

WOODPECKERS IN A CHANGING WORLD

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Attendants of the 7th international woodpecker conference during the excursion to Izki Natural Park on 25 February 2014. Photo: Jonathan Rubines .

Woodpeckers as model organisms in a changing world. Foreword to the 7th International Woodpecker Conference Proceedings

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The first international woodpecker conference took place in Uppsala, Sweden, in 1989. Since then, international meetings have regularly been organized by the Woodpecker Working Group of the German Ornithological Society (<http://www.fachgruppe-spechte.de/>). This issue of *Acta Ornithologica* contains the proceedings of the 7th International Woodpecker Conference held in Vitoria-Gasteiz, Spain, from 23 to 26 February 2014. With the title 'Woodpeckers in a Changing World', the conference aimed at bringing together researchers, conservationists, ornithologists, forest managers and woodpecker enthusiasts from across the globe to discuss threats to and opportunities for woodpeckers in the face of global environmental change. With more than one hundred delegates from 16 countries, the conference also provided an excellent international forum for discussions on how woodpecker research may improve our understanding of behaviour, ecology and conservation sciences farther away from this fascinating bird group. The scientific program consisted of 42 contributions, including 3 plenary talks, 22 other oral contributions and 17 posters. Thematically, topics ranged from behavioural ecology (9 contributions), habitat use/selection (8), population biology (7), conservation (6), community ecology (4), forest management (3), population genetics (2) to phylogenetics/phylogeography (2) and one methodological poster. The almost complete lack of foraging behaviour studies was surprising, because foraging behaviour has long been a core subject of research on woodpeckers. In turn, the absence of bioacoustic studies is in line with previous international woodpecker meetings

and clearly highlights an important knowledge gap in our understanding of woodpecker behaviour. A comparison with the 18 talks presented at the first international woodpecker conference in Uppsala, Sweden, 1989, reveals that the diversity of topics presented has increased over the 25 years. Thirty-nine % of the talks (7 of 18) at the Uppsala conference were related more or less directly to conservation of woodpeckers, the corresponding numbers for the Vitoria-Gasteiz conference being 16 % (4 of 25 talks) and 14 % (6 of 42 talks and posters combined), respectively. Community ecology (3 talks in Uppsala), population biology (3), behavioural ecology (2) and forest management (1) were represented to similar degrees in Uppsala and Vitoria-Gasteiz. Finally, and not surprisingly considering the methodological development that has occurred since 1989, the topics population genetics and phylogeny/phylogeography were not part of the oral contributions in Uppsala.

The papers in this issue are a sample of the oral and poster contributions presented at the conference and nicely reflect the diversity of topics discussed. On the basis of discussions that took place in Vitoria-Gasteiz, we introduce here the proceedings of the 7th International Woodpecker Conference and briefly examine the potential of woodpeckers as model organisms for research and conservation in a changing world.

Woodpeckers have been traditionally used as model organisms for conservation. For example, the Ivory-billed Woodpecker *Campephilus principalis* is one of the first and most relevant icons for conservation worldwide, whose probable

extinction still provokes an enormous debate among scientists and conservationists nowadays. Likewise, long-term studies on the ecology of Red-cockaded Woodpeckers *Picoides borealis* have provided not only the basis for reversing the negative trend of this endangered species, but also for guiding conservation efforts in endemic longleaf pine *Pinus palustris* forests of the south-eastern USA (Blanc & Walters 2009). In addition, woodpeckers have been used as model organisms to assess the impact of major drivers of biodiversity loss, such as habitat loss and fragmentation. To achieve this goal, numerous studies have evaluated fragmentation effects on the occurrence/abundance (Müller 1982, Pettersson 1985), demography (Mazgajski & Rejt 2006, Robles et al. 2008), or the persistence (Robles & Ciudad 2012) of woodpecker populations. Moreover, woodpeckers have been used as model organisms to assess the influence of the current climate change largely induced by humans on animal behaviour and range shifts of species (e.g., Schiegg et al. 2002, Cobben et al. 2012).

Because most woodpeckers are perfectly adapted to forest ecosystems, woodpeckers have historically caught the attention of forest ornithologists and ecologists. As primary cavity creators (i.e., ecosystem engineers), several woodpecker species provide key nest sites to secondary cavity-nesting birds in forests (e.g., Kosiński et al. 2010). Because nest site quality is a species-specific attribute, the role of woodpeckers as key ecosystem engineers will depend on the quantity and quality of cavities (i.e., nest sites) that each woodpecker species provides to secondary cavity users in a given habitat (Robles & Martin 2013, 2014), as well as on the availability of cavities provided by other agents (e.g., wind storms, rot-fungi) in relation to that of woodpecker cavities (Remm et al. 2006). However, despite extensive investigation on this topic, a proper knowledge of the role of woodpeckers as keystone suppliers of cavities deserves more research and requires experimental approaches that manipulate the access of targeted secondary cavity nesters to woodpecker cavities in a wide variety of forests and settings. Apart from the potential role of woodpeckers as key ecosystem engineers, the dependency of numerous woodpecker species on particular features such as dead/decayed wood for nesting and large trees for foraging makes woodpeckers excellent indicators of the quality particularly of managed forests in terms of structures and age (e.g., Pasinelli 2000 a,b, 2007, Zahner et al.

2012). In addition, some woodpecker species have been shown to be positively correlated with the occurrence and/or species richness of other organisms that depend on mature and old-growth forests, including birds, cryptogams and saproxylic beetles (e.g., Martikainen et al. 1998, Mikusinski et al. 2001, Drever et al. 2008, Roberge et al. 2008). Consequently, several woodpecker species are unique indicators of the ecological sustainability of forest management practices for the conservation of an important fraction of forest biodiversity.

The conference proceedings include examples that illustrate the utility of woodpeckers as model organisms to assess forest management effects on biodiversity. Lammertink (2014) provides an exciting analysis and review of the changes in the conservation status and taxonomy of the world's woodpeckers in the last 25 years. Besides reporting an increase in the number of threatened woodpecker species, Lammertink examines the threats to which woodpeckers are exposed, highlights the negative impact of deforestation and selective logging for the conservation of red-listed woodpeckers, and identifies priorities for woodpecker research and conservation worldwide. Later in this issue, Kumar et al. (2014) provide one of the first studies on the effects of forest management on woodpecker community structure in the tropics. Intensive management in sub-Himalayan dipterocarp forests appears to considerably reduce woodpecker abundances and species richness, probably due to removal of large trees and snags in this hotspot of woodpecker diversity. That intensive forest management practices might affect not only woodpecker community structure but also woodpecker reproduction is implied by Tremblay et al. (2014), who found a positive association between nestling weight gain in the Black-backed Woodpecker *Picoides arcticus* and the amount of old coniferous habitat in managed forest landscapes.

Aside from the role of woodpeckers in terms of biodiversity conservation in forests, studies on woodpeckers have helped furthering our knowledge of theories in ecological, behavioural and evolutionary sciences. For example, the long-term studies on Red-cockaded Woodpeckers and on Acorn Woodpeckers *Melanerpes formicivorus* have substantially improved our understanding of social behaviour in cooperative breeding systems (see e.g., Walters et al. 1992, Koenig et al. 2011). These long-term studies also exemplify the importance of studying species and the ecosystems they

inhabit over large temporal and spatial scales to understand the mechanisms underlying behavioural and ecological phenomena. In this issue, Koenig & Walters (2014) illustrate how the long-term study of Acorn Woodpeckers in California (i) has increased our knowledge on the evolution of cooperative breeding and delayed dispersal in birds, and (ii) can improve our general understanding of ecological and evolutionary theories.

Apart from the obvious relevancy of long-term studies, woodpecker studies that are more restricted in their duration and resources have also helped solving behavioural and ecological questions. Some examples of such studies are included in the proceedings of the conference. Jusino et al. (2014) provide a novel and non-destructive tool to accurately identify fungi species associated with cavities created by woodpeckers, which will be particularly useful in unravelling the relationships between trees, fungi and cavity-nesting birds underlying forest community structure. By examining the variation in the orientation of the entrance of woodpecker cavities in the northern hemisphere, Landler et al. (2014) found that regional climate is likely to be a selective force in shaping cavity construction. Finally, Leniowski et al. (2014) found that mates exhibit similar brightness of carotenoid-based red caps in the Middle Spotted Woodpecker *Dendrocopos medius*, and propose mutual mate choice and social competition as potential explanations for mutual carotenoid ornamentation.

Numerous institutions and persons contributed with their help and effort to the great success of the conference. We would like to thank the Provincial Council of Álava, the Hazi foundation and the Woodpecker Working Group of the German Ornithological Society for initiating and organizing the conference. In particular, we thank José María ("Chema") Fernández-García, Jonathan Rubines and their team from the local organizing committee for their fantastic efforts. We are very grateful to the EU LIFE+ project "Pro-Izki" (ref. LIFE10 NAT/ES/000572), the Provincial Council of Álava, the German Ornithological Society (DO-G), the Bundesverband Wissenschaftlicher Vogelschutz e.V. (BWV) and the Swiss Ornithological Institute Sempach for the financial support, and to Imaginería naturalista (Javier Murillo) and Gedomol for exhibiting their beautiful wooden sculptures and photos during the conference.

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Trends in threat status and priorities in conservation of the woodpeckers of the world

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Abstract. Taking the first IUCN Red List from 1988 as a starting point, I review trends in the threat status of the woodpecker species of the world, the geographical distribution of (near-) threatened woodpecker species, threat factors affecting these species, and the research output about them. Between 1988 and 2013 the number of genuinely Red Listed woodpeckers (categories Near Threatened and up) increased from 20 to 28 species and the number of species in the categories Vulnerable and up from 8 to 12. As percentage of recognised woodpecker species in the different years, the increase in Red Listed woodpecker species was even sharper. The geographical distribution of Red Listed woodpeckers stayed constant between 1988 and 2013, with over half of the species in Latin America, about one quarter in Asia, and none in Europe. A taxonomic reappraisal adopted by IUCN in 2014 raised the total number of recognised woodpecker species to 254 and of Red Listed woodpecker species to 42, of which 40% occur in Asia. Nearly all Red Listed woodpecker species on the 2013 list are threatened by deforestation. Out of 28 species, 10 are also threatened by selective logging, and these 10 are in higher threat categories. Woodpecker conservation research should focus in particular on the species sensitive to selective logging, to assess their within-habitat requirements and thresholds. The output of research on Red Listed woodpeckers in the past 25 years was heavily skewed to three North American species: Red-headed Woodpecker *Melanerpes erythrocephalus*, Red-cockaded Woodpecker *Picoides borealis* and Ivory-billed Woodpecker *Campephilus principalis*. I identify 10 priority species to focus woodpecker conservation research on, four from Latin America: Speckle-chested Piculet *Picumnus steindachneri*, Fernandina's Flicker *Colaptes fernandinae*, Black-bodied Woodpecker *Dryocopus schulzi*, Helmeted Woodpecker *Dryocopus galeatus*; and six from Asia: Okinawa Woodpecker *Dendrocopos noguchii*, Korean White-bellied Woodpecker *Dryocopus richardsi*, Great Slaty Woodpecker *Mulleripicus pulverulentus*, Red-collared Woodpecker *Picus rabieri*, Yellow-faced Flameback *Chrysocolaptes xanthocephalus* and White-rumped Woodpecker *Meiglyptes tristis*.

