi:10.1016/S0006-3207(02)00173-8

Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation* **70**, 265–276. doi:10.1016/0006-3207(94)90172-4

Olah, G., Vigo, G., Heinsohn, R., and Brightsmith, D. J. (2014). Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaws Ara macao macao in lowland Peru. *Journal for Nature Conservation* **22**, 176–185. doi:10.1016/j.jnc.2013.11.003

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0 Available at http://www.R-project.org.

Rendell, W. B., and Robertson, R. J. (1989). Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. *The Condor* **91**, 875–885. doi:10.2307/1368072

Renton, K., Salinas-Melgoza, A., De Labra-Hernández, M. Á., and De La Parra-Martínez, S. M. (2015). Resource requirements of parrots: Nest site selectivity and dietary plasticity of Psittaciformes. *Journal of Ornithology* **156**, 73–90. doi:10.1007/s10336-015-1255-9

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G., and Fuller, R. A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment* **12**, 395–402. doi:10.1890/130237

Saunders, D.L., and Tzaros, C. (2011). National Recovery Plan For The Swift Parrot Lathamus Discolor. BirdLife Australia, Melbourne

Stojanovic, D., Koch, A. J., Webb, M., Cunningham, R. B., Roshier, D., and Heinsohn, R. (2014a). Validation of a

landscape-scale planning tool for cavity dependent wildlife. *Austral Ecology* **39**, 579–586. doi:10.1111/aec.2014.39.issue-5

Stojanovic, D., Terauds, A., Westgate, M. J., Webb, M. H., Roshier, D., and Heinsohn, R. (2015). Exploiting the richest patch has a fitness payoff for the migratory swift parrot. *Journal of Animal Ecology* **84**, 1194–1201. doi:10.1111/1365-2656.12375

Stojanovic, D., Webb, M., Alderman, R., Porfirio, L., and Heinsohn, R. (2014b). Discovery of a novel predator reveals extreme but highly variable mortality for an endangered bird. *Diversity and Distributions* **20**, 1200–1207. doi:10.1111/ddi.12214

Stojanovic, D., Webb, M. H., Roshier, D., Saunders, D., and Heinsohn, R. (2012). Ground-based survey methods both overestimate and underestimate the abundance of suitable tree-cavities for the endangered swift parrot. *Emu* **112**, 350–356. doi:10.1071/MU11076

Stojanovic, D., Webb Nee Voogdt, J., Webb, M., Cook, H., and Heinsohn, R. (2016). Loss of habitat for a secondary cavity nesting bird after wildfire. *Forest Ecology and Management* **360**, 235–241. doi:10.1016/j.foreco.2015.10.040

Szabo, J. K., Khwaja, N., Garnett, S. T., and Butchart, S. H. M. (2012). Global patterns and drivers of avian extinctions at the species and subspecies level. *Plos ONE* **7**, e47080. doi:10.1371/journal.pone.0047080

Vanderwerf, E. A. (2012). Evolution of nesting height in an endangered Hawaiian forest bird in response to a non-native predator. *Conservation Biology* **26**, 905–911. doi:10.1111/cobi.2012.26.issue-5

Venables, W., and Ripley, B. (2002). 'Modern Applied Statistics with S,' 4th edn. (Springer: New York.)

Webb, M. H., Holdsworth, M. C., and Webb, J. (2012). Nesting requirements of the endangered swift parrot (*Lathamus discolor*). *Emu* **112**, 181–188. doi:10.1071/MU11014

Webb, M. H., Terauds, A., Tulloch, A., Bell, P., Stojanovic, D., and Heinsohn, R. (2017). The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems. *Conservation Biology*. doi:10.1111/cobi.12899

Webb, M. H., Wotherspoon, S., Stojanovic, D., Heinsohn, R., Cunningham, R., Bell, P., and Terauds, A. (2014). Location matters: Using spatially explicit occupancy models to predict the distribution of the highly mobile, endangered swift parrot. *Biological Conservation* **176**, 99–108. doi:10.1016/j.biocon.2014.05.017

Wiebe, K. L., and Swift, T. L. (2001). Clutch size relative to tree cavity size in Northern Flickers. *Journal of Avian Biology* **32**, 167–173. doi:10.1034/j.1600-048X.2001.320210.x