Frontiers in Ecology and the Environment

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

Kristina L Cockle, Kathy Martin, and Tomasz Wesołowski

Front Ecol Environ **2011; doi:10.1890/110013**

This article is citable (as shown above) and is released from embargo once it is posted to the *Frontiers* e-View site (www.frontiersinecology.org).

Please note: This article was downloaded from ***Frontiers*** **e-View**, a service that publishes fully edited and formatted manuscripts before they appear in print in *Frontiers in Ecology and the Environment*. Readers are strongly advised to check the final print version in case any changes have been made.

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

Kristina L Cockle[1,2,3*], Kathy Martin[1,4], and Tomasz Wesołowski[5]

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.

Front Ecol Environ 2011; doi:10.1890/110013

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.

[1]*Center for Applied Conservation Research, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada;* [2]*Proyecto Selva de Pino Paraná, Fundación de Historia Natural Félix de Azara, Departamento de Ciencias Naturales y Antropología, Universidad Maimónides, Buenos Aires, Argentina;* [3]*CICyTTP-CONICET, Diamante, Entre Ríos, Argentina* [*]*(kristinacockle@gmail.com);* [4]*Environment Canada, Delta, British Columbia, Canada;* [5]*Department of Avian Ecology, Wrocław University, Wrocław, Poland*

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-

© The Ecological Society of America

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 plastered-over non-excavated cavity 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

 © The Ecological Society of America

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 ($b_{excavated*Canada}$ = –2.83, standard error [SE] = 0.57, P < 0.0001; $b_{excavated*Poland}$ = –1.95, SE = 0.50, P < 0.0001). The yearly odds of loss were similar for both cavity types in Canada ($b_{excavated}$ = –0.143, SE = 0.28, P = 0.60, Akaike's information criterion $[AIC]_{model} > AIC_{null}$), but much higher for excavated than for decay-formed cavities in Poland (2.1 times higher, 95% confidence interval [CI]: 1.8–2.4; $b_{excavated}$ = 0.75, SE = 0.070, P < 0.0001) and Argentina (12.7 times higher; 95% CI: 4.7–34.0; $b_{excavated}$ = 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*)

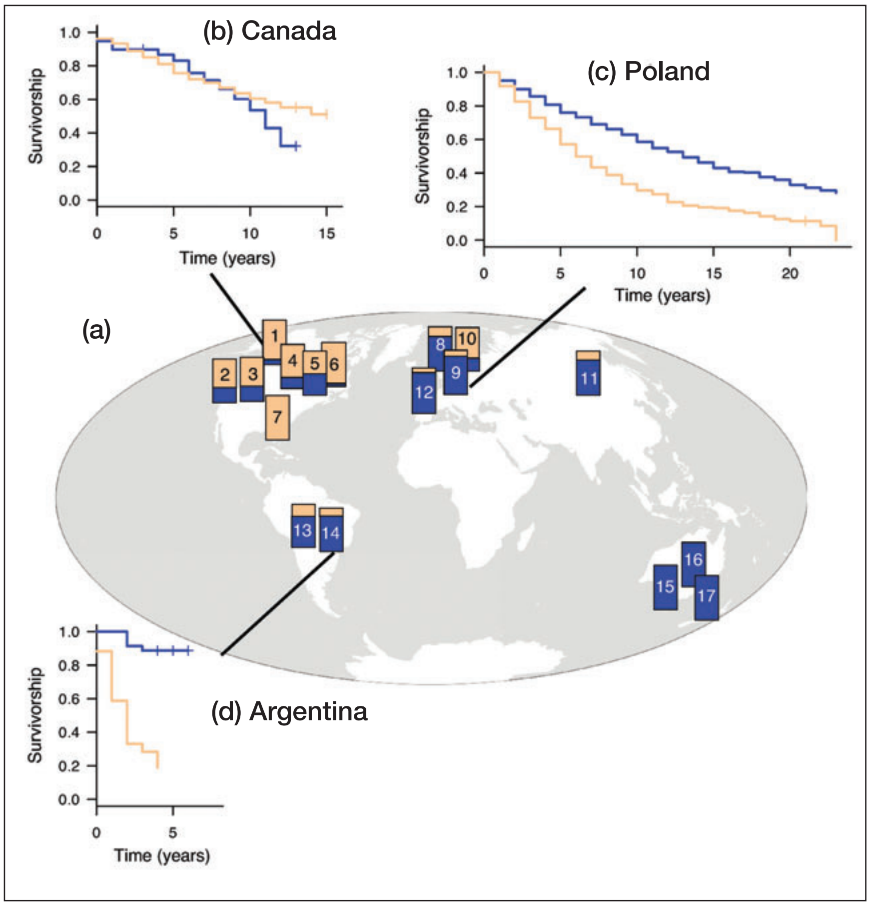

Figure 2. *(a) Proportion of non-excavator nests in excavated (orange) versus non-excavated (blue) cavities in 17 community studies around the world: (1) Aitken and Martin (2007); (2) Waters (1988); (3) Raphael and White (1984); (4) Stauffer and Best (1982); (5) Bavrlic (2008); (6) Drapeau (pers comm); (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).*

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

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

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

 © The Ecological Society of America

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) 1-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.