Key words: IUCN Red List, old-growth forest, selective logging, threat factors, conservation, woodpeckers

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INTRODUCTION

Woodpeckers are a near-cosmopolitan family of birds occurring on all continents except Australia and Antarctica. Most species in the family live in forests or woodland ecosystems but some are adapted to open areas with few or no trees. Some woodpecker species are rather flexible in their habitat requirements and can live in intensively managed forests or in tree plantations, whereas other species are closely dependent on natural or old-growth forests (Winkler & Christie 2002). When an old-growth specialist woodpecker species occurs in a restricted geographical range and there is considerable deforestation and forest

modification in its range, it is usually globally threatened, and a worrisome number of woodpecker species are now in this situation. Even so, the proportion of threatened species in the woodpecker family is relatively low, whereas it is markedly high in such bird families as pigeons or parrots (Bennett & Owens 1997). The difference in the proportion of threatened species between bird families is to a large extent related to the proportion of island endemic species in each family, which is rather low in woodpeckers. Independent from the family average of threatened species, woodpecker species that are old-growth or natural forest specialists are often among the most sensitive and visible vertebrates affected by changes

in forest ecosystems. As such, these woodpeckers make valuable indicators and umbrella species (Martikainen et al. 1998, Mikusiński et al. 2001, Kumar et al. 2011). Furthermore, as forests are the major reservoirs of biodiversity globally (Myers et al. 2000), conservation efforts for woodpecker species carry weight in biodiversity conservation beyond these single species.

A first perspective on the conservation of the woodpeckers of the world was presented by Short & Horne (1990). They discussed the taxonomy of the family, the distinction between specialised and generalised species and genera, the ecological attributes of woodpeckers including cavity excavation and foraging, woodpecker communities with high species diversity, and made recommendations for forest management supportive of the conservation of the European woodpecker diversity. They stressed that closely related woodpeckers may differ in their needs and demands on their environment. They did not identify the most threatened woodpeckers at the time or present a priority list of woodpecker species that needed research and conservation action. However around the same time, Collar & Andrew (1988) published the first Red List of threatened bird species of the world, which included 7 threatened and 10 near-threatened species of woodpeckers, partially following recommendations from Short (1982).

Taking Collar & Andrew (1988) as a starting point, I examine trends in the conservation status of the woodpecker species of the world over the past quarter century. I tally changes in the number of woodpecker species in different threat categories on iterations of the IUCN Red List during this period, and discuss the impact of taxonomic changes on recent and future lists. I examine the geographical distribution of Red Listed woodpecker species, the threat factors that affect these species, and patterns in the research effort on Red Listed woodpeckers. I identify priority species for conservation research and discuss options to increase the research output on these species.

METHODS

I reviewed woodpecker species listed on all 12 iterations of the IUCN Red List between 1988 and 2014. In Table 1 I present only the genuine category changes of Red Listed woodpecker species between years, those that reflect a change in threat situation rather than improved knowledge

of an unchanged situation, as indicated in the species accounts by BirdLife International in subsequent years. In order to be able to examine numerical trends over time, I included the status that I estimated for four newly recognised species on one to four early iterations of the list, before the recognition of these species. These species are Sulu Woodpecker *Dendrocopos ramsayi*, first recognised in 2000 and formerly considered a subspecies of Philippine Woodpecker *D. maculatus*; Choco Woodpecker *Veniliornis chocoensis*, first recognised in 1994 and formerly considered a subspecies of Red-stained Woodpecker *V. affinis*; Kaempfer's Woodpecker *Celeus obrieni*, first recognised in 2007 and formerly considered a subspecies of Rufous-headed Woodpecker *C. spectabilis*, and Andaman Woodpecker *Dryocopus hodgei*, first recognised in 1994 and formerly considered a subspecies of White-bellied Woodpecker *D. javensis*. In all four cases, the best available information indicated that the status between 1988 and the first evaluation was equal to the status at first evaluation. I treated the 2014 Red List separately as it is based on an expanded species list of del Hoyo & Collar (2014) and there is no information on past Red List status of newly recognised species, at least not in sufficient detail to estimate when in the past 26 years list category changes might have occurred. I then tallied the changes of woodpecker species in threat categories over the 26 year period, both as the number of species as well as the percentage of woodpecker species recognised by the IUCN in each list year. Following Collar (2013), the number of all recognised woodpecker species in 1988 was based on Morony et al. (1975), in 1994, 2000 and 2004 it was based on Sibley & Monroe (1990), and from 2007 onward it is based on yearly taxonomic checklists issued by BirdLife International. I define "Red Listed woodpeckers" as those that are in the categories Near-Threatened and up, and "threatened woodpeckers" as those that are in the categories Vulnerable and up. I reviewed the threat factors that affect Red Listed woodpeckers by scoring key words in the "Threats" sections in on-line species fact sheets (BirdLife International 2014b) and grouping these into broad and finer categories. I made no distinction between past or current threats but instead included all threats that affected a species during the 25 year window. I scored the number of publications on Red Listed woodpecker species by running a search for the scientific name of each species in the online Web of Science database, with "all years" and "all databases" filters. This

includes Zoological Record. The threat factor and research output analyses only include the 28 species Red Listed between 1988 and 2013, because information is too scant for species newly recognised and Red Listed in 2014. All statistical tests were performed in R (version 3.1.0, The R Foundation for Statistical Computing).

RESULTS AND DISCUSSION

Changes in woodpecker species and status on IUCN Red Lists 1988–2013

Between 1988 and 2013 eleven iterations of the IUCN Red List of birds of the world were published (Collar & Andrew 1988, Collar et al. 1994, BirdLife International 2000, 2004, 2007, 2008, 2009, 2010, 2011, 2012, 2013). During that period 35 woodpecker species were on one or more iterations of the list. There were 43 changes in the threat categories of these species. However, most of these category changes reflect improvements in the knowledge of the status of species rather than actual changes in the threat situation of species. Based on such improved knowledge, seven woodpecker species that figured in various iterations of the Red List were removed in revisions of the list: Rusty-necked Piculet *Picumnus fuscus*, Ochraceous Piculet *Picumnus limae*, Fine-barred Piculet *Picumnus subtilis*, Antillean Piculet *Nesocittes micromegas*, Ground Woodpecker *Geocolaptes olivaceus*, White-winged Woodpecker *Dendrocopos leucopterus*, and Robust Woodpecker *Campephilus robustus*.

There are 13 genuine changes in the Red List status of 28 genuinely listed woodpecker species during 1988–2013 (Table 1). Of the 13 changes, 12 involved a change to a higher threat category, and only one, the Red-cockaded Woodpecker *Picoides borealis*, showed an improvement from Vulnerable to Near-Threatened status. Of the 28 Red-Listed species, 16 remained in a constant threat category over the 25-year period, with most of these in the Near-Threatened category. One species, the Speckle-chested Piculet *Picumnus steindachneri* went through two changes, first from Near-Threatened to Vulnerable in 2000 and then from Vulnerable to Endangered in 2013. The remaining 11 species showed one category change.

The total number of woodpecker species on the Red List (categories Near-Threatened and up) steadily climbed from 20 to 28 species between 1988 and 2013 (Table 1). The number of threatened woodpeckers (categories Vulnerable and up)

climbed from 8 to 13 species between 1988 and 2012, then lowered to 12 species in 2013 with the downlisting of Red-cockaded Woodpecker. The number of woodpecker species in the highest threat categories of Endangered to Critically Endangered/Possibly Extinct stayed at a constant of 4 during 1988–2011, then climbed to 6 in 2012–2013 with the inclusion of Speckle-chested Piculet and Varzea Piculet *Picumnus varzeae*, following a model of future deforestation in the Amazonian basin by Bird et al. (2011). One species, Imperial Woodpecker *Campephilus imperialis*, is in the category Critically Endangered/Possibly Extinct as of 2012. By these measures, the number of Red Listed woodpeckers and their mean Red List status have sharply increased over the past quarter century.

Changes in woodpecker taxonomy and impact on Red List trends

The appearance of four newly split woodpecker species on the IUCN Red List between 1994 and 2007 (with asterisk in earlier years in Table 1) is representative of an increasing tendency in ornithology to elevate former subspecies (particularly allopatric and distinctive subspecies) to species level (Hazevoet 1996, Tobias et al. 2010, Gill 2014). The number of recognised species in the woodpecker family has increased from 198 species in Short (1982) to 219 species in BirdLife International (2013), and to 234 species in Gill & Donsker (2014). A large increase in recognised woodpecker species to 254 came with del Hoyo & Collar (2014), adopted by BirdLife International (2014a) (Table 2). Additional splits are recommended by Del-Rio et al. (2013) and Winkler et al. (2014). To examine trends in the number of Red Listed woodpecker species over time, one approach is to make an estimate of the Red List status of species on year iterations of the list before their elevation to species level, as I did in the previous section, so that trends can be examined among a constant suite of species. Another approach is to take the number of woodpecker species on a year iteration of the Red List and the total number of recognised woodpecker species in that year, and calculate the proportion of these numbers. Taking this approach (Table 3), the percentage of Red-Listed woodpecker species increased from 7.8% of recognised woodpecker species in 1988 to 12.8% in 2013, an increase by a factor of 1.6x. The percentage of threatened woodpecker species increased from 2.9% to 5.5%, a factor of 1.8x. These are even sharper increases than

Table 1. Red List categories of 28 woodpecker species genuinely appearing on 11 iterations of the IUCN Red List between 1988 and 2013, showing a total of 13 genuine changes. Cells are colour coded with increasing threat category. LC — Least Concern, NT — Near Threatened, VU — Vulnerable, EN — Endangered, CR — Critically Endangered, CR/PE — Critically Endangered/Possibly Extinct. * — Threat status of species estimated by the author for early years when taxa were not yet recognised as species and hence were not evaluated.

