

## The roles of predation, microclimate and cavity abundance in the evolution of New Zealand's tree-cavity nesting avifauna

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**Abstract** Tree-cavity nesting is common for a broad range of bird species throughout the world. However, the majority of information on the use of cavity nests is largely derived from the Northern Hemisphere with little data originating from tropical or southern temperate areas. We discuss 3 factors (predation, microclimate, and cavity abundance) that may have shaped the evolution of New Zealand's tree-cavity nesting birds. New Zealand's landbird fauna possesses the highest percentage (24%) of secondary tree-cavity nesters (7 orders and 12 families) of any region examined. Given the high occurrence of tree-cavity nesting in New Zealand's avifauna there may be environmental pressures that select for this form of nesting. Historically, birds were likely the main nest predators of New Zealand's cavity nesting birds and indications are that nest predation levels are not comparable to some continental habitats. This suggests that other factors such as microclimate or cavity abundance may have played a disproportionate or complementary role in influencing the high percentage of tree-cavity nesting in New Zealand. However, evidence is limited and any attempt to identify selection pressures on tree-cavity nesting must be balanced against phylogenetic concerns, as some birds were likely tree-cavity nesters before their arrival in New Zealand.

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### INTRODUCTION

Tree-cavity nesting birds (CNBs) are a ubiquitous component of the world's avifauna and over 50 years of research has been focused on disentangling the forces that shape cavity nesting behaviour in birds (von Haartman 1957; Nilsson 1984; Nilsson 1986; Newton 1994; Newton 1998). There appear to be 3 main factors implicated in the evolution of cavity nesting behaviour: predation pressure, characteristics of cavity microclimate, and the availability of cavities (Gibbons & Lindenmayer 2002). Predation is the greatest cause of nest loss in

many birds (Nilsson 1984). Most studies examining predation have found that birds choose, and are more likely successful in, the strongest/safest cavities (Nilsson 1984). The greater safety of cavity nests relative to open-cup nests is believed to arise because of their concealed or camouflaged locations and small entrance diameters that limit predator access (Alerstam & Högstedt 1981; Fisher & Wiebe 2006). The properties that contribute to a predator-resistant cavity (dense living wood with a small entrance hole) may also contribute to maintaining an optimal microclimate (through reduced convection and conduction). Species have been shown to preferentially select the most thermally advantageous cavities (Chruszcz & Barclay 2002;

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Lausen & Barclay 2003; Neubaum *et al.* 2006) and have demonstrated higher reproductive success when nesting in microclimatically higher quality cavities (Wiebe 2001). Cavity abundance may function to limit the densities of CNBs under certain instances, especially under heavy management practices, as forest age is a critical factor to plentiful cavity formation (Newton 1994).

Cavity formation is vital to nest site selection for CNBs, whether formation is through natural sources or facilitated by primary cavity nesters (PCNs). Cavity selection has historically served as a basis for dividing CNBs, as some species (e.g. woodpeckers) possess the capacity to excavate their own nest sites (PCNs), while secondary CNBs (SCNs) cannot excavate their own nest sites and depend on existing cavities. It is thought that PCNs may be somewhat less constrained in site selection because of their ability to excavate (Hooge *et al.* 1999), but the relative contribution of predation pressure, suitability of microclimate, and abundance of nest sites in shaping these constraints is unclear. Although numerous studies have examined each of these 3 factors individually, there seems to be complex trade-offs between external factors (e.g. cavity integrity and predation rate) with internal factors (e.g. microclimate) in selecting cavities (Remm *et al.* 2006). Determining how a range of factors is balanced may be critical as site selection has major consequences for overall reproductive success for a variety of cavity nesting species worldwide (Nilsson 1984; Nilsson 1986; Wesolowski & Tomialojć 2005).

Despite the cosmopolitan occurrence of CNBs, numerous regions have received little empirical study (Bai *et al.* 2003; Monterrubio-Rico & Escalante-Pliego 2006; Tomasevic & Estades 2006; Cockle *et al.* 2008). The majority of research has focused on species within North America and Eurasia with limited data coming from tropical regions or southern temperate areas (Tomasevic & Estades 2006; Boyle *et al.* 2008; Cornelius *et al.* 2008). This bias towards studies conducted in the Northern Hemisphere may be problematic given that life-history traits, such as clutch size, differ in the Southern Hemisphere (Martin 2002; Franklin & Wilson 2003).