Acknowledgements

KLC and KM thank Natural Sciences and Engineering Research Council of Canada (Canada Graduate Scholarship and Strategic Grant), Killam Foundation, Rufford Small Grants for Nature Conservation, Lindbergh Foundation, Columbus Zoo and Aquarium, Environment Canada, British Ornithologists' Union, Aves Argentinas/BirdLife International, Cleveland Zoo, and Oregon Zoo for funding and equipment. Ministerio de Ecología and RNR (Misiones) granted permits for fieldwork in Argentina. We thank P Drapeau, J Remm, and H Robles for unpublished data, and K Wiebe, A Norris, A Bodrati, R Elner, A Edworthy, D Irwin, D Srivastava, P Marshall, S Simard, and C Krebs for helpful comments on the study.

References

Aitken KEH and Martin K. 2004. Nest cavity availability and selection in aspen–conifer groves in a grassland landscape. *Can J Forest Res* **34**: 2099–2109.

Aitken KEH and Martin K. 2007. The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western Canada. *J Ornithol* **148(S2)**: S425–34.

Bai M, Wichmann F, and Mühlenberg M. 2003. The abundance of tree holes and their utilization by hole-nesting birds in a primeval boreal forest of Mongolia. *Acta Ornithol* **38**: 95–102.

Bavrlic K. 2008. The effects of partial harvesting on cavity-nesting birds in the Carolinian forests of southwestern Ontario: habitat responses and species interactions (MSc thesis). Peterborough, Canada: Trent University.

Blakely TJ, Jellyman PG, Holdaway RJ, *et al.* 2008. The abundance, distribution and structural characteristics of tree-holes in *Nothofagus* forest, New Zealand. *Austral Ecol* **33**: 963–74.

Blanc L and Walters JR. 2008. Cavity-nest webs in a longleaf pine ecosystem. *Condor* **110**: 80–92.

Carlson A, Sandström U, and Olsson K. 1998. Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. *Ardea* **86**: 109–19.

Cockle K. 2010. Nesting ecology and community structure of cavity-nesting birds in the Neotropical Atlantic forest (PhD dissertation). Vancouver, Canada: University of British Columbia.

Cockle KL, Martin K, and Drever MC. 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biol Conserv* **143**: 2851–57.

Cockle K, Martin K, and Wiebe K. 2011. Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. *Biotropica* **43**: 228–36.

Cornelius C, Cockle K, Politi N, *et al.* 2008. Cavity-nesting birds in Neotropical forests: cavities as a potentially limiting resource. *Ornitol Neotrop* **19(S)**: 253–68.

Crawley MJ. 2007. The R book. Chichester, UK: John Wiley and Sons.

Daily GC, Ehrlich PR, and Haddad NM. 1993. Double keystone bird in a keystone species complex. *P Natl Acad Sci USA* **90**: 592–94.

Drever MC, Aitken KEH, Norris AR, and Martin K. 2008. Woodpeckers as reliable indicators of bird richness, forest health and harvest. *Biol Conserv* **141**: 624–34.

Drever MC and Martin K. 2010. Response of woodpeckers to changes in forest health and harvest: implications for conservation of avian biodiversity. *Forest Ecol Manag* **259**: 958–66.

Evelyn MJ and Stiles DA. 2003. Roosting requirements of two frugivorous bats (*Sturnira lilium* and *Arbiteus intermedius*) in fragmented Neotropical forest. *Biotropica* **35**: 405–18.

Gibbons P and Lindenmayer D. 2002. Tree hollows and wildlife conservation in Australia. Collingwood, Australia: CSIRO Publishing.

Jones CG, Lawton JH, and Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–86.

Koch AJ, Munks SA, Driscoll D, and Kirkpatrick JB. 2008a. Does hollow occurrence vary with forest type? A case study in wet and dry *Eucalyptus obliqua* forest. *Forest Ecol Manag* **255**: 3938–51.

Koch AJ, Munks SA, and Woehler EJ. 2008b. Hollow-using vertebrate fauna of Tasmania: distribution, hollow requirements and conservation status. *Aust J Zool* **56**: 323–49.

Lindenmayer DB, Cunningham RB, Donnelly CF, *et al.* 1993. The abundance and development of cavities in *Eucalyptus* trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecol Manag* **60**: 77–104.

Lindenmayer DB, Cunningham RB, Tanton MT, and Smith AP. 1990. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia. II. The loss of trees with hollows and its implications for the conservation of Leadbeater's possum *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae). *Biol Conserv* **54**: 133–45.

Marsden SJ and Pilgrim JD. 2003. Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain, PNG. *Ibis* **145**: 45–53.

Martin K, Aitken KEH, and Wiebe KL. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* **106**: 5–19.

Mikusiński G, Gromadzki M, and Chylarecki P. 2001. Woodpeckers as indicators of forest bird diversity. *Conserv Biol* **15**: 208–15.

Newton I. 1998. Population limitation in birds. San Diego, CA: Academic Press.

Politi N, Hunter Jr M, and Rivera L. 2010. Availability of cavities for avian cavity nesters in selectively logged subtropical montane forests of the Andes. *Forest Ecol Manag* **260**: 893–906.

R Development Core Team. 2009. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Raphael MG and White M. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monogr* **86**: 3–66.

Remm J, Lõhmus A, and Remm K. 2006. Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? *Forest Ecol Manag* **221**: 267–77.

Robles H, Ciudad C, and Matthysen E. 2011. Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: the role of traditional management practices. *Forest Ecol Manag* **261**: 1428–35.

Stauffer DF and Best LB. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. *Wilson Bull* **94**: 329–37.

Tabachnick BG and Fidell LS. 2001. Using multivariate statistics, 4th edn. Boston, MA: Allyn & Bacon.

