Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide

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In forests worldwide, tree-cavity supply can limit populations of the 10–40% of bird and mammal species that require cavities for nesting or roosting. Conservation efforts aimed at cavity-using communities have often focused on woodpeckers because, as cavity excavators, they are presumed to control cavity supply. We show that avian excavators are the primary cavity producers in North America (77% of nesting cavities), but not elsewhere (26% in Eurasia and South America; 0% in Australasia). We studied survivorship of 2805 nest cavities and found similar persistence of cavities created by woodpeckers and those created by decay in Canada, but low persistence of woodpecker-excavated cavities in Poland and Argentina. Outside of North America, the ephemeral nature of many woodpecker cavities may render most cavity-using vertebrates critically dependent on the slow formation of cavities by damage and decay. The future of most cavity-using communities will therefore be highly dependent on changing forest policies to stem the current loss of old trees.

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The formation and persistence of tree cavities are key ecological processes that influence the abundance, diversity, and conservation of cavity-nesting and cavity-roosting vertebrates in forests and savannas worldwide (von Haartman 1957; Lindenmayer *et al.* 1990; Evelyn and Stiles 2003; Marsden and Pilgrim 2003). Because most cavity users cannot create their own cavities, their populations can be limited by the availability of existing cavities (Newton 1998). Birds that produce tree cavities ("excavators") are therefore considered a top priority for the conservation of cavity-using communities because they can directly affect the abundance and diversity of vertebrates that require but cannot create cavities ("non-excavators") (Daily *et al.* 1993; Jones *et al.* 1994; Mikusiński *et al.* 2001; Martin *et al.* 2004; Aitken and Martin 2007; Blanc and Walters 2008; Drever *et al.* 2008). However, tree cavities may also be created over many years by fungal decay and insects, as well as from mechanical damage by fire and wind (Gibbons and Lindenmayer 2002; Figure 1). Where such decay processes provide an important source of nesting cavities, conservation policies for cavity-nesting birds should explicitly address requirements for the formation of non-excavated cavities. Here, we examine the role of avian excavators versus decay processes in forming tree cavities globally and test the hypothesis that differential cavity persistence explains geographic differences in the rates at which the two types of cavities are used for nesting.

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Methods

Proportion of excavated versus non-excavated cavities used by non-excavators

We compiled data on the proportion of nests of non-excavator birds that were found in cavities created by excavators versus those formed only by damage and decay processes, by carefully reviewing all published studies of whole communities of non-excavator birds and contacting colleagues for unpublished data. We did not compare data on the proportions of available cavities between forests because very few studies have determined the suitability of non-excavated cavities. Also, definitions of what constitutes a cavity vary widely between studies, depending on the species of birds or types of decay formations present in the community.

Cavity abundance and persistence

We studied nest cavities from 1995 to 2010 in mature and logged temperate mixed forest near William's Lake, British Columbia, Canada (51°52'N, 122°21'W; n = 779 excavated and n = 39 non-excavated cavities); from 1979 to 2004 in primeval temperate mixed forest at Białowieża National Park, Poland (52°41'N, 23°52'E; n = 539 excavated and n = 1368 non-excavated cavities); and from 2004 to 2010 in primary and logged subtropical Atlantic mixed forest near San Pedro, Misiones, Argentina (26°38'S, 54°07'W; n = 34 excavated and n = 46 non-

Figure 1. *Variation in excavated and non-excavated tree cavities used for nesting. (a) Northern saw-whet owl (*Aegolius acadicus*) at nest cavity excavated by northern flicker (*Colaptes auratus*) at Riske Creek, Canada. (b) Maroon-bellied parakeet (*Pyrrhura frontalis*) at non-excavated crack cavity in the trunk of a live parana pine (*Araucaria angustifolia*), Misiones, Argentina. (c) Non-excavated bulge cavity used by collared flycatchers (*Ficedula albicollis*) in Białowieża National Park, Poland. (d) Eurasian nuthatch (*Sitta europaea*) at a non-excavated cavity with plastered-over edges in Białowieża National Park, Poland. (e) Vinaceous parrot (*Amazona vinacea*) nestling in non-excavated cavity in Misiones, Argentina. (f) Magellanic woodpecker (*Campephilus magellanicus*) nestling in excavated cavity in Patagonia, Argentina.*