Common name	Scientific name	IUCN Red List Category (year)										
		1988	1994	2000	2004	2007	2008	2009	2010	2011	2012	2013
White-bellied Piculet	<i>Picumnus spillogaster</i>	LC	LC	LC	LC	LC	LC	LC	LC	LC	VU	VU
Guianan Piculet	<i>Picumnus minutissimus</i>	LC	LC	LC	LC	LC	LC	LC	LC	LC	NT	NT
Speckle-chested Piculet	<i>Picumnus steindachneri</i>	NT	NT	VU	VU	VU	VU	VU	VU	VU	VU	EN
Varzea Piculet	<i>Picumnus varzeae</i>	LC	LC	LC	LC	LC	LC	LC	LC	LC	EN	EN
Tawny Piculet	<i>Picumnus fulvescens</i>	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Mottled Piculet	<i>Picumnus nebulosus</i>	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Guadeloupe Woodpecker	<i>Melanerpes herminieri</i>	LC	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Krynsna Woodpecker	<i>Campethera notata</i>	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Sterling's Woodpecker	<i>Dendropicos stierlingi</i>	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Sulu Woodpecker	<i>Dendrocopos ramsayi</i>	VU*	VU*	VU	VU	VU	VU	VU	VU	VU	VU	VU
Arabian Woodpecker	<i>Dendrocopos doriae</i>	NT	NT	VU	VU	VU	VU	VU	VU	VU	VU	VU
Okinawa Woodpecker	<i>Dendrocopos noguchii</i>	CR	CR	CR	CR	CR	CR	CR	CR	CR	CR	CR
Red-cockaded Woodpecker	<i>Picoides borealis</i>	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	NT
Choco Woodpecker	<i>Veniliornis chocoensis</i>	NT*	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
White-browed Woodpecker	<i>Piculus aurulentus</i>	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Fernandina's Flicker	<i>Colaptes fernandinae</i>	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU
Kaempfer's Woodpecker	<i>Celeus obrieni</i>	EN*	EN*	EN*	EN*	EN	EN	EN	EN	EN	EN	EN
Helmeted Woodpecker	<i>Dryocopus galeatus</i>	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU	VU
Black-bodied Woodpecker	<i>Dryocopus schulzi</i>	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Andaman Woodpecker	<i>Dryocopus hodgii</i>	NT*	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Guayaquil Woodpecker	<i>Campephilus guayaquilensis</i>	LC	LC	NT	NT	NT	NT	NT	NT	NT	NT	NT
Imperial Woodpecker	<i>Campephilus imperialis</i>	CR	CR	CR	CR	CR	CR	CR	CR	CR	CR/PE	CR/PE
Ivory-billed Woodpecker	<i>Campephilus principalis</i>	CR	CR	CR	CR	CR	CR	CR	CR	CR	CR	CR
Red-collared Woodpecker	<i>Picus rabieri</i>	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT	NT
Olive-backed Woodpecker	<i>Dinopium rafflesii</i>	LC	LC	NT	NT	NT	NT	NT	NT	NT	NT	NT
Buff-necked Woodpecker	<i>Meiglyptes tukki</i>	LC	LC	NT	NT	NT	NT	NT	NT	NT	NT	NT
Great Slaty Woodpecker	<i>Mulleripicus pulverulentus</i>	LC	LC	LC	LC	LC	LC	LC	VU	VU	VU	VU

Table 2. Woodpecker species newly added to the IUCN 2014 Red List after taxonomic reappraisals by del Hoyo & Collar (2014).

Common name	Scientific name	2014 IUCN Red List category	Common name	Formerly subspecies of	Scientific name
Splendid Woodpecker	<i>Campephilus splendens</i>	NT	Crimson-bellied Woodpecker		<i>Campephilus haematogaster</i>
Javan Flameback	<i>Chrysocolaptes strictus</i>	VU	Greater Flameback		<i>Chrysocolaptes lucidus</i>
Red-headed Flameback	<i>Chrysocolaptes erythrocephalus</i>	EN	Greater Flameback		<i>Chrysocolaptes lucidus</i>
Yellow-faced Flameback	<i>Chrysocolaptes xanthocephalus</i>	EN	Greater Flameback		<i>Chrysocolaptes lucidus</i>
Spot-throated Flameback	<i>Dinopium everetti</i>	NT	Common Flameback		<i>Dinopium javanense</i>
White-rumped Woodpecker	<i>Meiglyptes tristis</i>	EN	Buff-rumped Woodpecker		<i>Meiglyptes tristis</i>
Chequer-throated Yellownappe	<i>Chrysophlegma humii</i>	NT	Chequer-throated Yellownappe		<i>Chrysophlegma mentale</i>
Javan Yellownappe	<i>Chrysophlegma mentale</i>	NT	Chequer-throated Yellownappe		<i>Chrysophlegma mentale</i>
Sumatran Woodpecker	<i>Picus dedemi</i>	NT	Grey-faced Woodpecker		<i>Picus canus</i>
Ringed Woodpecker	<i>Celeus torquatus</i>	NT	Ringed Woodpecker		<i>Celeus torquatus</i>
Atlantic Black-breasted Woodpecker	<i>Celeus tinnunculus</i>	VU	Ringed Woodpecker		<i>Celeus torquatus</i>
Northern Sooty Woodpecker	<i>Mulleripicus funebris</i>	NT	Sooty Woodpecker		<i>Mulleripicus funebris</i>
Southern Sooty Woodpecker	<i>Mulleripicus fuliginosus</i>	VU	Sooty Woodpecker		<i>Mulleripicus funebris</i>
Amami Woodpecker	<i>Dendrocopos owstoni</i>	NT	White-backed Woodpecker		<i>Dendrocopos leucotos</i>

the increases outlined in the previous section among a constant suite of species: an increase of Red Listed woodpecker species from 20 to 28 (factor 1.4x) and of threatened species from 8 to 12 (factor 1.5x). Nevertheless, the more conservative increase figures from trends in species numbers in the constant suite are arguably a fairer index of trends, because as more subspecies are lifted to species level, average global range size of species drops, hence global populations are smaller, and this increases the probability of species meeting Red List criteria. This issue is exacerbated by the taxonomic approach by del Hoyo & Collar (2014) which adds many small-range species to the list. Their splits are welcome as an improved recognition of actual biodiversity and the improved focus they provide on taxa of conservation concern. However, changes in woodpecker taxonomy do complicate assessments of status trends over time among Red Listed woodpecker species.

As part of further re-evaluations of species status of woodpecker taxa, including with molecular techniques, priority should be given to clarifying the potential species status of taxa that are threatened or probably threatened, including *Dryocopus javensis richardsi* of North Korea (Sonobe & Izawa 1987), *Piculus chrysochloros polyzonus* of coastal Atlantic Forest in southern Brazil, and *P. c. paraensis* of northeast Brazil (Del-Rio et al. 2013).

Red List trends in woodpeckers compared to other birds

Bennett & Owens (1997) reported that on the IUCN Red List of Collar et al. (1994) the woodpecker family had a lower proportion of threatened species than birds in general. The same is true for the 1988 and 2013 iterations of the Red List. In 1988, of all woodpecker species 3.4% were threatened and 8.3% were Red Listed (these numbers are as they appeared on the 1988 list and are not corrected to genuinely listed species based on later insights, thus numbers differ from those in Tables 1 and 3), compared to 11.6% threatened species and 18.7% Red Listed species among all other birds (Collar & Andrew 1988). In 2013, of all woodpecker species 5.5% were threatened and 12.8% were Red Listed, compared to 13.2% threatened species and 22.0% Red Listed species among all other birds. The number of woodpecker species of conservation concern appears to have increased faster between 1988 and 2013 than the comparable number of other birds: the number of threatened woodpecker species increased by a

Table 3. Total number of recognised woodpecker species, number of species in IUCN Red List Categories, and percentage of Red Listed woodpecker species relative to recognised species during 1988–2013. Numbers from the 2014 Red List are based the different taxonomy of del Hoyo & Collar (2014) and are added for comparison. The increase factors were calculated over the years 1988 versus 2013.

	year											increase factor
	1988	1994	2000	2004	2007	2008	2009	2010	2011	2012	2013	(2014)
Number of recognised species	204	216	216	216	218	218	218	218	218	219	219	(254)
Near-Threatened species	10	13	14	14	14	14	14	14	14	15	16	(24)
Vulnerable species	3	3	6	6	6	6	6	7	7	8	6	(9)
Endangered species	0	0	0	0	1	1	1	1	1	2	3	(6)
Critically Endangered sp.	3	3	3	3	3	3	3	3	3	2	2	(2)
Critic. End/ Possib. Ex. sp	0	0	0	0	0	0	0	0	0	1	1	(1)
Percentage (%) of												
Red Listed (NT+) species	7.8	8.8	10.6	10.6	11.0	11.0	11.0	11.5	11.5	12.8	12.8	(16.5)
Threatened (VU+) species	2.9	2.8	4.2	4.2	4.6	4.6	4.6	5.0	5.0	5.9	5.5	(7.1)
(Cri.) Endangered/PE (EN+) species	1.5	1.4	1.4	1.4	1.8	1.8	1.8	1.8	1.8	2.3	2.7	(1.2)
												1.6x
												1.8x
												1.8x

factor of 1.6x (1.1x in other birds) and Red Listed woodpecker species by 1.5x (1.1x in other birds). However the differences in these increase rates are not significant (Fisher exact test, $p = 0.73$ for threatened species and $p = 0.65$ for Red Listed species).