In New Zealand, tree-cavity nesting species are unusual because they occur without major PCNs (see methods for the limited importance of kingfishers as tree cavity providers) or a major suite of climbing terrestrial nest predators (a few arboreal reptiles). Even the number of potential avian egg/nest predators (see below) is likely to be low relative to other biogeographic regions. Therefore, the historical and present forces driving behaviour of the cavity nesting community are largely unknown and many assumptions regarding cavity nesting

**Table 1.** Occurrence of cavity and obligate cavity nesting birds as a percentage of the total number of landbird species present from various regions. Derived from Monterrubio-Rico and Escalante-Pliego (2006) with adjustments made to exclude PCNs.

	Landbird species	% Cavity nesting ( <i>n</i> )	% Obligate cavity nesting ( <i>n</i> )
New Zealand	95	24 (23)	11 (10)
Australia	531	18 (94)	11 (57)
Europe	419	14 (60)	5 (22)
Mexico	657	14 (93)	9 (62)
North America	484	10 (48)	5 (24)
Southern Africa	643	9 (55)	6 (36)

can be questioned. For example, does the absence of a PCN limit the number of available tree cavities and does the lack of a major suite of native climbing terrestrial vertebrates influence the predation rate on CNBs? Given that tree cavity nesting is common (Table 1) and occurs independently in numerous families of New Zealand birds (Table 2), there may be environmental pressures within New Zealand that select for this form of nesting for some species. Therefore, our objectives are to characterize the cavity nesting community and discuss the forces that may have contributed to the evolution of tree-cavity nesting within New Zealand.

### Background and scope

The New Zealand archipelago and its approximately 600 offshore islands have remained isolated from the continental landmasses for at least 80 million years (Worthy & Holdaway 2002; Worthy *et al.* 2006). Recent human colonization in the last 800 years has resulted in the large-scale conversion of lowland forests to farming with only 22% of the original forest cover remaining and the introduction of non-native mammalian predators (Clout & Gaze 1984). At least since the Miocene, 3 species of bats were the only terrestrial mammals to occupy New Zealand prior to human settlement (Worthy *et al.* 2006). This isolation resulted in birds filling most of the niches usually occupied by terrestrial mammals (Worthy & Holdaway 2002) and the only comparable situation for a major landmass in the world is Hawaii (Loope *et al.* 1988). The landbird fauna of New Zealand is largely Australasian in origin but with a high degree of endemism (Worthy & Holdaway 2002).

For the purpose of this study, the landbird fauna of New Zealand will be considered to consist primarily of those species present and breeding during the Holocene prior to human settlement

**Table 2.** Number of species of landbird families and number (%) that are tree cavity-nesters in New Zealand.

Family	Order	No. species	No. tree cavity nesters (%)
Emeidae	Dinornithiformes	8	0 (0)
Dinornithidae	Dinornithiformes	3	0 (0)
Apterygidae	Apterygiformes	3	0 (0)
Accipitridae	Falconiformes	4	1 (25)
Phasianidae	Galliformes	1	0 (0)
Rallidae	Gruiformes	13	0 (0)
Aptornithidae	Gruiformes	2	0 (0)
Columbidae	Columbiformes	1	0 (0)
Psittacidae	Psittaciformes	7	5 (71)
Cuculidae	Cuculiformes	2	1 (50)
Strigidae	Strigiformes	2	2 (100)
Aegothelidae	Caprimulgiformes	1	0 (0)
Alcedinidae	Coraciiformes	1	1 (100)
Anatidae	Anseriformes	15	3 (20)
Scolopacidae	Charadriiformes	3	0 (0)
Acanthisittidae	Passeriformes	6	2 (33)
Hirundinidae	Passeriformes	1	0 (0)
Motacillidae	Passeriformes	1	0 (0)
Sylviidae	Passeriformes	2	0 (0)
Pachycephalidae	Passeriformes	3	1 (33)
Acanthizidae	Passeriformes	2	0 (0)
Monarchidae	Passeriformes	1	0 (0)
Eopsaltriidae	Passeriformes	3	3 (100)
Zosteropidae	Passeriformes	1	0 (0)
Meliphagidae	Passeriformes	2	1 (50)
Notiomystidae	Passeriformes	1	1 (100)
Callaeidae	Passeriformes	3	2 (66)
Paradisaeidae	Passeriformes	1	0 (0)
Corvidae	Passeriformes	2	0 (0)

(approx. 14<sup>th</sup> century). Species were considered part of the New Zealand landbird fauna that historically or presently breed on the main landmasses and major outlying islands (Kermadec Is, 30° S to Campbell I, 52° S). We considered landbirds to include those families that habitually reside in terrestrial habitats and that forage away from aquatic or marine habitats. Rails (Rallidae) and waterfowl (Anatidae) were included within the landbird fauna as they