Therneau T and Lumley T. 2009. Survival: survival analysis, including penalized likelihood. R Package Version 2.35–4. http://cran.r-project.org/web/packages/survival/index.html. Viewed 21 Apr 2011.

von Haartman L. 1957. Adaptation in hole-nesting birds. *Evolution* **11**: 339–47.

Waters JR. 1988. Population and habitat characteristics of cavity-nesting birds in a California oak woodland (MSc thesis). Arcata, CA: Humboldt State University.

Wesołowski T. 2007. Lessons from long-term hole-nester studies in a primeval temperate forest. *J Ornithol* **148(S2)**: S395–S405.

 © The Ecological Society of America

Los pájaros carpinteros, la degradación natural de la madera, y el futuro de las comunidades de vertebrados que anidan en huecos

Kristina L Cockle, Kathy Martin, y Tomasz Wesołowski

Traducción de: Cockle, KL, K Martin, y T Wesołowski. 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and the Environment. doi: 10.1890/110013. www.frontiersinecology.org

Resumen

En los bosques del mundo, 10-40% de las especies de aves y mamíferos requieren huecos en árboles para anidar o pernoctar, y la cantidad de estas cavidades puede limitar sus poblaciones. Los esfuerzos para conservar las comunidades que usan huecos han enfocado frecuentemente en los pájaros carpinteros porque se presume que como excavadores ellos controlan la fuente de huecos. Nosotros demostramos que las aves excavadoras son los principales productores de huecos en Norteamérica (77% de los huecos usados para anidar), pero no en otros continentes (26% en Eurasia y Sudamérica; 0% en Australasia). Estudiamos la persistencia de 2805 huecos usados para anidar, y encontramos una persistencia similar entre los huecos creados por pájaros carpinteros y los creados por degradación natural en Canada, pero baja persistencia o durabilidad de los huecos excavados por carpinteros en Polonia y Argentina. El hecho de que los huecos de pájaros carpinteros sean tan efímeros fuera de Norteamérica genera que la mayoría de los vertebrados que usan huecos dependan criticamente en la lenta formación de huecos por daños y degradación. El futuro de la mayoría de las comunidades que usan huecos entonces dependerá en que cambiemos las políticas forestales para reducir la actual pérdida de árboles viejos.