Threat factors affecting Red-Listed woodpecker species

Three broad categories and 10 finer categories of threats drive population declines in the 28 species of woodpecker on the 2013 IUCN Red List (Table 4). In broad categories, habitat loss is the most important threat factor, affecting all Red Listed species except one. The exception is the Imperial Woodpecker for which ca. 80% of original forest cover in its range still exists, although nearly all of that has been strongly modified by logging of large timber and extraction of dead trees for paper pulp (Lammertink et al. 1996). Habitat modification affects 18 species, and increased mortality from unnatural causes affects 4 species. Specifically, hunting affects or affected the two largest *Campephilus* woodpeckers, and predation by introduced species affects two woodpecker species that are small island endemics, Guadeloupe Woodpecker *Melanerpes herminieri* and Okinawa Woodpecker *Dendrocopos noguchii*. Also in finer categories, within habitat loss, the main factor is deforestation for large scale agriculture and urbanization, affecting 25 species. Within habitat modification, the main threat factor is selective logging, affecting 10 species. In other words, these are the species that are dependent on old-growth or near-natural forests. Given the often repeated emphasis on the importance of old-growth or near-natural forests for conservation of woodpeckers (Tanner 1942, Mikusiński & Angelstam 1998, Czeszczewik & Walankiewicz 2006, Virkkala 2006), it is surprising that only 10 out of 28 globally threatened woodpeckers depend on such habitats. Nevertheless, the 10 Red Listed woodpeckers that are affected by selective logging are on average in higher threat categories than the 18 that are not (Wilcoxon $W = 46$, $p = 0.02$), underlining the importance of conservation of old-growth and natural forest for the most threatened woodpeckers. The higher threat categories of old-growth dependent woodpecker species can be explained in part by the scarcity of such habitats world-wide (FAO 2010, Lindenmayer et al. 2014), and in part by these species being negatively affected both by deforestation as well as by habitat modification

Table 4. Threat factors affecting 28 woodpecker species on the 2013 IUCN Red List. Source: BirdLife International (2014b) species fact sheets.

Threat factor	N species affected by factor	Species
Habitat loss	27	all species except <i>Campephilus imperialis</i>
Deforestation, for industrial agriculture and urbanisation	25	
Deforestation, small holder forest clearance	15	
Artificial lakes	3	<i>Picumnus varzeae</i> , <i>P. nebulosus</i> , <i>Ceuleus obrieni</i>
Habitat modification	18	
Selective logging	10	
Grazing	4	
Forest fire damage	4	
Suppression of forest fire	1	<i>Picoides borealis</i>
Destruction of nest trees by parrot trappers	1	<i>Colaptes fernandinae</i>
Increased mortality	4	
Hunting	2	<i>Campephilus imperialis</i> , <i>C. principalis</i>
Predation by exotic species	2	<i>Melanerpes herminieri</i> , <i>Dendrocopos noguchii</i>

through selective logging in the remaining forests; that is, nearly everywhere in their global ranges. The 10 Red Listed woodpecker species that are affected by selective logging are: Speckle-chested Piculet, Okinawa Woodpecker, Red-cockaded Woodpecker, Fernandina's Flicker, Helmeted Woodpecker, Black-bodied Woodpecker, Imperial Woodpecker, Ivory-billed Woodpecker, Red-collared Woodpecker, and Great Slaty Woodpecker (BirdLife International 2014b).

Geographical distribution of Red Listed woodpeckers

In 2013, Red Listed woodpecker species were distributed as follows over the world: Latin America and Caribbean 57%, Asia 21%, North America 11%, Africa 11%, Europe 0% (Table 5). This is not different from the distribution of all woodpecker species in 2013, nor from the distribution of Red Listed woodpeckers in 1988 (Fisher exact test, $n = 21$, $p = 1$ and $p = 0.93$, respectively). Both in 1988 and 2013, Latin America had the largest number of Red Listed woodpecker species followed by Asia. In both years, in Latin American the percentage of Red Listed species was higher than the percentage of all woodpecker species, whereas in Asia the percentage of Red Listed species was below the percentage of all woodpecker species. After the reappraisals in 2014 of woodpecker taxonomy and Red List status of woodpeckers, 11 Asian woodpecker species were added to the Red List (Table 2). In 2014, Latin America remains ahead over Asia in overall woodpecker species richness (45% versus 29%) as well as in Red Listed woodpeckers (47% versus 40%). However, in 2014 for the first time, the percentage of Red Listed woodpeckers in Asia (40%) is higher than would be expected based on its overall woodpecker species richness (29%), whereas Latin America now has a percentage of Red Listed woodpeckers (47%) similar to its overall woodpecker richness (45%). The relatively high number of threatened woodpecker species in Asia in 2014 reflects both high deforestation rates in Asia (Hansen et al. 2013) as well as an under-recognition of woodpecker species richness in Asia in previous decades.

The number and percentage of threatened woodpecker species in Africa have been consistently modest between 1988 and 2013 and the percentage is even lower in 2014 (Table 5). The low woodpecker species richness and a low number of sympatric woodpecker species anywhere on the continent could mean less niche stacking among

Table 5. Geographical distribution of all recognised woodpecker species and of Red Listed (RL) woodpecker species in 1988, 2013 and 2014. The 2014 numbers are based on the new taxonomy of del Hoyo & Collar (2014).

	1988				2013				2014			
	All species		RL species		All species		RL species		All species		RL species	
	N	%	N	%	N	%	N	%	N	%	N	%
Latin America	100	46	11	52	114	47	16	57	126	45	20	47
Asia	59	27	4	19	66	27	6	21	81	29	17	40
North America	22	10	3	14	23	10	3	11	24	9	3	7
Africa	28	13	3	14	28	12	3	11	35	13	3	7
Europe	10	5	0	0	10	4	0	0	11	4	0	0

the species and hence more flexibility to forest disturbance. Furthermore, most of Africa's woodpeckers are medium sized; there are few small species and no large species, whereas small and large species are more frequent than expected among Red Listed woodpecker species (Mikusiński 2006). Finally, the rate and extent of deforestation in Africa is lower than that in Latin America and Asia (Hansen et al. 2013).

Europe has no globally threatened woodpecker species: despite population declines and local extinctions of several species in western and northern Europe these same species have large or stable populations in eastern Europe and/or in parts of Eurasia (Mikusiński & Angelstam 1998). The Middle Spotted Woodpecker *Dendrocopos medius*, a European near-endemic and mature forest specialist, may have gone through a rapid global decline in the decades before the first Red List evaluation in 1988, but currently it has a stable or increasing global population (BirdLife International 2014b).

Research output on Red Listed woodpecker species

Although there has been a considerable output of 693 papers on 28 Red Listed woodpeckers between 1988 and 2013, this production is heavily skewed towards three North American species that account for 86% of these papers, with Red-cockaded Woodpecker alone accounting for 435 papers (Table 6). Outside of North America, Kaempfer's Woodpecker was most intensively published about with 14 papers. Seventeen species had between one and ten papers, and 7 species had no publications about them since 1988. For most Red Listed woodpecker species, information on their ecology and habitat requirements remains scant (Winkler & Christie 2002), and much research remains to be done to facilitate informed measures for improving the situation of these woodpeckers.

PRIORITY SPECIES FOR RESEARCH AND CONSERVATION PROJECTS

To set priorities for research among Red Listed woodpecker species, I argue that the species that are affected by selective logging are most in need of research, to assess their within-habitat and landscape requirements and thresholds, and to so derive measures to stabilise and recover populations of these species. This as opposed to woodpecker species that are affected primarily by deforestation, but that can tolerate considerable within-habitat modification. Such species are best helped not with detailed research but with conservation projects aimed at maintaining forest cover through sustainable use within their areas of occurrence, actions that typically would not be aimed solely at these woodpeckers but at forest biodiversity in general. Nevertheless, some research on woodpecker species on the outside of this dichotomy remains necessary, especially on those that are in the Endangered threat category: Varzea Piculet and Kaempfer's Woodpecker.

The 10 Red Listed woodpecker species that are affected by selective logging are often in the higher threat categories, an additional reason to prioritise these species for research. Two of the 10, Imperial Woodpecker and Ivory-billed Woodpecker, are at the verge of extinction if not extinct. Despite occasional reports of both species, organised searches to locate surviving individuals in recent decades have been fruitless (Lammertink & Estrada 1995, Lammertink et al. 1996, Rohrbaugh et al. 2007, 2009, Lammertink et al. 2011, Moskwik et al. 2013). If credible reports of either of these two species would again emerge, efforts for documentation, research and recovery would be the top priority in woodpecker conservation, but until then no practical research programme can be executed for these two species. A third species, Red-cockaded Woodpecker, is the only of the Red Listed woodpecker species which

Table 6. The number of papers published on 28 Red Listed woodpecker species prior to 1988 and since 1988, and the threat category of the species on the 2013 IUCN Red List.

Common name	Scientific name	IUCN (2013)	Region	N papers	
				pre-1988	post-1988
White-bellied Piculet	<i>Picumnus spilogaster</i>	VU	Latin America	2	0
Guianan Piculet	<i>Picumnus minutissimus</i>	NT	Latin America	1	0
Speckle-chested Piculet	<i>Picumnus steindachneri</i>	EN	Latin America	2	0
Varzea Piculet	<i>Picumnus varzeae</i>	EN	Latin America	1	3
Tawny Piculet	<i>Picumnus fulvescens</i>	NT	Latin America	1	4
Mottled Piculet	<i>Picumnus nebulosus</i>	NT	Latin America	1	4
Guadeloupe Woodpecker	<i>Melanerpes herminieri</i>	NT	Latin America	3	6
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	NT	North America	120	73
Knysna Woodpecker	<i>Campethera notata</i>	NT	Africa	3	6
Stierling's Woodpecker	<i>Dendropicos stierlingi</i>	NT	Africa	3	1
Sulu Woodpecker	<i>Dendrocopos ramsayi</i>	VU	Asia	0	0
Arabian Woodpecker	<i>Dendrocopos doriae</i>	VU	Africa	2	2
Okinawa Woodpecker	<i>Dendrocopos noguchii</i>	CR	Asia	3	4
Red-cockaded Woodpecker	<i>Picoides borealis</i>	NT	North America	98	435
Choco Woodpecker	<i>Veniliornis chocoensis</i>	NT	Latin America	4	0
White-browed Woodpecker	<i>Piculus aurulentus</i>	NT	Latin America	2	6
Fernandina's Flicker	<i>Colaptes fernandinae</i>	VU	Latin America	3	2
Kaempfer's Woodpecker	<i>Celeus obrieni</i>	EN	Latin America	1	14
Helmeted Woodpecker	<i>Dryocopus galeatus</i>	VU	Latin America	2	10
Black-bodied Woodpecker	<i>Dryocopus schulzi</i>	NT	Latin America	1	3
Andaman Woodpecker	<i>Dryocopus hodgei</i>	NT	Asia	0	0
Guayaquil Woodpecker	<i>Campephilus guayaquilensis</i>	NT	Latin America	1	0
Imperial Woodpecker	<i>Campephilus imperialis</i>	CR/PE	Latin America	4	8
Ivory-billed Woodpecker	<i>Campephilus principalis</i>	CR	North and Latin America	46	88
Red-collared Woodpecker	<i>Picus rabieri</i>	NT	Asia	2	2
Olive-backed Woodpecker	<i>Dinopium rafflesii</i>	NT	Asia	2	5
Buff-necked Woodpecker	<i>Meiglyptes tukki</i>	NT	Asia	10	7
Great Slaty Woodpecker	<i>Mulleripicus pulverulentus</i>	VU	Asia	10	10

has improved in conservation status during the past 25 years (Table 1), after intensive research and recovery efforts (Conner et al. 2001). This species remains dependent on appropriate management and restoration of its habitat. Additional research to monitor and guide these continued efforts is welcome, but given the extensive body of knowledge on this species, such research is not an international priority. Excluding these three species, and including two recent additions from the 2014 IUCN Red List and one likely future split, results in the following list of ten woodpecker species for which conservation research is urgent.