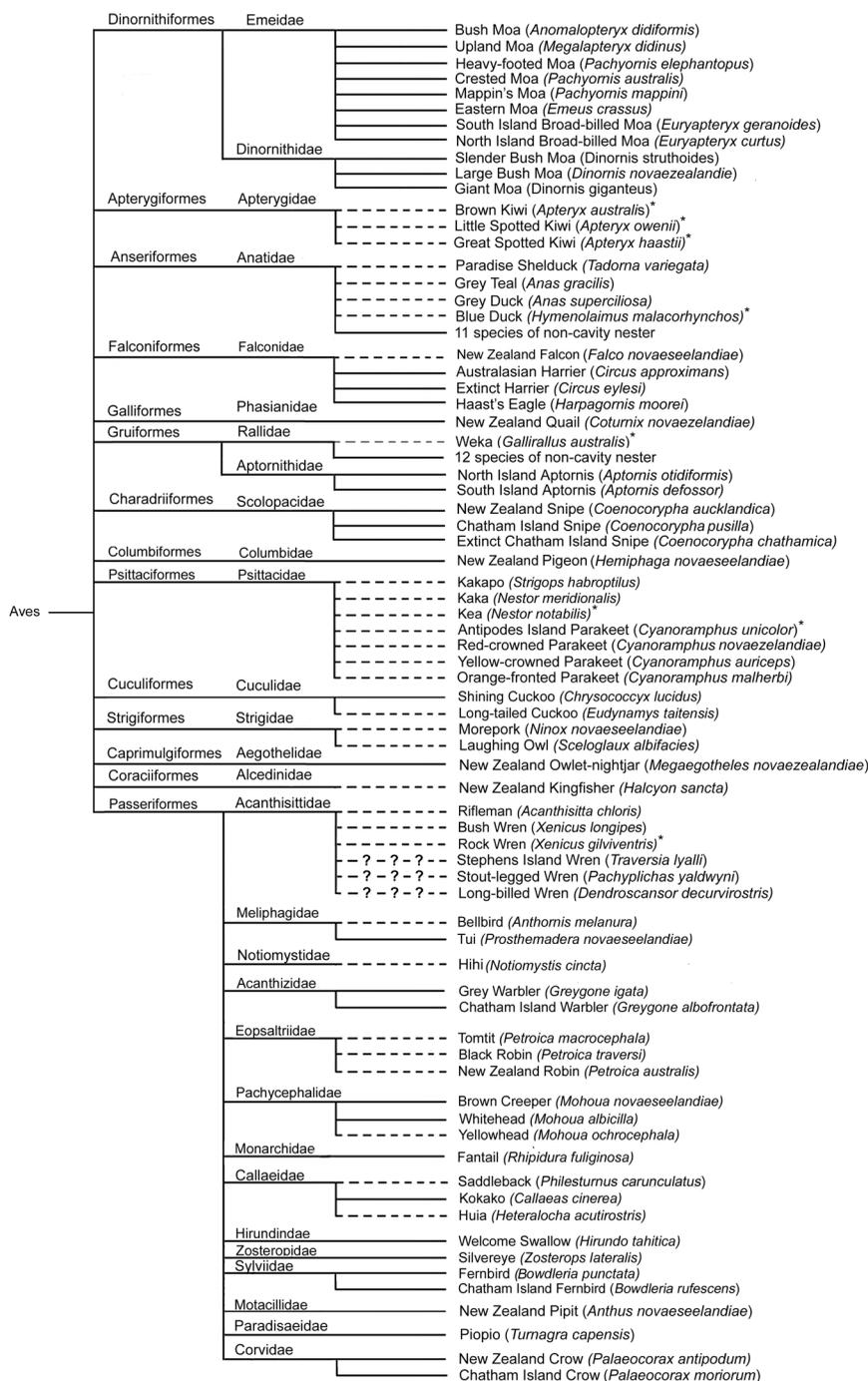
are not wholly wetland species in New Zealand and some species nest within cavities (Heather & Robertson 1996; Worthy & Holdaway 2002). Two species, the silvereye (*Zosterops lateralis*) and welcome swallow (*Hirundo tahitica*), which arrived unassisted after European settlement, were also included. We follow Robertson and Medway's (2003) use of specific nomenclature and conservation status, which maintains many species at subspecific level, with amendments based on Boon *et al.* (2001), Worthy and Holdaway (2002), and Driskell *et al.* (2007). Nesting habits of all species follow Heather and Robertson (1996), and Worthy and Holdaway (2002). However, many nesting habits could not be determined as numerous species ( $n = 35$ ) went extinct prior to or during European settlement and to be conservative, we assumed these birds were non-cavity nesters. We only examined those species that nest in tree cavities and reside in forested habitats for this study, as the literature primarily focuses on tree-cavity nesting (but see Camprodon *et al.* 2008), even though some species only nest in alternate cavity types (e.g., ground cavities; Fig. 1).