excavated cavities). Avian excavators known to create tree cavities at these sites include seven woodpecker species and two passerine species (Passeriformes) in Canada (Martin *et al.* 2004); seven woodpecker species and two passerine species in Poland (Wesołowski 2007); and 10 woodpecker species and two trogon species (*Trogon* spp) in Argentina (Cockle 2010) (Table 1). (For additional details on the study areas, see: Martin *et al.* [2004]; Wesołowski [2007]; Cockle [2010].) We found cavity nests by following adult birds; listening for begging chicks; watching for birds to enter and leave cavities; and observing cavity contents using ladders, mirrors, pole-mounted video cameras, and by climbing trees. Once located, cavities were checked every year thereafter, to determine whether they were still usable; cavities were considered to be no longer usable when (1) the tree fell; (2) the branch supporting the cavity fell from the tree; (3) the cavity walls collapsed; or (4) bark grew over and closed the cavity opening.

Statistical analyses

We calculated how long the cavity was available for birds to use (cavity life span) from the year the cavity was first found to be used until the year it was no longer usable (0–23 years). Since cavities were not always found in their first year of use, our calculations of life span should be considered as minimum estimates. We used the "Survival" package (Therneau and Lumley 2009) in R version 9.2.2 (R Development Core Team 2009) to create a Cox's proportional hazard model that predicted the odds of cavity loss based on the following explanatory variables: (1) site (country), (2) formation process (excavated or non-excavated), and (3) site × formation interaction. Cox's proportional hazard method models failure rate (loss of cavity) as a log-linear function of covariates, whereby regression coefficients ß are the natural logarithm of the odds of failure. This method allowed us to include cavities that were still usable at the end of the study (right-censored data; Tabachnick and Fidell 2001; Crawley 2007). Upon finding a significant site × formation interaction, we built a separate Cox's proportional hazard model for each site, with only formation process as an explanatory variable.

Results and discussion

Excavators produced 77% of cavities used by non-excavators in North America (range: 50–99%; $n = 7$ sites), but only 25% in South America (20–30%; $n = 2$), 27% in Eurasia (10–69%; $n = 5$), and 0% in Australia and New Zealand (no excavators present; Figure 2). We found no published, community-wide studies that reported use of excavated versus non-excavated cavities by nesting birds anywhere in Africa, south and Southeast Asia, or northern South America, and we strongly encourage field studies in these regions – especially in strictly tropical forests – to determine whether the pattern holds. There are three potential reasons for the regional differences we found. Excavated cavities may be produced at higher rates, may persist longer, or may be selected preferentially by non-excavators in North America. Evidence suggests that excavated cavities may be avoided by non-excavators in some parts of Europe (Remm *et al.* 2006; Wesołowski 2007; but see Robles *et al.* 2011) but neither avoided nor selected in North or South America (Aitken and Martin 2007; Cockle *et al.* 2011). Cavity production rates could differ between regions because of biogeographical differences in excavator species abundance, richness, or behavior, or in tree species traits. Cavity persistence rates could differ between regions because of differences in cavity attributes, tree species, climate, fungal colonization, and other decay processes. There are no clear biogeographical differences in the species pool of excavators that would explain the greater use of excavated cavities by birds in North America (excepting continents that lack excavators; Table 2; Figure 2).

To evaluate the cavity persistence hypothesis, we compared persistence rates for excavated and decay-formed cavities in Canada, Poland, and Argentina. The global model predicting cavity loss showed a significant interaction between site and cavity type ($b_{\text{excavated*Canada}} = -2.83$, standard error [SE] = 0.57, $P < 0.0001$; $b_{\text{excavated*Poland}} = -1.95$, SE = 0.50, $P < 0.0001$). The yearly odds of loss were similar for both cavity types in Canada ($b_{\text{excavated}} = -0.143$, SE = 0.28, $P = 0.60$, Akaike's information criterion $[\text{AIC}]_{\text{model}} > \text{AIC}_{\text{null}}$), but much higher for excavated than for decay-formed cavities in Poland (2.1 times higher, 95% confidence interval [CI]: 1.8–2.4; $b_{\text{excavated}} = 0.75$, SE = 0.070, $P < 0.0001$) and Argentina (12.7 times higher, 95% CI: 4.7–34.0; $b_{\text{excavated}} = 2.54$, SE = 0.50, $P < 0.0001$; Table 2; Figure 2). Excavators in Canada created about 55% of their cavities in living trees (almost all in tree stems) that remained intact and available to other species for more than a decade (Martin *et al.*

Table 1. Species of birds known to excavate cavities at study sites in Canada, Poland, and Argentina