Speckle-chested Piculet (EN) has twice moved up in Red List category over the past 26 years while there was no research dedicated to this species during that period (Tables 1 and 6). It is endemic to a small range of about 160 by 60 km in two valleys in northern Peru, where it occurs in tropical and lower montane forests at 1100–2200 m elevation and is known from a few locations only (Schulenberg & Sedgwick 2012, BirdLife International 2014b). It is threatened by deforestation for

agriculture and pasture and by selective logging and intrusion into remaining forest areas by an expanding human population. Research is needed into its exact geographic range, habitat requirements and disturbance tolerance, and identification of sites with population strongholds.

Okinawa Woodpecker (CR) is restricted to a range of about 55 by 12 km in the northeast of Okinawa Island, Japan, where an estimated population of 100 to 390 mature individuals survives (BirdLife International 2014b) although this may be an underestimate considering the size of the range. It frequents old-growth forest, particularly for foraging, and it is threatened by deforestation, selective logging, and predation by introduced mongoose and feral cats. Research is needed into its population density in forests of different ages and structures, movements and dispersal between old-growth forest remnants, and rates of predation by introduced mammals, all topics best examined in a radio telemetry study. Approximately 14% of the range area of the bird is on U.S. military bases on the island ([http:// en.wikipedia.org/wiki/File:](http://en.wikipedia.org/wiki/File:)

US_military_bases_in_Okinawa.svg) and although this adds complexity to research and conservation actions, it also means there may be opportunities to fund research into this species through U.S. Department of Defense grants.

Fernandina's Flicker (VU) of Cuba has a total population of 400–530 mature individuals (BirdLife International 2014b) divided between five widely separated sub-populations that probably have little exchange between one another. It is a bird of open palm savannahs and it is threatened by clearance for agriculture, logging, and the cutting of cavity trees by parrot trappers. The main population in Zapata Swamp appears to have declined at least 20% between 1998 and 2007 (BirdLife International 2014b). A doctorate study by A. Serrano is under way of a community of cavity nesting birds including Fernandina's Flicker in the Delta del Cauto Protected Area in Granma province (E. Iñigo-Elias pers. comm.). Research that is needed includes periodic transect counts to monitor population trends in all of the sub-populations.

Helmeted Woodpecker (VU) of the southern Atlantic Forest has a global population of between 2,500 and 10,000 individuals (BirdLife International 2014b). Generally scarce, it reaches its best densities in mature forest stands. It is threatened by deforestation and selective logging. Its population strongholds are in the Serra de Paranapiacaba, São Paulo, Brazil, and in Misiones Province, Argentina, where I am making a radio-tracking study of this species since 2012. The goals of this research are to assess density, landscape use, nesting ecology and foraging ecology of Helmeted Woodpecker in logged and mature forests, as well as its co-existence with two large woodpecker species, Lineated Woodpecker *Dryocopus lineatus* and Robust Woodpecker *Campephilus robustus*.

Black-bodied Woodpecker (NT) of xeric woodlands in the Chaco region of north-central Argentina, southern Bolivia, and western Paraguay has a tentative global population estimate of ca. 7,000 mature individuals (BirdLife International 2014b). It is threatened by selective logging and deforestation for agriculture. The rate of deforestation in its range has increased since 2000 and is among the highest deforestation rates globally (Hansen et al. 2013). Research is needed to assess its degree of tolerance to selective logging, improve estimates of its global population status and trends, and to assess to what extent the Chaco areas that are currently being cleared, overlap with stronghold areas of this woodpecker species.

Red-collared Woodpecker (NT) of lowland forests in Laos, Vietnam and Cambodia is generally scarce and is declining due to forest loss and degradation. Research is needed into its tolerance to habitat disturbance, population trends, and nearly all basic aspects of its biology (Winkler & Christie 2002).

Great Slaty Woodpecker (VU) is the largest woodpecker in Southeast Asia. It uses large trees for both foraging and nesting and shows marked population declines with selective logging of mature forests (Lammertink et al. 2009, Baral 2011, Kumar & Shahabuddin 2012). It is threatened by rapid rates of deforestation and logging of old-growth forest including in its strongholds in Myanmar, Cambodia and Borneo (Lammertink et al. 2009, Hansen et al. 2013). Research is needed to assess the reproductive rate and the long-term viability of reduced populations in disturbed forests, and to assess priority sites for conservation of old-growth habitat, particularly in Myanmar.

Yellow-faced Flameback of the Philippine islands Panay, Negros, Guimaras and Masbate has suffered from deforestation and hence habitat loss of between 92% and 100% on the four islands (Curio 2002, and <http://www.google.com/earth/>), and the only recent records come from Negros. Its total population may be below 500 mature individuals, and research is needed to assess its current distribution, densities, reproductive success, and habitat requirements. The other recently Red Listed splits from the Greater Flameback complex (Javan Flameback and Red-headed Flameback, Table 2) are also of research interest but are better known than Yellow-faced Flameback, and both occur in several protected areas.

White-rumped Woodpecker of Java appears to be extremely rare and, as all Javan forest endemics, contends with the effects of extensive deforestation and fragmentation, pressure from a dense human population on remaining forests including in protected areas, and indiscriminate large scale bird trapping. Whereas the sister taxon Buff-rumped Woodpecker *Meiglyptes grammithorax* is common and tolerant to forest disturbance elsewhere in the Sundaic region (Lammertink 2004, Styring & Hussin 2004), White-rumped Woodpecker has not been recorded in intensive surveys of forest birds in Java (van Balen 1999) and there appear to have been only two sightings in the past 50 years, both by D. Liley at Gunung Halimun in 1994 (S. van Balen and D. Liley pers. comm.). Surveys are needed to clarify the current status and distribution of White-rumped Woodpecker, perhaps using playback initially of sounds

of Buff-rumped Woodpecker as there are no known recordings of White-rumped Woodpecker. **Korean White-bellied Woodpecker** *Dryocopus [javensis] richardsi*: if species level status is confirmed for this taxon it would rank among the most critically endangered woodpecker species. It is extinct in South Korea and on Tsushima island (Japan) and is now down to a population of probably less than 40 individuals in North Korea, if still extant (Fiebig 1993). Surveys and protective measures for this taxon are very urgent but also highly challenging given the political situation and socio-economic pressures in North Korea.

For each of the priority species, recommended research actions should be accompanied by, or followed up by, conservation actions. This includes communication of results to land managers and governments, a search for solutions with local stakeholders, and an inclusion of desired improvements in environmental education, as well as strategic alignment with conservation efforts for other biodiversity.

CONCLUDING REMARKS

An emphasis in research priorities on woodpeckers that are affected by selective logging, including globally and regionally threatened species, puts a spotlight on the importance of the protection of old-growth forests in the ranges of each of these species. Old-growth forests are usually the habitats where specialist woodpeckers reach their best densities and best reproductive rates (Tanner 1942, Carlson & Aulén 1992, Lammertink et al. 2009) and these forests are indispensable as reference sites in research and as population strongholds. Globally, conservation strategies have moved away from the total protection of habitats to the development of sustainable, multiple uses by community stakeholders (Naughton-Treves et al. 2005). There is a lot of merit to this current approach and it is often the only viable option for the conservation management of large landscapes. Nevertheless, the strict protection of generally small and few old-growth remnants in forest ecosystems must remain in focus. There is an important role for biologists working with specialist woodpecker species in advocating the importance of old-growth protection and the restoration to old-growth conditions in select, formerly logged areas.

Up to the present, the bulk of woodpecker research is concentrated in North America and Europe (Mikusiński 2006), and is often aimed at

regionally threatened species that have secure populations elsewhere, or at common species in behavioural or ecological research. While there are valid motivations for these research avenues, it is imperative that woodpecker researchers dedicate more of their expertise and resources to globally threatened woodpecker species, to help prevent an erosion of woodpecker diversity from global extinctions. Research groups working with woodpeckers should include more PhD and student projects about globally threatened woodpeckers. Researchers with main projects in the northern hemisphere could dedicate field research on threatened woodpeckers outside their main field seasons. For some threatened species, information is so scant that even a short project of several weeks can yield important new information. Woodpecker conservation research would further be stimulated by the creation of a grant fund dedicated to this family, similar to existing funds for raptors, cranes, and parrots.

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STRESZCZENIE

[Zmiany w ocenie stopnia zagrożenia wyginięciem oraz priorytety w ochronie dzięciołów]

Posługując się Czerwoną Listą Gatunków Zagrożonych Międzynarodowej Unii Ochrony Przyrody i Jej Zasobów (IUCN) z 1988 r. jako punktem odniesienia, opisano zmiany, jakie

zachodziły w ciągu ostatnich 25 lat w ocenie statusu zagrożenia dzięciołów na świecie, w rozmieszczeniu geograficznym gatunków z Czerwonej Listy i czynnikach wskazywanych jako odpowiedzialne za zmiany ich liczebności. Przeanalizowano także liczbę publikacji dotyczących zagrożonych gatunków dzięciołów.