Differences among geographic regions in the proportion of species that are facultative CNBs were tested using correspondence analysis in SPSS 16.0 (SPSS Institute, Inc. 2007). Correspondence analysis is a technique to ordinate categorical attributes in a low dimensional space by converting the chi-square values for each cell to similarity measures, with positive values indicating greater association, which places these groups closer together on the perceptual map (Fig. 2).

### Characterisation of New Zealand's cavity nesters

New Zealand's landbird fauna consists of only 95 species (out of a total 240 species) that breed on the main landmasses and within the territorial oceans and possessions (Table 1). Cavity nesting is common in the landbirds (Table 1; Fig. 1) and spread among 7 orders and 12 families (Table 2). Three endemic families (Callaeidae, Acanthisittidae, Notiomystidae) also possess some members whom nest in cavities. A fourth family (Meliphagidae) is species rich (182 species worldwide); however, only 2 species are known to nest in cavities, one of which occurs in New Zealand.

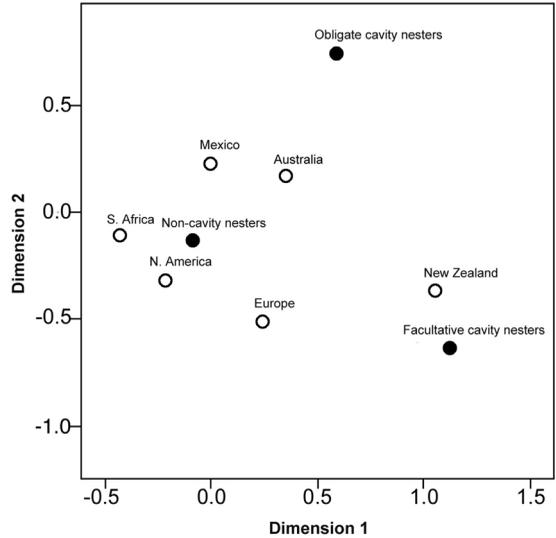
New Zealand has the highest percentage of CNBs in its landbird fauna with 23 species (24%) known to nest in tree cavities (Table 1). Of the total landbird fauna, 10 (11%) are considered obligate cavity nesters (nest in cavities nearly 100% of the time; e.g. yellowheads (*Mohua ochrocephala*)). Facultative cavity nesting (FCN) is common with 13 (14%) species of landbirds using tree cavities only a proportion of the time. Correspondence analysis clearly reveals how distinct New Zealand's landbirds are in terms of its facultative CNBs ( $\chi^2 =$



**Fig. 1.** Native landbird species in New Zealand, with nesting habits derived from Heather & Robertson (1996). Dashed lines represent species that occasionally nest in cavities; solid lines represent non-cavity nesting species or whose nesting habitats are unknown. Taxonomic names correspond to class, order, family and species; to save space numerous species of non-cavity nesting waterfowl (Anatidae) and rail (Rallidae) are not named. Lines connect taxonomic groups but do not infer phylogenetic distances. An "\*" denotes species that nest in cavities but rarely in tree-cavities and were not considered in the analysis. A "?" indicates 3 extinct species whose nesting habitats are unknown but may have been cavity nesters due to a taxonomic relationship with extant New Zealand wrens.

**Table 3.** Nest habits and substrates of *Petroica* spp. and Pachycephalidae in Australia and New Zealand. Cavity substrate indicates species nesting in tree cavities (tree), earth or rock cavities (ground), and under bark (bark). N/A are species with open-cup nests. Data from Higgins *et al.* (2006).