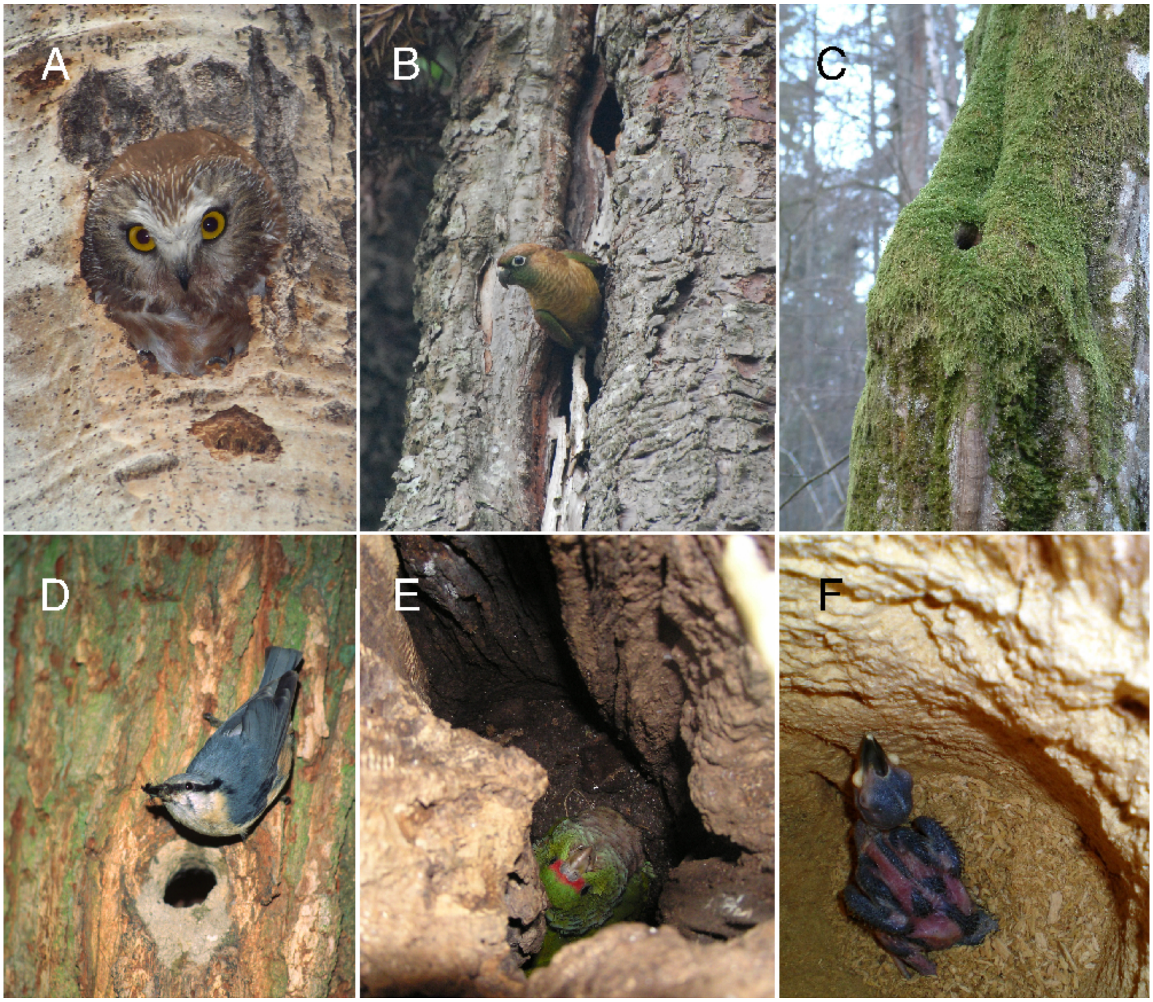

Figura 1. *Variación en los huecos excavados y no-excavados usados para nidificar. (a)* Aegolius acadicus *en un hueco excavado por* Colaptes auratus *en Riske Creek, Canadá (A Adams). (b) Piriquita (*Pyrrhura frontalis*) en una grieta en el tronco de un pino paraná (*Araucaria angustifolia*) viva, Misiones, Argentina (G Robledo). (c) Hueco no-excavado usado por* Ficedula albicollis *en Parque Nacional Bialowieza, Polonia. (d)* Sitta europea *en hueco no-excavado, con entrada reducida por material (F Fabijanski) (e) Pichón de loro vinoso (*Amazona vinacea*) en un hueco no-excavado en Misiones, Argentina (N Fariña). (f) Pichón de Carpintero Gigante (*Campephilus magellanicus*) en un hueco excavado en la Patagonia, Argentina (L Chazarreta)*

La formación y la persistencia de los huecos en árboles son procesos ecológicos claves que influyen en la abundancia, la diversidad, y la conservación de los vertebrados que anidan y pernoctan en huecos en bosques y savanas en todo el mundo (von Haartman 1957; Lindenmayer et al. 1990; Evelyn y Stiles 2003; Marsden y Pilgrim 2003). Como la mayoría de los usadores de huecos no pueden crear sus propios huecos, sus poblaciones pueden ser limitadas por la disponibilidad de huecos existentes (Newton 1998). Las aves que producen los huecos en los árboles ("excavadoras") entonces son consideradas una alta prioridad para la conservación de las comunidades que usan huecos, porque pueden afectar directamente la abundancia y diversidad de los vertebrados que requieren huecos pero que no pueden crearlos ("no excavadores") (Daily et al. 1993; Jones et al. 1994; Mikusinski et al. 2001; Martin et al. 2004; Aitken y Martin 2007; Blanc y Walters 2008; Drever et al. 2008). Sin embargo, los huecos en árboles pueden ser creados durante muchos años por la degradación de los hongos e insectos, como también por daños mecánicos de fuego y viento (Gibbons and Lindenmayer 2002; Figura 1). Donde estos procesos de degradación proveen una fuente importante de huecos para anidar, las políticas de conservación para las aves que anidan en huecos deberían apuntar explicitamente a los requisitos para la formación de huecos no-excavados. Aquí examinamos, a nivel global, el rol de las aves excavadoras vs. procesos de degradación en la formación de huecos en árboles, y testeamos la hipótesis sobre las diferencias en la persistencia entre los dos tipos de huecos que puedan explicar las diferencias geográficas en el uso de los dos tipos de huecos para anidar.

Métodos

Proporción de huecos excavados vs no-excavados, usados por las aves no excavadoras

Compilamos datos sobre la proporción de nidos de aves no excavadoras que se encontraron en huecos creados por aves excavadoras vs. aquellos formados solo por daños y degradación, revisando cuidadosamente todos los estudios publicados sobre comunidades enteras de aves no excavadoras y contactando a nuestros colegas para obtener datos no publicados. No comparamos datos sobre las proporciones de huecos disponibles entre diferentes bosques, porque muy pocos estudios han determinado la aptitud de los huecos no excavados. También, las definiciones de lo que constituye un hueco varían entre estudios, dependiendo de las especies de aves o tipos de degradación presentes en la comunidad.

Abundancia y persistencia de huecos

Estudiamos huecos usados para anidar entre 1995 y 2010 en bosque templado mixto maduro y sujeto a tala, cerca de William's Lake, British Columbia, Canadá (51˚52'N, 122˚21'W; *n* = 779 huecos excavados y *n* = 39 huecos no-excavados); de 1979 a 2004 en bosque mixto templado primario en Parque Nacional Białowieża, Polonia (52˚41'N, 23˚52'E; *n* = 539 huecos excavados y *n* = 1368 huecos no-excavados); y de 2004 a 2010 en bosque Atlántico mixto subtropical primario y sujeto a tala, cerca de San Pedro, Misiones, Argentina (26˚38'S, 54˚07'W; *n* = 34 huecos excavados y *n* = 46 huecos no-excavados). Las aves conocidas como excavadoras de huecos en estos sitios incluyen siete especies de pájaros carpinteros y dos especies de passeriformes en Canadá (Martin et al. 2004); siete especies de pájaros carpinteros y dos especies de passeriformes en Polonia (Wesołowski 2007); y 10 especies de pájaros carpinteros y dos especies de trogones (*Trogon* spp) en Argentina (Cockle 2010) (Tabla 1). (Para más detalles sobre las áreas de estudio, ver: Martin et al. [2004]; Wesołowski [2007]; Cockle [2010].) Para encontrar nidos en huecos, seguimos a las aves adultas; escuchamos pichones pidiendo alimento; buscamos aves entrando o saliendo de los huecos; y observamos el contenido de los huecos usando escaleras, espejos, cámaras de video montado en postes, y trepando los árboles. Una vez localizados, los huecos fueron revisados cada año para determinar si aún las aves los podrían usar; consideramos que el hueco ya no era útil cuando (1) el árbol se había caido; (2) la rama que tenía el hueco se había caido del árbol, (3) las paredes del hueco habían colapsado, (4) la corteza había crecido y cerrado la entrada del hueco.