W okresie pomiędzy 1988 a 2013 r. zostało opublikowanych 11 wydań Czerwonej Listy IUCN. Uwzględniając zmiany związane ze wzrastającą liczbą informacji o statusie i liczebności gatunku, wśród 28 gatunków zanotowano w tym okresie 13 zmian w kategorii stopnia zagrożenia, 12 z nich dotyczyły zwiększenia stopnia zagrożenia i tylko w przypadku dzięcioła skromnego status zmienił się z „narażony” na „bliski zagrożenia” (Tab. 1). Liczba gatunków dzięciołów wykazywanych na Czerwonej Liście tj. w kategoriach począwszy od „bliskie zagrożenia” i wyżej wzrosła z 20 do 28 gatunków, zaś w grupie zagrożonych wyginięciem tj. kategoriach począwszy od „narażone” i wyżej — z 8 do 12 (odpowiednio wzrost o 1,6 i 1,8 raza — Tab. 3). Rozmieszczenie geograficzne gatunków dzięciołów wykazywanych w Czerwonej Liście nie zmieniło się od 1988 r. — połowa tych gatunków zasiedla Amerykę Łacińską, a jedna czwarta Azję. W Europie nie ma obecnie gatunku, który mógłby być zaliczony do którejś z kategorii zagrożenia (Tab. 5). W związku ze zmianami taksonomicznymi, zwłaszcza z podniesieniem do rangi gatunku wielu podgatunków (Tab. 2), liczba gatunków dzięciołów wzrosła do 254. Zmiany te spowodowały wzrost liczby gatunków dzięciołów na Czerwonej Liście do 42, z których 40% zasiedla Azję (Tab. 5).

Utrata i zmiany zachodzące w siedliskach, oraz wzrost śmiertelności to główne grupy zagrożeń dla analizowanych 28 gatunków dzięciołów. Wśród nich 10 jest zagrożonych przez selektywne pozyskiwanie drewna — są to gatunki klasyfikowane w kategoriach „zagrożone wyginięciem” (Tab. 4).

Badania naukowe i działania ochronne powinny koncentrować się przede wszystkim na gatunkach wrażliwych na wyręb selektywny. Dotychczas badania naukowe prowadzone na zagrożonych gatunkach dzięciołów skupiały się przede wszystkim na trzech gatunkach północno-amerykańskich — dzięciurze krasnogłowym, dzięciole skromnym i dzięciole wielkodziobym (Tab. 6). Autor przedstawia listę 10 priorytetowych gatunków, które wymagają jak najszybszych badań i zabiegów ochronnych: 4 zasiedlających Amerykę Łacińską i 6 — Azję.

What we don't know, and what needs to be known, about the cooperatively breeding Acorn Woodpecker *Melanerpes formicivorus*

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Abstract. The Acorn Woodpecker *Melanerpes formicivorus* is one of a small number of woodpecker species that are cooperative breeders, living in family groups of up to 15 individuals of both sexes and all ages and exhibiting a complex mating system involving multiple cobreeders of both sexes (polygynandry). Although much has been learned concerning the social organisation and ecology of this species, over 45 years of research at Hastings Reservation, central coastal California, USA, has left us with a large number of unanswered questions ranging from relatively minor issues such as why adults have white eyes and why juveniles have a plumage similar to adult males to more major issues such as how cavity limitation could act as a driver of their unique social behaviours and how brood reduction is adaptive. Here we briefly discuss some of these questions and speculate as to how they might be addressed by future work. Long-term studies are important as a means of addressing many demographic and behavioural questions, but are even more valuable as a means of generating new questions that would have been overlooked without detailed knowledge of natural history and general ecology.

Key words: Acorn Woodpeckers, *Melanerpes*, caching behaviour, cooperative breeding, eye colour, food storage, juvenile plumage, social behaviour, cavity

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INTRODUCTION

Cooperative breeding, whereby some individuals help raise young that are not their own (Koenig & Dickinson 2004), is found in an estimated 9% of birds worldwide (Cockburn 2006) and is widely distributed taxonomically (Arnold & Owens 1999). Of the 182 species of true woodpeckers (subfamily Picinae) recognised by Winkler & Christie (2002), the proportion known or suspected to live in family groups and exhibit cooperative breeding is similar, with approximately 18 (9.8%) in this category. Of these, eight (44%) are members of the genus *Melanerpes*, a relatively large Neotropical genus of 22 species with eclectic and often diverse food habits, only rarely including the classical woodpecker habit of excavating for wood-boring larvae.

With over a third of species in this genus exhibiting cooperative breeding, *Melanerpes* exhibits far more sociality than any other major

woodpecker genus and, although a critical phylogenetic analysis has yet to be performed, would appear to contain significantly more cooperative breeders than expected, similar to several genera of passerine birds including *Campylorhynchus* wrens, *Malurus* fairy-wrens, *Pomatostomus* babblers, and *Cyanocorax* jays (Edwards & Naeem 1993). Studies of at least one other social *Melanerpes* species — the colonial Hispaniolan Woodpecker *M. striatus* — is ongoing, but otherwise none of the other highly social species in this genus has been studied in detail, and cooperative breeding is known only anecdotally in several.

Here we emphasise not what is known about the cooperatively breeding Acorn Woodpecker — one of the most extensively studied of all species in the family (Mikusiński 2006) — but rather what we do *not* know about its ecology, behaviour, and evolution. This wealth of questions is striking because it follows 45 years of work and two long-term studies of this species, including our own

ongoing study at Hastings Reservation in central coastal California, USA, started in 1968 by Michael and Barbara MacRoberts (1976), and that of Peter Stacey and his colleagues in Water Canyon, New Mexico, conducted between 1975 and 1984 (Stacey 1979a, b, Stacey & Ligon 1987).

A BRIEF SUMMARY OF ACORN WOODPECKER SOCIAL BEHAVIOUR

Acorn Woodpeckers live in permanently territorial, polygynandrous family groups that typically include three factions: a coalition of between one and six males that compete for matings within the group, a coalition of one to three females that lay eggs communally in the same nest cavity, and up to 10 helpers that are offspring of the breeders from prior nests (Koenig et al. 1995b). Group composition is highly variable, however. Of 1547 group-years of data at our study site in central coastal California between 1972 and 2012, 39% of group-years consisted of a simple pair of birds, while 45% contained at least two cobreeder males, 23% two joint-nesting females, and 58% at least one helper. Helpers are of both sexes, although a modest majority (57.4% of 1294 helper-years between 1972 and 2012) were males, in the same direction as the slight but significant sex bias of fledglings (Koenig et al. 2001). Geographic variation is also considerable, with groups in a population studied in southwestern New Mexico being significantly smaller than the California population and exhibiting very little if any joint-nesting (Koenig & Stacey 1990), and those in a third population in southeastern Arizona being almost entirely pairs and generally migratory (Stacey & Bock 1978).

Kinship is a critical feature of Acorn Woodpecker societies. Cobreeder male coalitions are almost always brothers, a father and his sons, or a mixture of the two, whereas joint-nesting females are sisters or a mother and daughter. Despite this pattern of close genetic relatedness within groups, incest is rare, and helpers do not breed in their natal group (Koenig et al. 1998, Haydock et al. 2001). Instead, reproductive vacancies created by the death of the breeders (either males or females) within a group are filled by a coalition of (former) helpers (related to each other but unrelated to birds in the group that has the vacancy) from elsewhere. Once a vacancy is filled, however, helpers of the sex opposite that of the vacancy are able to inherit and cobreed along with their same-sex

parents. Thus incest avoidance, rather than reproductive competition, is the primary driver of reproductive roles within groups.

Reproductive vacancies are often vigorously contested in 'power struggles' among coalitions of same-sex helpers, events that provide unequivocal evidence that helping is 'making the best of a bad job' and that helpers fight for the opportunity to give up their helper status and become breeders in the population.

Until recently, we assumed that the primary feature of the biology of Acorn Woodpeckers limiting dispersal and the creation of new territories in this species was primarily related to their granaries — snags or trees in which birds drill small holes in which they store acorns from the oaks (genus *Quercus* and *Notholithocarpus*) with which they are closely associated (Koenig & Mumme 1987). Recently, however, we have tested this hypothesis experimentally and found that, although granaries are important, cavities excavated by the birds and suitable for nesting are even more limiting (E. Walters and W. Koenig, unpublished data).

Groups exhibit a considerable range of apparently highly cooperative behaviours, including communal acorn storage, granary defence, and nesting, along with equally impressive competitive behaviours in the form of mate-guarding by males (Mumme et al. 1983a) and egg-destruction by joint-nesting females (Mumme et al. 1983b, Koenig et al. 1995a). Helpers contribute to most group functions, but the fitness consequences of helpers differ significantly depending on the sex of the helper and the size of the acorn crop (see below).

The effects of the acorn crop are dramatic. In years of large acorn crops, the breeding season, which typically will have ended in June or July, will start again in August or September as acorns mature. Such autumn nests fledge young as late as early November (Koenig & Stahl 2007). After a winter hiatus, groups will then resume nesting the following spring and potentially have two successive nests. In contrast, in poor crop years, birds are forced to abandon their territories, only occasionally returning the following spring after spending the winter off the territory (Hannon et al. 1987).

The acorn crop has other, more subtle effects as well. In particular, the effect of male helpers, measured as the increase in offspring produced per nest attributable to each helper, changes with the size of the acorn crop, being highly positive in

good acorn crop years and negative in poor years, opposite the expectation of the hypothesis that helpers are necessary, and thus more beneficial, when ecological conditions are poor (Koenig et al. 2011). In contrast, female helpers have a positive but statistically non-significant effect on offspring production that does not vary with the acorn crop.

Regardless of which sex of helper one considers, the indirect (kin-selected) fitness benefits helpers gain by increasing the reproductive success of their parents are small compared to the advantages of breeding, thus supporting the hypothesis that helping is an inferior option compared to breeding. In addition to these kin-selected benefits, however, there are several potential direct fitness advantages that helpers could be gaining by provisioning offspring. For example, they could be gaining experience that helps them as breeders later in life (the 'skills hypothesis') or be helping in order to keep breeders from forcing them out of the group (the 'pay-to-stay hypothesis'). We have, however, as yet failed to find evidence for any of these potential direct fitness benefits (Koenig & Walters 2011).

WHAT WE DO NOT KNOW

Questions that elude us, even after more than 45 years of continuous effort, fall into several categories. Those we focus on here are divided arbitrarily into questions specific to Acorn Woodpeckers and those that are more generally applicable to woodpeckers or cooperatively breeding species.