	Cavity nesting	Fidelity	Cavity substrate
<b><i>Petroica</i> spp.</b>			
<b>New Zealand</b>			
<i>Petroica macrocephala</i>	Yes	Facultative	Tree
<i>Petroica australis</i>	Yes	Facultative	Tree
<i>Petroica traversi</i>	Yes	Facultative	Tree, Ground
<b>Australia</b>			
<i>Petroica multicolor</i>	Yes	Facultative	Tree
<i>Petroica goodenovii</i>	No	Non-cavity	N/A
<i>Petroica phoenicea</i>	Yes	Facultative	Tree, Ground, Bark
<i>Petroica rosea</i>	No	Non-cavity	N/A
<i>Petroica rodinogaster</i>	No	Non-cavity	N/A
<b>Pachycephalidae</b>			
<b>New Zealand</b>			
<i>Mohoua albigilla</i>	No	Non-cavity	N/A
<i>Mohoua ochrocephala</i>	Yes	Obligate	Tree
<i>Mohoua novaeseelandiae</i>	No	Non-cavity	N/A
<b>Australia</b>			
<i>Falcunculus frontatus</i>	No	Non-cavity	N/A
<i>Oreoica gutturalis</i>	Yes	Facultative	Tree
<i>Pachycephala olivacea</i>	No	Non-cavity	N/A
<i>Pachycephala rufogularis</i>	No	Non-cavity	N/A
<i>Pachycephala inornata</i>	No	Non-cavity	N/A
<i>Pachycephala pectoralis</i>	No	Non-cavity	N/A
<i>Pachycephala melanura</i>	No	Non-cavity	N/A
<i>Pachycephala simplex</i>	No	Non-cavity	N/A
<i>Pachycephala rufiventris</i>	No	Non-cavity	N/A
<i>Pachycephala lanioides</i>	No	Non-cavity	N/A
<i>Colluricincla megarrhyncha</i>	Yes	Facultative	Tree
<i>Colluricincla boweri</i>	No	Non-cavity	N/A
<i>Colluricincla woodwardi</i>	Yes	Facultative	Ground
<i>Colluricincla harmonica</i>	Yes	Facultative	Tree



**Fig. 2.** Correspondence analysis using data derived from Table 1. Type of nest substrate use given by solid circles and country or region by open circles. Closeness of points indicates a nearer relationship among groups, which reveals the distinct separation of New Zealand in numbers of facultative CNBs and the proximity in the number of non-CNBs in all other sampled regions of the world.

57.4, *df* = 10, *P* < 0.001; Fig. 2). The proportion of nest types varies for FCNs in some New Zealand species, such as South I saddlebacks (*Philesturnus c. carunculatus*), which used tree cavities a majority of the time in 2 island populations (54% and 80%, respectively), while a 3rd island population depended on a non-tree substrate, flax (*Phormium cookianum*), for nesting (67%; Hooson & Jamieson 2003). Eight species of landbird typically nest in ground burrows, as they are flightless or occur in alpine habitats but were not treated as cavity nesters because they rarely nest in tree cavities (Fig. 1). The New Zealand kingfisher (*Halcyon sancta*) is the only bird species capable of excavating its own cavities (PCN), although they typically nest in earthen banks and their importance in providing cavities in forests is limited, even though they may routinely enter forested habitats (Heather & Robertson 1996).

**Phylogenetic considerations for determining nest substrate**

Understanding past evolutionary scenarios is likely to be complex, especially when attempting to understand the origin of cavity nesting in birds (Collias & Collias 1984; Brightsmith 2005a). Cavity nesting is likely to have evolved numerous times independently in the various groups of birds and cavity nesting may be ancestral in many groups of birds (von Haartman 1957; Collias & Collias 1984).

**Table 4.** Mean cavity production of New Zealand (*Nothofagus* spp.) tree species compared to selected continental tree species. Sample sizes indicate number of trees measured in each habitat with minimum entrance diameter that signified a cavity. Adapted from and see Blakely *et al.* (2008) for sources.

Species	Country	<i>n</i>	Cavities/tree	Minimum entrance (cm)
<i>Nothofagus fusca</i>	New Zealand	10	17.4	1.0
<i>Nothofagus menziesii</i>	New Zealand	10	8.1	1.0
<i>Nothofagus solandri</i>	New Zealand	10	4.9	1.0
<i>Nothofagus</i> spp.	New Zealand	78	0.7	1.7
<i>Nothofagus</i> spp.	New Zealand	120	0.3	1.7
<i>Dacrycarpus dacrydioides</i>	New Zealand	5	7.8	1.0
<i>Prumnopitys ferruginea</i>	New Zealand	5	15.2	1.0
<i>Prumnopitys taxifolia</i>	New Zealand	5	8.6	1.0
<i>Acer saccharum</i>	USA	1201	3.2	2.0
<i>Corymbia colaphylla</i>	Australia	40	1.9	2.0
<i>Eucalyptus leucoxydon</i>	Australia	40	7.8	1.0
<i>Eucalyptus marginata</i>	Australia	112	3.3	2.0
<i>Fagus grandifolia</i>	USA	1489	3.1	2.0
<i>Quercus</i> spp.	USA	2791	4.1	2.0