Table 1. Especies de aves conocidas como excavadoras en los sitios de estudio en Canadá, Polonia, y Argentina

Canadá	***Polonia***	***Argentina***
Woodpeckers		
Sphyrapicus nuchalis	*Picus canus*	*Picumnus temminckii*
Picoides pubescens	*Dryocopus martius*	*Melanerpes candidus*
Picoides villosus	*Dendrocopos major*	*Melanerpes flavifrons*
Picoides dorsalis	*Dendrocopos medius*	*Veniliornis spilogaster*
Picoides arcticus	*Dendrocopos leucotos*	*Piculus aurulentus*
Colaptes auratus	*Dendrocopos minor*	*Colaptes melanochloros*
Dryocopus pileatus	*Picoides tridactylus*	*Colaptes campestris*
		Dryocopus galeatus
		Dryocopus lineatus
		Campephilus robustus
Otras excavadoras		
Poecile atricapillus	*Parus montanus*	*Trogon surrucura*
Sitta canadensis	*Parus cristatus*	*Trogon rufus*

Análisis estadísticos

Calculamos cuánto tiempo el hueco estuvo disponible para la utilizacion de las aves (vida útil del hueco), desde el año en que encontramos el hueco hasta el año en que ya no era útil (0-23 años). Como no siempre encontramos los huecos en su primer año de uso, nuestros cálculos de la vida útil del hueco deberían considerarse estimaciones mínimas. Usamos el paquete "Survival" (Therneau y Lumley 2009) en R versión 9.2.2 (R Development Core Team 2009) para crear un modelo Cox's Proportional Hazard que predice los odds de pérdida del hueco basado en las siguientes variables explicatorias: (1) sitio (país), (2) proceso que formó el hueco (excavado o no excavado), y (3) interacción entre sitio y proceso que formó el hueco. El método de Cox's Proportional Hazard modela la probabilidad de fracaso (pérdida del hueco) como una función log-lineal de los co-variables, en donde los coeficientes de la regresión ß son el logaritmo natural de los odds de fracaso. Este método nos permitió incluir los huecos que aún eran útiles al final del estudio (Tabachnick y Fidell 2001; Crawley 2007). Encontramos una interacción significativa entre sitio y proceso de formación, entonces luego construimos un modelo diferente para cada sitio, con el proceso de formación como la única variable explicatoria.

Resultados y discusión

Los excavadores produjeron el 77% de los huecos usados por aves no excavadoras en Norteamérica (rango: 50-99%; *n* = 7 sitios), pero solo el 25% en Sudamérica (20-30%; *n* = 2), 27% en Eurasia (10-69%; *n* = 5) y 0% en Australia y Nueva Zelanda (donde no hay aves excavadoras; Figura 2). No encontramos ningún estudio publicado de una