ISSUES LARGELY RESTRICTED TO ACORN WOODPECKERS

Why do adults have white eyes?

Fledgling Acorn Woodpeckers have dark eyes that gradually fade to the white eye colour of adults by the time of the postjuvinal moult, 3 to 4 months after fledging (Spray & MacRoberts 1975; Fig. 1). Intriguingly, all four of the 22 species of *Melanerpes* that have light eyes are either cooperative breeders (*M. candidus*, *M. formicivorus*, and *M. cruentatus*) or colonial (*M. striatus*). In addition, the Ground Woodpecker *Geocolaptes olivaceus*, one of the few non-*Melanerpes* woodpecker species that is a cooperative breeder, has light eyes as both adults and juveniles. Although this overall pattern suggests a relationship between sociality and light eyes, no such relationship has been noted in other taxa and comparably light eyes are found in

several species of *Dryocopus* and *Campephilus* woodpeckers, none of which is social.

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What we don't know, and what needs to be known, about the cooperatively breeding Acorn Woodpecker *Melanerpes formicivorus*

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Abstract. The Acorn Woodpecker *Melanerpes formicivorus* is one of a small number of woodpecker species that are cooperative breeders, living in family groups of up to 15 individuals of both sexes and all ages and exhibiting a complex mating system involving multiple cobreeders of both sexes (polygynandry). Although much has been learned concerning the social organisation and ecology of this species, over 45 years of research at Hastings Reservation, central coastal California, USA, has left us with a large number of unanswered questions ranging from relatively minor issues such as why adults have white eyes and why juveniles have a plumage similar to adult males to more major issues such as how cavity limitation could act as a driver of their unique social behaviours and how brood reduction is adaptive. Here we briefly discuss some of these questions and speculate as to how they might be addressed by future work. Long-term studies are important as a means of addressing many demographic and behavioural questions, but are even more valuable as a means of generating new questions that would have been overlooked without detailed knowledge of natural history and general ecology.

Key words: Acorn Woodpeckers, *Melanerpes*, caching behaviour, cooperative breeding, eye colour, food storage, juvenile plumage, social behaviour, cavity

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INTRODUCTION

Cooperative breeding, whereby some individuals help raise young that are not their own (Koenig & Dickinson 2004), is found in an estimated 9% of birds worldwide (Cockburn 2006) and is widely distributed taxonomically (Arnold & Owens 1999). Of the 182 species of true woodpeckers (subfamily Picinae) recognised by Winkler & Christie (2002), the proportion known or suspected to live in family groups and exhibit cooperative breeding is similar, with approximately 18 (9.8%) in this category. Of these, eight (44%) are members of the genus *Melanerpes*, a relatively large Neotropical genus of 22 species with eclectic and often diverse food habits, only rarely including the classical woodpecker habit of excavating for wood-boring larvae.

With over a third of species in this genus exhibiting cooperative breeding, *Melanerpes* exhibits far more sociality than any other major

woodpecker genus and, although a critical phylogenetic analysis has yet to be performed, would appear to contain significantly more cooperative breeders than expected, similar to several genera of passerine birds including *Campylorhynchus* wrens, *Malurus* fairy-wrens, *Pomatostomus* babblers, and *Cyanocorax* jays (Edwards & Naeem 1993). Studies of at least one other social *Melanerpes* species — the colonial Hispaniolan Woodpecker *M. striatus* — is ongoing, but otherwise none of the other highly social species in this genus has been studied in detail, and cooperative breeding is known only anecdotally in several.

Here we emphasise not what is known about the cooperatively breeding Acorn Woodpecker — one of the most extensively studied of all species in the family (Mikusiński 2006) — but rather what we do *not* know about its ecology, behaviour, and evolution. This wealth of questions is striking because it follows 45 years of work and two long-term studies of this species, including our own

ongoing study at Hastings Reservation in central coastal California, USA, started in 1968 by Michael and Barbara MacRoberts (1976), and that of Peter Stacey and his colleagues in Water Canyon, New Mexico, conducted between 1975 and 1984 (Stacey 1979a, b, Stacey & Ligon 1987).

A BRIEF SUMMARY OF ACORN WOODPECKER SOCIAL BEHAVIOUR

Acorn Woodpeckers live in permanently territorial, polygynandrous family groups that typically include three factions: a coalition of between one and six males that compete for matings within the group, a coalition of one to three females that lay eggs communally in the same nest cavity, and up to 10 helpers that are offspring of the breeders from prior nests (Koenig et al. 1995b). Group composition is highly variable, however. Of 1547 group-years of data at our study site in central coastal California between 1972 and 2012, 39% of group-years consisted of a simple pair of birds, while 45% contained at least two cobreeder males, 23% two joint-nesting females, and 58% at least one helper. Helpers are of both sexes, although a modest majority (57.4% of 1294 helper-years between 1972 and 2012) were males, in the same direction as the slight but significant sex bias of fledglings (Koenig et al. 2001). Geographic variation is also considerable, with groups in a population studied in southwestern New Mexico being significantly smaller than the California population and exhibiting very little if any joint-nesting (Koenig & Stacey 1990), and those in a third population in southeastern Arizona being almost entirely pairs and generally migratory (Stacey & Bock 1978).

Kinship is a critical feature of Acorn Woodpecker societies. Cobreeder male coalitions are almost always brothers, a father and his sons, or a mixture of the two, whereas joint-nesting females are sisters or a mother and daughter. Despite this pattern of close genetic relatedness within groups, incest is rare, and helpers do not breed in their natal group (Koenig et al. 1998, Haydock et al. 2001). Instead, reproductive vacancies created by the death of the breeders (either males or females) within a group are filled by a coalition of (former) helpers (related to each other but unrelated to birds in the group that has the vacancy) from elsewhere. Once a vacancy is filled, however, helpers of the sex opposite that of the vacancy are able to inherit and cobreed along with their same-sex

parents. Thus incest avoidance, rather than reproductive competition, is the primary driver of reproductive roles within groups.

Reproductive vacancies are often vigorously contested in 'power struggles' among coalitions of same-sex helpers, events that provide unequivocal evidence that helping is 'making the best of a bad job' and that helpers fight for the opportunity to give up their helper status and become breeders in the population.

Until recently, we assumed that the primary feature of the biology of Acorn Woodpeckers limiting dispersal and the creation of new territories in this species was primarily related to their granaries — snags or trees in which birds drill small holes in which they store acorns from the oaks (genus *Quercus* and *Notholithocarpus*) with which they are closely associated (Koenig & Mumme 1987). Recently, however, we have tested this hypothesis experimentally and found that, although granaries are important, cavities excavated by the birds and suitable for nesting are even more limiting (E. Walters and W. Koenig, unpublished data).

Groups exhibit a considerable range of apparently highly cooperative behaviours, including communal acorn storage, granary defence, and nesting, along with equally impressive competitive behaviours in the form of mate-guarding by males (Mumme et al. 1983a) and egg-destruction by joint-nesting females (Mumme et al. 1983b, Koenig et al. 1995a). Helpers contribute to most group functions, but the fitness consequences of helpers differ significantly depending on the sex of the helper and the size of the acorn crop (see below).

The effects of the acorn crop are dramatic. In years of large acorn crops, the breeding season, which typically will have ended in June or July, will start again in August or September as acorns mature. Such autumn nests fledge young as late as early November (Koenig & Stahl 2007). After a winter hiatus, groups will then resume nesting the following spring and potentially have two successive nests. In contrast, in poor crop years, birds are forced to abandon their territories, only occasionally returning the following spring after spending the winter off the territory (Hannon et al. 1987).

The acorn crop has other, more subtle effects as well. In particular, the effect of male helpers, measured as the increase in offspring produced per nest attributable to each helper, changes with the size of the acorn crop, being highly positive in

good acorn crop years and negative in poor years, opposite the expectation of the hypothesis that helpers are necessary, and thus more beneficial, when ecological conditions are poor (Koenig et al. 2011). In contrast, female helpers have a positive but statistically non-significant effect on offspring production that does not vary with the acorn crop.

Regardless of which sex of helper one considers, the indirect (kin-selected) fitness benefits helpers gain by increasing the reproductive success of their parents are small compared to the advantages of breeding, thus supporting the hypothesis that helping is an inferior option compared to breeding. In addition to these kin-selected benefits, however, there are several potential direct fitness advantages that helpers could be gaining by provisioning offspring. For example, they could be gaining experience that helps them as breeders later in life (the 'skills hypothesis') or be helping in order to keep breeders from forcing them out of the group (the 'pay-to-stay hypothesis'). We have, however, as yet failed to find evidence for any of these potential direct fitness benefits (Koenig & Walters 2011).

WHAT WE DO NOT KNOW

Questions that elude us, even after more than 45 years of continuous effort, fall into several categories. Those we focus on here are divided arbitrarily into questions specific to Acorn Woodpeckers and those that are more generally applicable to woodpeckers or cooperatively breeding species.

ISSUES LARGELY RESTRICTED TO ACORN WOODPECKERS

Why do adults have white eyes?

Fledgling Acorn Woodpeckers have dark eyes that gradually fade to the white eye colour of adults by the time of the postjuvinal moult, 3 to 4 months after fledging (Spray & MacRoberts 1975; Fig. 1). Intriguingly, all four of the 22 species of *Melanerpes* that have light eyes are either cooperative breeders (*M. candidus*, *M. formicivorus*, and *M. cruentatus*) or colonial (*M. striatus*). In addition, the Ground Woodpecker *Geocolaptes olivaceus*, one of the few non-*Melanerpes* woodpecker species that is a cooperative breeder, has light eyes as both adults and juveniles. Although this overall pattern suggests a relationship between sociality and light eyes, no such relationship has been noted in other taxa and comparably light eyes are found in

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What is the functional significance of these patterns? There is no comparative analysis of juvenile plumage patterns in woodpeckers, and thus we do not know how common or rare it is for juveniles of this group to resemble adult males rather than adult females. Possibly there is



Fig 1. Two fledglings on the right (note dark eyes and male-like crown plumage) begging from an adult (with white eye on the left). Also note the granary limb pock-marked with storage holes used for storing acorns. Photo © by Marie Read.

a connection with dominance, since males are generally dominant over females within birds of the same (breeder or helper) status (Hannon et al. 1987). Why this would not apply to birds in Colombia is unknown. This character would be relatively easy to manipulate experimentally, however, and behavioural observations, although difficult, could potentially reveal the fitness consequences of juvenile plumage, at least at the intraspecific level.