A single selective agent is unlikely to be responsible for cavity nesting in the great diversity of cavity nesting organisms, and phylogeny can play an important role in determining cavity nest substrate (von Haartman 1957; Gibbons & Lindenmayer 2002). For example, species that arrive in new habitats may continue to nest in cavities if the current environment does not select against the behaviour. Some groups of birds (e.g. kingfishers) possessed long evolutionary histories of cavity nesting prior to their colonization of new habitats in New Zealand. Additionally, some groups of CNBs in New Zealand (e.g. Australasian *Petroica*, yellowheads in the family Pachycephalidae) have close relatives in Australia, which also exhibit cavity nesting (Table 3), suggesting that some CNBs in New Zealand may have arrived with the cavity nesting habit previously established.

Conversely, no members of the honeyeaters (Meliphagidae) are considered to be cavity nesters in Australia. However, the bellbird (*Anthornis melanura*) of New Zealand is one of only 2 honeyeaters known to nest in cavities worldwide in this diverse species rich family, which may indicate selection towards cavity nesting in this species. Other families are endemic to New Zealand, yet many members of these are cavity nesters with no known affinities to modern CNBs in Australia (Ewen *et al.* 2006). The families Notiomystidae, Callaeidae and Acanthistidae are characterized by having many members who are

cavity nesters (Fig. 1) and have long evolutionary histories in New Zealand (Ericson *et al.* 2002; Ewen *et al.* 2006). If conditions in New Zealand select for cavity nesting, the long evolutionary histories of these species in New Zealand may be partially responsible for the high occurrence of cavity nesting observed in these families.

### The role of predation in the evolution of cavity nesting

The literature is largely silent on causal mechanisms for bird species to transition towards cavity nesting (Brightsmith 2005a). Gibbons and Lindenmayer (2002) suggest predation may have played a role in the evolution of cavity nesting in Australia. The authors demonstrated that for some mammal groups, cavity nesting is more common in open forested habitats in Australia compared to denser forests in Papua New Guinea, which suggests that selective forces may be operating to favor cavity nesting in more open forests. They propose that transitions towards more open forested habitats, which occurred in the late Miocene, may have also caused birds to seek greater safety by breeding in cavities (difficult to access by larger bodied predators), as species with exposed feeding niches (increased visibility in open forests) are more likely to be followed back to their nest by predators (but see Wesolowski 1983). However, the only evidence the author presents is that of the association

between the opening of forests in the late Miocene in Australia and the radiation of its CNBs, but the exact mechanism or mechanisms behind this radiation is unknown.

The best evidence for the role of predation in the evolution of cavity nesting comes from Brightsmith (2005a, 2005b). He found that 2 orders of ancestrally tree CNBs (Psittaciformes and Trogoniformes) likely have undergone numerous independent transitions towards cavity nesting in alternate nesting cavities (e.g. termite mounds). Alternate nest cavities were associated with increases in nestling period compared to tree-cavity nests, which suggests that non-tree cavities are safer nest sites, as lower predation rates are thought to allow the extension of offspring development (Lack 1968; Bosque & Bosque 1995; Martin 1995). Therefore, the authors suggest that predation may be linked to past cavity-nest niche shifts in these orders and those selective forces are possibly still operating as some of these species retain the ability to nest in tree cavities. Although this evidence only relates to nest site transitions within existing CNBs, the transition from open-cup nesting to cavity nesting has been documented in phylogenetic studies of the family Hirundinidae and subfamily Tityrinae (Winkler & Sheldon 1993; Barber & Rice 2007). However, the authors provided no solid evidence that predation was behind these transitions, or any other factors, such as cavity abundance or microclimate (see below). Nevertheless, numerous studies have suggested that cavity nests provide safer nesting sites from predators compared to open-cup nests (Lack 1954; Nilsson 1984; Martin & Li 1992; Wesolowski & Tomialojć 2005; Fontaine *et al.* 2007). Therefore, it is possible that predation may select for a changeover to cavity nesting, given that it has been associated with transitions between other nesting substrates but more study is needed.