Canada	*Poland*	*Argentina*
Woodpeckers		
Red-naped sapsucker (*Sphyrapicus nuchalis*)	Grey-headed woodpecker (*Picus canus*)	Ochre-collared piculet (*Picumnus temminckii*)
Downy woodpecker (*Picoides pubescens*)	Black woodpecker (*Dryocopus martius*)	White woodpecker (*Melanerpes candidus*)
Hairy woodpecker (*Picoides villosus*)	Great spotted woodpecker (*Dendrocopos major*)	Yellow-fronted woodpecker (*Melanerpes flavifrons*)
American three-toed woodpecker (*Picoides dorsalis*)	Middle spotted woodpecker (*Dendrocopos medius*)	White-spotted woodpecker (*Veniliornis spilogaster*)
Black-backed woodpecker (*Picoides arcticus*)	White-backed woodpecker (*Dendrocopos leucotos*)	White-browed woodpecker (*Piculus aurulentus*)
Northern flicker (*Colaptes auratus*)	Lesser spotted woodpecker (*Dendrocopos minor*)	Green-barred woodpecker (*Colaptes melanochloros*)
Pileated woodpecker (*Dryocopus pileatus*)	Three-toed woodpecker (*Picoides tridactylus*)	Campo flicker (*Colaptes campestris*)
		Helmeted woodpecker (*Dryocopus galeatus*)
		Lineated woodpecker (*Dryocopus lineatus*)
		Robust woodpecker (*Campephilus robustus*)
Other excavators		
Black-capped chickadee (*Poecile atricapillus*)	Willow tit (*Parus montanus*)	Surucua trogon (*Trogon surrucura*)
Red-breasted nuthatch (*Sitta canadensis*)	Crested tit (*Parus cristatus*)	Black-throated trogon (*Trogon rufus*)