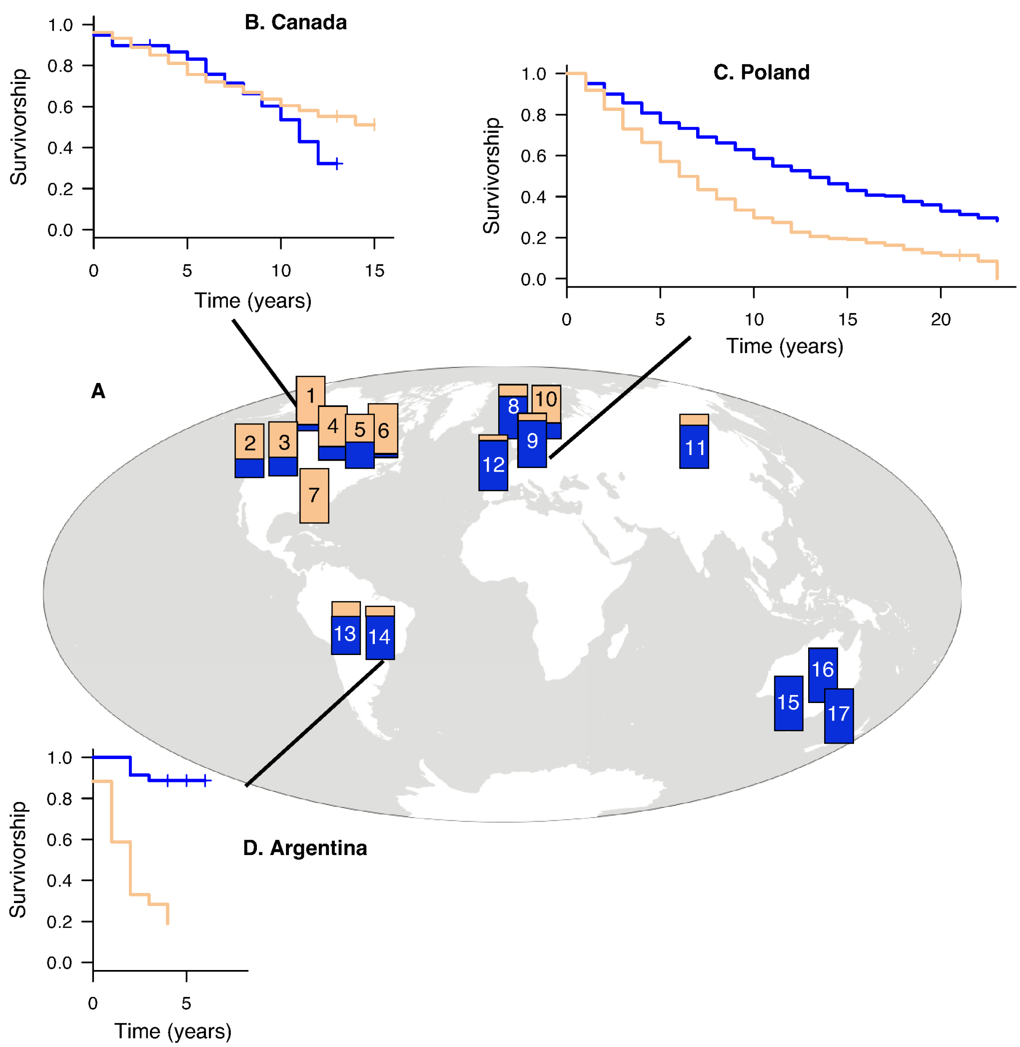

Figura 2. *(a) Proporción de nidos de aves en huecos excavados (naranja) vs. no-excavados (azul) en 17 estudios de comunidades alrededor del mundo: (1) Aitken y Martin (2007); (2) Waters (1988); (3) Raphael y White (1984); (4) Stauffer y Best (1982); (5) Bavrlic (2008); (6) Drapeau (pers comm); (7) Blanc y Walters (2008); (8) Carlson et al. (1998); (9) Wesolowski (2007); (10) Remm (pers comm); (11) Bai et al. (2003); (12) Robles (pers comm); (13) Politi en Cornelius et al. (2008); (14) Cockle (2010); (15) Koch et al. (2008b); (16) Gibbons y Lindenmayer (2002); (17) Blakely et al. (2008). (b-d) Supervivencia de huecos excavados y no-excavados en sitios de Canadá, Polonia y Argentina. Cruzes en las lineas indican censoreo en los datos (ej huecos que aún eran útiles al final del período de obervación).*

comunidad entera que reportó el uso de las aves de huecos excavados vs no excavados en ningún lugar de África, sur o sudeste de Asia, o norte de Sudamérica, entonces recomendamos estudios de campo en estas regiones – especialmente en bosques estrictamente tropicales – para determinar si el patrón que encontramos es robusto. Hay tres razones potenciales que explicarían las diferencias regionales que encontramos. Es posible que en Norteamérica haya mayor producción de huecos excavados, que estos huecos sobrevivan más tiempo en el ambiente, o que sean seleccionados preferencialmente por los no excavadores. Hay evidencia que las aves no excavadoras podrían evitar los huecos excavados en algunas partes de Europa (Remm et al. 2006; Wesołowski 2007; pero ver Robles et al. 2011) pero no parecen evitarlos ni seleccionarlos en Norteamérica o Sudamérica (Aitken y Martin 2007; Cockle et al. 2011). La taza de producción de los huecos podría diferir entre regiones por diferencias biogeográficas en las características de las especies de árboles o en la abundancia, riqueza, o comportamiento de las especies de aves excavadoras. La taza de persistencia de los huecos podría diferir entre regiones por diferencias en las características de los huecos, especies de árboles, clima, colonización por parte de hongos, y otros procesos de degradación. No hay diferencias claras biogeográficas en las especies de aves excavadoras que explicarían el mayor uso de huecos excavados por las aves en Norteamérica (excepto los continentes que no tienen excavadores; Tabla 2; Figura 2).

Tabla 2. Riqueza de especies de aves excavadoras y no-excavadoras, densidad de huecos, y persistencia (tiempo de vida) mediana estimada para huecos excavados y no-excavados en sitios de Canadá, Polonia y Argentina

	Riqueza de especies		*Densidad de huecos (número por ha)*		*% de nidos de no-excavadoras en huecos excavados*	*Persistencia de huecos (años)*	
	Excavadoras	*No-excavadoras*	*Excavados*	*No-excavados*		*Excavado*	*No-excavado*
Canadá	9	22	11,2	1,1	90	14	14
Polonia	9	22	5	>11	16	6	13
Argentina	12	57	0,5	4,0	20	2	25

Para evaluar la hipótesis de la persistencia de los huecos, comparamos la taza de persistencia entre huecos excavados y huecos formados por degradación en Canadá, Polonia y Argentina. El modelo global que predecía la pérdida de los huecos mostró una interacción significativa entre el sitio y el tipo de hueco ($b_{excavado*Canada} = -2.83$, SE = 0.57, $P < 0.0001$; $b_{excavado*Polonia} = -1.95$, SE = 0.50, $P < 0.0001$). Los odds anuales de pérdida de hueco eran similares entre los dos tipos de huecos en Canadá ($b_{excavado} = -0.143$, SE = 0.28, P = 0.60, $AIC_{modelo} > AIC_{nulo}$), pero mucho mayores para los huecos excavados que para huecos formados por degradación en Polonia (2.1 veces mayores, 95% CI: 1.8-2.4; $b_{excavado} = 0.75$, SE = 0.070, $P < 0.0001$) y Argentina (12.7 veces mayores; 95% CI: 4.7-34.0; $b_{excavado} = 2.54$, SE = 0.50, $P < 0.0001$; Tabla 2; Figura 2). Las aves excavadoras en Canadá crearon aproximadamente 55% de sus huecos en árboles vivos (casi siempre en el tronco) que permanecían intactos y disponibles para otras especies durante más de una década (Martin et al. 2004; Tabla 2; Figura 3). En contraste, las excavadoras en Polonia y Argentina principalmente crearon sus huecos en ramas muertas o árboles muertos que caían o se desintegraban rápidamente, proveyendo solamente un recurso efimero para la nidificación de otras especies (Wesołowski 2007; Cockle et al. 2011; Tabla 2; Figura 3).