Globally, there is a great diversity of predators with specialized techniques suited to defeat cavity nests (Wesolowski & Tomialojć 2005; Brightsmith 2005b; Wesolowski 2007a). However, New Zealand was inhabited by few predators (largely avian) able to routinely access arboreal cavities (Morepork *Ninox novaeseelandiae*, New Zealand falcon *Falco novaeseelandiae*, an extinct harrier *Circus eylesi*, laughing owl *Sceloglaux albifacies*, long-tailed cuckoo *Eudynamis taitensis*, New Zealand raven *Corvus antipodum*), although anecdotal evidence exists that bats and reptiles may have been nest predators (A. Cree, *pers. comm.*). If predation favours cavity nesting, then it is possible that native predators were able to replicate high predation levels observed in continental habitats, which possess a more diverse assemblage of predators. However, evidence indicates that native predators in New Zealand do not duplicate these

predation levels (Innes *et al.* 2010). In fact, Bosque and Bosque (1995) demonstrated that lengthened nesting periods in some groups of New Zealand birds were an indication of the release from high predation pressures. Therefore, the New Zealand avifauna may challenge the role of predation in the evolutionary transition from open nesting to cavity nesting, and therefore other factors associated with cavity nesting may have been involved in shaping nesting behavior. How birds balance other selective pressures within the context of a predator-proof cavity remains unresolved (Albano 1992; Fisher & Wiebe 2006).

### Microclimate of cavity nests

Factors that determine nest microclimate include wind speed, gas composition or humidity, yet temperature is likely the most critical component during reproduction (Ar & Sidis 2002). Reproduction is an energetically costly period during a bird's life due to the vulnerability of bird eggs to ambient temperatures, the high energy expenditure associated with incubation, and the costs of thermoregulation to nestlings (Webb 1987; Wachob 1996; Reid *et al.* 2000; Deeming 2002; Dawson *et al.* 2005). Thermally advantageous nest sites may be of potential importance to some bird species as they likely reduce fluctuations in ambient temperature (Rhodes *et al.* 2009), allowing the parents to devote less of their own energy to maintaining conditions for successful reproduction (Dawson *et al.* 2005).

Gibbons and Lindenmayer (2002) propose many scenarios under which the thermal advantages of cavities could have favoured the evolution of cavity nesting, including during the transition toward endothermy (e.g., hollows provide energy savings), for insulative/protective properties during communal roosting, or for protection from temperate climate conditions, although support for any of these scenarios is largely speculative. Regardless, natural selection would likely favour those individuals that could transition towards the most thermally beneficial nest sites (Tieleman *et al.* 2008). Cavities go a long way to providing these conditions due to their superior thermal properties (Wachob 1996; Wiebe 2001). Consequently, selecting a microclimatically high quality cavity may translate into reproductive benefits, as experimental evidence indicates increased internal cavity temperatures foster successful reproduction (Yom-Tov & Wright 1993; Bryan & Bryant 1999; Reid *et al.* 2000; Dawson *et al.* 2005).

With a limited number of investigations, it is not easy to make conclusions regarding the importance of microclimate for cavity nesters within New Zealand (but see Rhodes *et al.* 2009). Some areas of

New Zealand may be exposed to harsher weather conditions (cold temperatures and increased rain) compared to some continental areas (Bosque & Bosque 1995; O' Donnell 2002) and this may result in increased nestling mortality (Bosque & Bosque 1995). Cavity nesting is known to better protect some birds from extremes in weather, such as cold temperatures or abundant rainfall (Collias & Collias 1984). Open-cup nests are known to experience cooler temperatures (but see Lyon & Montgomerie 1987) compared to cavity nests, which may slow embryo growth and cause abnormal development (Webb 1987; Godard *et al.* 2007). Additionally, Godard *et al.* (2007) demonstrated that open-cup nests were more conducive to egg microbial infection than eggs contained in cavity nests, which has implications for hatchability. Therefore, the impact of microclimate may vary for differing nest types, and cavities may protect nesting birds from the deleterious effects of a poor microclimate in certain situations. However, Collias (1997) suggested that of the basic types of nests (cavity, open-cup, domed) each have distinct advantages in a diverse range of ecological situations and it is thought that open-cup nests, which can be placed in a much more variable range of locations, may have played a role in the current diversity of passerine birds.

#### Availability of nest sites for cavity nesting birds

Competition for cavities seems to be a recent phenomenon for some SCNs from an evolutionary perspective (Wesolowski 2007a; 2007b). When researchers in the past investigated questions regarding the limits on cavity nester densities, they suggested that cavity abundance was the main limiting factor for these populations (Newton 1994). This was based on the fact that most studies occurred in heavily modified forests in Europe and North America, which because of management techniques do not reach an age suitable for cavity formation (Newton 1994; Brightsmith 2005b). Similarly, provisioning nest boxes to site-limited populations within these forests raised breeding densities above non-provisioned levels, giving the appearance of site-limitation (Newton 1994). Now, it seems that under primeval or old-growth conditions in some forests, cavities are in super-abundance (Brightsmith 2005b; Aitken & Martin 2007; Wesolowski 2007a).