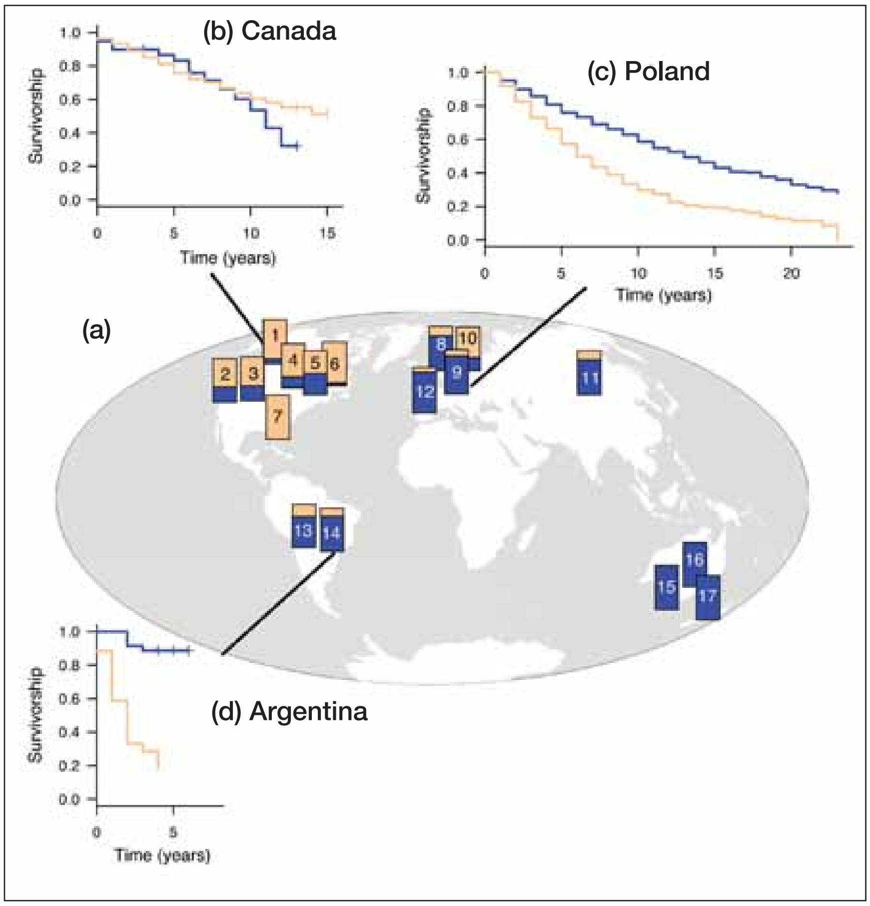

Figure 2. *(a) Proportion of non-excavator nests in excavated (orange) versus non-excavated (blue) cavities in 17 community studies around the world: (1) Aitken and Martin (2007); (2) Waters (1988); (3) Raphael and White (1984); (4) Stauffer and Best (1982); (5) Bavrlic (2008); (6) Drapeau (pers comm); (7) Blanc and Walters (2008); (8) Carlson* et al. *(1998); (9) Wesołowski (2007); (10) Remm (pers comm); (11) Bai* et al. *(2003); (12) Robles (pers comm); (13) Politi in Cornelius* et al. *(2008); (14) Cockle (2010); (15) Koch* et al. *(2008b); (16) Gibbons and Lindenmayer (2002); (17) Blakely* et al. *(2008). (b–d) Survivorship of excavated and non-excavated cavities at sites in Canada, Poland, and Argentina. Crosses on the lines indicate censoring in the data (eg cavities still standing at the end of the observation period).*

2004; Table 2; Figure 3). In contrast, excavators in Poland and Argentina primarily created cavities in dead branches or dead trees that fell or disintegrated quickly, providing only an ephemeral nesting resource for other species (Wesołowski 2007; Cockle *et al.* 2011; Table 2; Figure 3).

Although much attention has been paid to the role of woodpeckers as cavity producers, we found that outside North America most non-excavators rely on cavities formed by damage and decay, processes that act over many years to create cavities primarily in large old trees (Lindenmayer *et al.* 1993; Gibbons and Lindenmayer 2002; Cockle *et al.* 2011). In Australia, for example, eucalypts (*Eucalyptus* spp) may begin to form non-excavated cavities at around 100 years of age, but large cavities are rare in trees younger than 220 years of age (Gibbons and Lindenmayer 2002; Koch *et al.* 2008a). In North America, woodpeckers may mitigate the impacts of forest loss or disturbance by excavating suitable nesting cavities in relatively younger, deciduous trees that are less likely to be harvested (Drever and Martin 2010). Outside North America, however, there is widespread resource competition between forest industries (eg logging) and cavity-using vertebrates (Gibbons and Lindenmayer 2002; Cockle *et al.* 2010; Politi *et al.* 2010). This conflict may be especially problematic in the little-studied tropical forests that harbor most cavity-using species worldwide. Our study highlights the urgent need to stem the loss of large old trees in order to conserve the predominant global process of tree cavity formation by decay that supports the exceptionally diverse cavity-using vertebrate communities outside of North America.

In much of the world, forest policies focus on stipulating the lower diameter limits of trees that can be harvested. Such policies help protect young trees but, unfortunately, promote harvest of large old trees, the very trees needed by cavity-nesting vertebrates. Instead of, or in addition to, such policies, governments and forest certification agencies should require forestry companies to conserve a sufficient supply of old trees for wildlife, and to ensure a long-term supply of these trees through careful management of forest age and size structure. It is not sufficient to conserve trees that appear to contain cavities, because most cavities (especially non-excavated cavities) seen from the ground

Table 2. Species richness of avian excavators and non-excavators, density of cavities, and estimated median life span of cavities for excavated and non-excavated cavities at sites in Canada, Poland, and Argentina

	Species richness		*Cavity density (# ha^{-1})*		*Percent of non-excavator nests in excavated cavities*	*Cavity life span (years)*	
	Excavators	*Non-excavators*	*Excavated*	*Non-excavated*		*Excavated*	*Non-excavated*
Canada	9	22	11.2	1.1	90	14	14
Poland	9	22	5	>11	16	6	13
Argentina	12	57	0.5	4.0	20	2	25

Figure 3. *Ontogeny of cavities excavated by two congeneric woodpeckers, northern flicker (*Colaptes auratus*) in Canada (a–c) and green-barred woodpecker (*Colaptes melanochloros*) in Argentina (d–f). (a) Newly excavated cavity. (b) Cavity 2 years old and still usable. (c) Cavity at least 13 years old and still usable; occupied at least three times by northern flickers and once by red squirrels (*Tamiasciurus hudsonicus*). (d) Green-barred woodpecker at its partly excavated cavity. (e) One-year-old cavity, still usable. (f) Cavity rendered unusable because the branch fell within 6 months of excavation.*

may be unsuitable for wildlife (Cockle *et al.* 2010), and dead trees with many obvious cavities often indicate past rather than current or future resource availability (Aitken and Martin 2004). In western Canada, wildlife tree policies focus on maintaining a range of tree types rather than only on current cavity-bearing trees, and thus have good potential to support a diverse community of cavity-using wildlife in timber production areas. We encourage the adoption of similar policies, tailored to local conditions and cavity types, throughout the managed forests of the world.

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