Figura 3. *Con el paso del tiempo, huecos excavados por dos especies de carpinteros del mismo género,* Colaptes auratus *en Canadá (a-c) y* Colaptes melanochloros *en la Argentina (d-f). (a) Hueco nuevamente excavado (A Adams). (b) Hueco de 2 años, aún útil (A Edworthy). (c) Hueco que tiene un mínimo de 13 años y aún es útil; ocupado por lo menos tres veces por* Colaptes auratus *y una vez por ardillas (*Tamiasciurus hudsonicus*) (A Edworthy). (d)* Colaptes melanochloros *en su hueco parcialmente excavado (S Vitale). (e) Hueco de un año, aún útil. (f) Hueco que dejó de ser útil porque la rama cayó dentro de los 6 meses, después de que fue excavado.*

Aunque se ha prestado mucha atención al rol de los pájaros carpinteros como productores de huecos, encontramos que fuera de Norteamérica la mayoría de los no excavadores dependen de los huecos formados por daños y degradación, procesos que actuan durante muchos años para crear huecos principalmente en árboles grandes y viejos (Lindenmayer et al. 1993; Gibbons y Lindenmayer 2002; Cockle et al. 2011). En Australia, por ejemplo, los eucaliptos (*Eucalyptus* spp) pueden empezar a formar huecos no-excavados alrededor de los 100 años de edad, pero los huecos grandes son raros en los árboles con menos de 220 años (Gibbons y Lindenmayer 2002; Koch et al. 2008a). En Norteamérica, los pájaros carpinteros podrían mitigar los impactos de la pérdida o disturbio del bosque al excavar huecos aptos para la nidificación en árboles relativamente más jóvenes, decíduos, que tienen menos probabilidad de ser cosechados (Drever y Martin 2010). Fuera de Norteamérica, sin embargo, hay mucha competencia por los recursos entre las industrias forestales (e.j., industria maderera) y los vertebrados que requieren huecos (Gibbons y Lindenmayer 2002; Cockle et al. 2010; Politi et al. 2010). Este conflicto puede ser especialmente problemático en los bosques tropicales poco estudiados que albergan la mayoría de las especies que usan huecos. Nuestro estudio destaca la necesidad urgente de detener la pérdida de árboles grandes y viejos para poder conservar los procesos de degradación que forman la mayoría de los huecos en el mundo y así mantienen comunidades excepcionalmente diversas de vertebrados.

En gran parte del mundo, las políticas forestales hacen enfoque en estipular los diámetros mínimos de los árboles que pueden ser cosechados. Estas políticas ayudan a proteger a los árboles jóvenes, pero lamentablemente promocionan la cosecha de árboles grandes viejos, exactamente los árboles indispensables para los vertebrados que anidan en huecos. En cambio de estas políticas, o en adición a ellos, los gobiernos y agencias de certificación de madera deberían requerir que las empresas madereras conserven una fuente suficiente de árboles viejos para la fauna silvestre, y que aseguren una fuente de estos árboles a largo plazo a través de un manejo cuidadoso de la estructura de edad y tamaño de árboles en el bosque. No es suficiente conservar los árboles que parecen contener huecos hoy, porque la mayoría de los huecos identificados desde el suelo (especialmente los huecos no excavados) no serían aptos para la fauna silvestre (Cockle et al. 2010), y los árboles muertos con muchos huecos obvios frecuentemente indican disponibilidad del recurso en el pasado y no en la actualidad o en el futuro (Aitken y Martin 2004). En el oeste de Canada, hay políticas que apuntan a conservar algunos árboles para la fauna silvestre, enfocando en mantener una variedad diversa de tipos de árboles y no solo árboles que contienen huecos hoy; estas políticas muestran buen potencial para mantener una comunidad diversa de animales que usan huecos, en áreas bajo explotación forestal. Recomendamos políticas similares, adaptadas a las condiciones y tipos de cavidades locales, en todos los bosques bajo manejo.

Agradecimientos

KLC y KM agradecen al Natural Sciences and Engineering Research Council of Canada (Canada Graduate Scholarship y Strategic Grant), Killam Foundation, Rufford Small Grants for Nature Conservation, Lindbergh Foundation, Columbus Zoo and Aquarium, Environment Canada, British Ornithologists' Union, Aves Argentinas/BirdLife International, Cleveland Zoo, y Oregon Zoo, por fondos y equipos. El Ministerio de Ecología y RNR (Misiones) otorgó los permisos para el trabajo de campo en la Argentina. Agradecemos a P Drapeau, J Remm, y H Robles por sus datos no publicados, y K Wiebe, A Norris, A Bodrati, R Elner, A Edworthy, D Irwin, D Srivastava, P Marshall, S Simard, y C Krebs por comentarios útiles sobre el estudio. K Cockle y A Bodrati realizaron la traducción.

Referencias

Aitken KEH and Martin K. 2004. Nest cavity availability and selection in aspen–conifer groves in a grassland landscape. *Can J Forest Res* **34**: 2099–2109.