It is thought that abundant availability of cavities in some primeval forests may have played a role in the transition towards cavity nesting in various vertebrates by providing more opportunities for evolution to occur (Gibbons & Lindenmayer 2002). Presently, Australian forests are capable of producing abundant levels of cavities, even in the absence of PCN vertebrates, which in some habitats provide

the majority of cavities (Gibbons *et al.* 2000; Aitken & Martin 2007). However, the current prevalence of cavities may not have always been the situation in Australia, as the rain forests that once dominated the landscape may not have offered the same degree of cavity abundance as *Eucalyptus* spp. presently do. Gibbons and Lindenmayer (2002) suggested that the same expansion of *Eucalyptus* spp. forests in Australia, which possibly fostered increases in predation (see above), also provided a previously unavailable abundance of cavities suitable for exploitation. Their evidence consists of the fact that cavity nesting vertebrates underwent a radiation during this time of forest transition, which suggests that a broadly abundant array of cavities possibly was a component that facilitated the evolution of some cavity nesting species in Australia, but this evidence may be confounded by a simultaneous increase in cavity predation (see above).

The role that cavity abundance played in the evolution of cavity nesting birds in New Zealand is unknown. No evidence exists, as in Australia, of a range expansion or transition of forests more suitable to cavity formation that coincided with a radiation of cavity nesting vertebrates. Historically, no PCNs existed in New Zealand forests but some habitats, such as Australia, indicate that PCNs may not be necessary to support a cavity nesting community due to plentiful natural cavity formation (Gibbons & Lindenmayer 2002). Of the few currently studied forest habitats in New Zealand, indications are that the forests are capable of generating cavity densities above those observed in some continental habitats (Blakely & Didham 2008; Blakely *et al.* 2008). Additionally, certain tree species are more conducive to cavity formation (Table 4) and given that various *Nothofagus* spp. have historically undergone numerous range contractions and expansions, suggests that levels of cavity abundance may have fluctuated in the past (Veblen *et al.* 1996). How these fluctuations affected the abundances of cavity-nesting birds is unknown as many do not occur in *Nothofagus* spp. forests (Worthy & Holdaway 2002).

Establishing current levels of cavity formation is important, as it at least suggests that an array of non-limiting cavities could have existed. However, understanding whether cavities presently occur in overabundance above those levels able to be used by vertebrates is difficult, as the historical cavity nesting community has been modified heavily with introduced competitors and predators (Wilson 2004). Cavities may exist in current habitats that would otherwise have been filled if novel predators were not suppressing bird abundances. With our current lack of knowledge about the contemporary structure of native cavity producing forests it is difficult to make projections about past abundances

of cavities and their influences on the evolution of CNBs.

### Balancing selection pressures

A comprehensive review of the literature on the evolution and ecology of cavity nesting in birds is well beyond the scope of this article, but excellent reviews exist that can be consulted (Newton 1994; Gibbons & Lindenmayer 2002; Aitken & Martin 2007; Wesolowski 2007a). We have discussed here 3 possible factors relating to the evolution of cavity nesting. Other hypotheses exist, such as trees that facilitate their own cavity formation to collect nutrients from mammalian wastes (Gibbons & Lindenmayer 2002), although no evidence for this exists from New Zealand (few arboreal mammals), therefore this hypothesis was not treated here. There was unlikely to have been one single factor that has contributed to the evolution of cavity nesting in vertebrates throughout their history, including within New Zealand. The taxonomically/phylogenetically broad occurrence of cavity nesting in New Zealand likely requires a synthesis of previous hypotheses to attempt to explain the evolution of cavity nesting, as evidence superseding one force over the other is lacking. However, it seems that the effects of nest predation may be minimized in New Zealand, as native predators do not replicate the current levels of predation by introduced mammals (Innes *et al.* 2010). If predation were the primary evolutionary cause of cavity nesting, we would not expect to see such a large percentage of cavity nesting within the landbird fauna when historic predation levels were likely low compared to some continental habitats. While evidence suggests that predation may have been responsible for the diversification and evolution of at least some of Australia's cavity nesting fauna (which possesses an abundant and diverse assemblage of predators), evidence from New Zealand may indicate a lesser role for predation in shaping the evolution of cavity nesting, except in the context of a phylogenetic 'hold-over' from their Australian ancestors. Whether cavity abundance or microclimate played important roles in the abundance of CNBs once landbirds colonized New Zealand, principally from Australasia (Worthy & Holdaway 2002), remains to be examined.

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