Aitken KEH and Martin K. 2007. The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western

Canada. *J Ornithol* **148(S2)**: S425–34.
Bai M, Wichmann F, and Mühlenberg M. 2003. The abundance of tree holes and their utilization by hole-nesting birds in a primeval boreal forest of Mongolia. *Acta Ornithol* **38**: 95–102.
Bavrlic K. 2008. The effects of partial harvesting on cavity-nesting birds in the Carolinian forests of southwestern Ontario: habitat responses and species interactions (MSc thesis). Peterborough, Canada: Trent University.
Blakely TJ, Jellyman PG, Holdaway RJ, *et al*. 2008. The abundance, distribution and structural characteristics of tree-holes in *Nothofagus* forest, New Zealand. *Austral Ecol* **33**: 963–74.
Blanc L and Walters JR. 2008. Cavity-nest webs in a longleaf pine ecosystem. *Condor* **110**: 80–92.
Carlson A, Sandström U, and Olsson K. 1998. Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. *Ardea* **86**: 109–19.
Cockle K. 2010. Nesting ecology and community structure of cavity-nesting birds in the Neotropical Atlantic forest (PhD dissertation). Vancouver, Canada: University of British Columbia.
Cockle KL, Martin K, and Drever MC. 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biol Conserv* **143**: 2851–57.
Cockle K, Martin K, and Wiebe K. 2011. Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. *Biotropica* **43**: 228–36.
Cornelius C, Cockle K, Politi N, *et al*. 2008. Cavity-nesting birds in Neotropical forests: cavities as a potentially limiting resource. *Ornitol Neotrop* **19(S)**: 253–68.
Crawley MJ. 2007. The R book. Chichester, UK: John Wiley and Sons.
Daily GC, Ehrlich PR, and Haddad NM. 1993. Double keystone bird in a keystone species complex. *P Natl Acad Sci USA* **90**: 592–94.
Drever MC, Aitken KEH, Norris AR, and Martin K. 2008. Woodpeckers as reliable indicators of bird richness, forest health and harvest. *Biol Conserv* **141**: 624–34.
Drever MC and Martin K. 2010. Response of woodpeckers to changes in forest health and harvest: implications for conservation of avian biodiversity. *Forest Ecol Manag* **259**: 958–66.
Evelyn MJ and Stiles DA. 2003. Roosting requirements of two frugivorous bats (*Sturnira lilium* and *Arbiteus intermedius*) in fragmented Neotropical forest. *Biotropica* **35**: 405–18.
Gibbons P and Lindenmayer D. 2002. Tree hollows and wildlife conservation in Australia. Collingwood, Australia: CSIRO Publishing.
Jones CG, Lawton JH, and Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–86.
Koch AJ, Munks SA, Driscoll D, and Kirkpatrick JB. 2008a. Does hollow occurrence vary with forest type? A case study in wet and dry *Eucalyptus obliqua* forest. *Forest Ecol Manag* **255**: 3938–51.
Koch AJ, Munks SA, and Woehler EJ. 2008b. Hollow-using vertebrate fauna of Tasmania: distribution, hollow requirements and conservation status. *Aust J Zool* **56**: 323–49.
Lindenmayer DB, Cunningham RB, Donnelly CF, *et al*. 1993. The abundance and

development of cavities in *Eucalyptus* trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecol Manag* **60**: 77–104.

Lindenmayer DB, Cunningham RB, Tanton MT, and Smith AP. 1990. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia. II. The loss of trees with hollows and its implications for the conservation of Leadbeater's possum *Gymnobelideus leadbeateri* McCoy (Marsupialia: Petauridae). *Biol Conserv* **54**: 133–45.

Marsden SJ and Pilgrim JD. 2003. Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain, PNG. *Ibis* **145**: 45–53.

Martin K, Aitken KEH, and Wiebe KL. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* **106**: 5–19.

Mikusinski G, Gromadzki M, and Chylarecki P. 2001. Woodpeckers as indicators of forest bird diversity. *Conserv Biol* **15**: 208–15.

Newton I. 1998. Population limitation in birds. San Diego, CA: Academic Press.

Politi N, Hunter Jr M, and Rivera L. 2010. Availability of cavities for avian cavity nesters in selectively logged subtropical montane forests of the Andes. *Forest Ecol Manag* **260**: 893–906.

R Development Core Team. 2009. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Raphael MG and White M. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monogr* **86**: 3–66.

Remm J, Lõhmus A, and Remm K. 2006. Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? *Forest Ecol Manag* **221**: 267–77.

Robles H, Ciudad C, and Matthysen E. 2011. Tree-cavity occurrence, cavity occupation and reproductive performance of secondary cavity-nesting birds in oak forests: the role of traditional management practices. *Forest Ecol Manag* **261**: 1428–35.

Stauffer DF and Best LB. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. *Wilson Bull* **94**: 329–37.

Tabachnick BG and Fidell LS. 2001. Using multivariate statistics, 4th edn. Boston, MA: Allyn & Bacon.

Therneau T and Lumley T. 2009. Survival: survival analysis, including penalized likelihood. R Package Version 2.35–4. http://cran.r-project.org/web/packages/survival/index.html.Viewed 21 Apr 2011.

von Haartman L. 1957. Adaptation in hole-nesting birds. *Evolution* **11**: 339–47.

Waters JR. 1988. Population and habitat characteristics of cavitynesting birds in a California oak woodland (MSc thesis). Arcata, CA: Humboldt State University.

Wesołowski T. 2007. Lessons from long-term hole-nester studies in a primeval temperate forest. *J Ornithol* **148(S2)**: S395–S405.