What is the functional significance of runt eggs?

Runt eggs are unusually small eggs that are deficient in some way, usually because they contain no yolk, and thus do not hatch (Koenig 1980a). They are found in all avian taxa but are generally quite rare; among woodpeckers in general, for example, the mean frequency of runt eggs is approximately 0.5% (Koenig 1980b). In contrast, the incidence of runt eggs in Acorn Woodpeckers is nearly an order of magnitude greater, being 4.8% in museum collections and around 3% among eggs at our study site in central coastal California (Koenig 1980b). In groups with a single female breeder, runt eggs composed 2.3% of 1661 eggs (Koenig et al. 2009). Their frequency among groups with joint-nesting females is apparently much higher, but is difficult to quantify because a

high proportion of them are destroyed: of 24 runt eggs noted during our study of egg destruction by joint-nesting females, 19 (79%) were destroyed prior to the onset of incubation (Koenig et al. 1995a). Thus, our estimates of the frequency of runt eggs is most likely an underestimate.

Runt eggs are particularly common in the nests of joint-nesting females and typically are laid immediately prior to the laying of a normal egg and clutch. The exact nature of the association between runt eggs and joint-nesting remains obscure, however. Koenig et al. (1995a) considered four hypotheses: (1) runt eggs are a synchronising signal indicating when and where a female will lay her eggs; (2) they provide a critical nutritional benefit to the female that destroys them; (3) they minimise the energetic losses due to egg destruction; and (4) the production of runt eggs increases the opportunity for the last-to-lay female to destroy a normal egg laid by a cobreeder. None of these hypotheses was strongly supported. Behavioural observations provide some support for the last of these hypotheses, however: in 5 of 17 nesting attempts (29%), a female that laid a runt egg destroyed both her own egg and a normal egg laid on the same day by her joint-nesting female, typically resulting in the first female laying one egg more in the completed clutch than the

number of (normal) eggs in the clutch contributed by the second joint-nesting female.

These findings suggest that runt eggs may help bias egg ownership within a joint clutch in favour of the bird laying the abnormally small egg. Our attempt to estimate the fitness consequences of laying a runt egg, however, indicates that they are minimal. Thus, the functional basis for the uniquely high incidence of runt eggs in Acorn Woodpeckers remains unclear.

Why does reproductive success increase linearly with the acorn crop?

The size of a granary places an upper limit on the number of acorns that can be securely stored by a group of Acorn Woodpeckers. The bulk of nesting takes place in March to June, many months after acorns are stored in the fall. Consequently, one would expect there to be a clear threshold set by the number of acorns that can be stored, beyond which a larger acorn crop would have little or no effect on the reproductive performance of the population the subsequent spring.

Contrary to this expectation, reproductive success appears to increase linearly with the overall size of the acorn crop, with no indication of a threshold (Fig. 2). What circumvents the expected threshold? One possibility is that acorns remain on the trees longer when the crop is large, thus reducing the length of time birds are dependent on their stored acorns (Koenig et al. 2014). It seems likely, however, that the mechanism is more complex, and that birds somehow capitalise on larger acorn crops in ways other than through their storage facilities so as to better survive the winter and be in better condition when the spring breeding season begins.

Partial support for birds being in better condition following large acorn crops comes from the finding that the relationship between the acorn crop and winter fattening was significantly positive, at least for males (Koenig et al. 2005). The mechanism behind this effect is unknown, although food supplementation experiments offer an opportunity for testing alternative hypotheses.

Why do Acorn Woodpeckers hide copulations, and what is the function of pre-roost mounting?

Although there is a considerable literature on copulation frequency in birds (Birkhead et al. 1987, Møller & Birkhead 1992), there is little regarding birds that hide their mating activities. Acorn Woodpeckers are one such species: mounting — both of females by males and vice-versa — is

observed just prior to roosting in the evening, when emerging from roost holes in the morning, and during power struggles (Koenig 1981), but such 'pre-roost mounting' is aseasonal, unrelated to age, sex, or status within a group, and does not appear to be a prelude to copulation (MacRoberts & MacRoberts 1976). In contrast, mountings leading to copulation during a female's fertile period are rarely observed. Thus the first question is: what is the function of pre-roost mounting? The second is: where and when does copulation take place? We have no idea concerning the answer to the first of these problems, while the most likely answer to the second is that copulations take place inside roost cavities, although this has yet to be confirmed.

The third, and perhaps most perplexing question, is: why are copulations hidden? One hypothesis is that copulating secretly confuses paternity and facilitates the ability of females to recruit male help in the provisioning of their young (Stacey 1982). Comparative evidence, however, fails to support this conjecture. For example, the cooperatively breeding Florida Scrub-Jay *Aphelocoma coerulescens* is similarly secretive in its mating behaviour but strictly monogamous both socially and genetically (Quinn et al. 1999), whereas copulations in the monogamous and cooperatively breeding Red-cockaded Woodpecker *Picoides borealis* are readily and commonly observed (Haig et al. 1994).

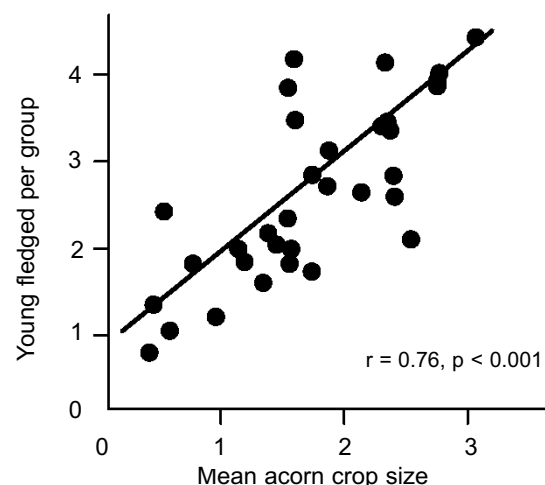


Fig. 2. The correlation between the size of the overall acorn crop ($\ln$ -transformed number of acorns counted in standardised 30-sec counts on marked trees) and the mean number of young fledged per group the following spring at Hastings Reservation, Monterey County, California, USA. A linear regression is plotted. Data from 1981 to 2013.

One hypothesis is that colonial hole-nesting species may copulate within cavities as a means of reducing interference whereas solitary species copulate outside of cavities where interference is less likely to be a problem (Birkhead et al. 1987). Clearly a more thorough comparative analysis of copulatory behaviour in cooperative breeders is warranted and would be needed to understand the functional significance of this trait.

MORE GENERAL ISSUES

Why do so few secondary cavity nesters use old Acorn Woodpecker cavities?

There is currently considerable interest in woodpeckers as keystone 'ecosystem engineers' excavating cavities that are used by secondary-cavity-nesting species in 'nest-web' communities (Martin & Eadie 1999, Martin et al. 2004, Robles & Martin 2014). In the oak savanna habitat of central coastal California there is a rich community of secondary-cavity nesting species, including Western Bluebirds *Sialia mexicana*, Ash-throated Flycatchers *Myiarchus cinerascens*, Oak Titmice *Baeolophus inornatus*, and Violet-green Swallows *Tachycineta thalassina*, as well as Dusky-footed Woodrats *Neotoma fuscipes*, various mice species (*Peromyscus* spp.), and several other less common species. None of these species appear to commonly use Acorn Woodpecker cavities at our study site, however. Since 1998 we have followed nesting cavities used by Acorn Woodpeckers and recorded nest reuse 271 times over a total of 1283 cavity-years. Of the 488 cases in which apparently useable cavities were reused (38.0% of cavity-years), 325 (66.6% of cases of cavity reuse) were by Acorn Woodpeckers and 120 (24.6% of cavity reuse) were by the introduced European Starling *Sturnus vulgaris*. Species other than these two were recorded using cavities in only 43 cavity-years (8.8% of cavity reuse). The most frequent of these other species was introduced European Honeybees *Apis mellifera*, which inhabited cavities previously used by Acorn Woodpeckers in 16 cavity-years (3.3% of cavity reuse), followed by Dusky-footed Woodrats (8 cavity-years, 1.6% of cavity reuse). Bird species, all of which were recorded using cavities on only one or two occasions, included Western Bluebirds, Oak Titmice, Ash-throated Flycatchers, Northern Flickers *Colaptes auratus*, Western Screech-Owls *Megascops kennicottii*, and Saw-whet Owls *Aegolius acadicus*.

Acorn Woodpeckers are by far the most common cavity-excavating species in this habitat.

Nonetheless, they appear to be a minor contributor to cavities used by other species in the community with the exception of introduced European Starlings. Why other species fail to take greater advantage of this resource is unclear. One possibility is that the starlings outcompete other species and keep them from using Acorn Woodpecker cavities (Weitzel 1988), but such interference by introduced starlings does not appear to be general (Koenig 2003). Furthermore, old Acorn Woodpecker cavities at our study site frequently go unused even when European Starlings are not present: of previously used nesting cavities that were apparently still useable, 56% were not used for nesting by any species in any one year. Although this does not preclude the possibility that some cavities were used for non-nesting activities such as roosting, it is consistent with the hypothesis that starlings are not a major factor keeping other species from using old Acorn Woodpecker nest cavities for their own use. Alternatively, natural cavities suitable to the various native species may not be limiting, similar to the situation found in some other undisturbed forests such as Białowieża National Park in eastern Poland, where competition for nest sites is of minor importance and woodpecker species are not a keystone provider of cavities (Wesołowski 2007).

What is the adaptive significance of brood reduction?

One advantage of the groups that result from the combination of delayed dispersal by offspring and mate-sharing (polygynandry) is that, with up to a dozen adults feeding at a nest, more nestlings can be raised than if only a pair provisioned young. Indeed, larger groups fledge more young, but brood reduction is still common, with 16% of nestlings perishing due to starvation between hatching and fledging (Koenig & Mumme 1987). Of these, the vast majority — 55 of 72 (76%) followed by Stanback (1991) — perished within 3 days of hatching, and young from eggs that hatch more than 24 h after the first egg hatches almost invariably die, regardless of group size or ecological conditions. In other words, brood reduction was common even in highly productive years following large acorn crops and among large groups with multiple cobreeders and helpers.

Brood reduction is common in birds and generally thought to be related to the dependence on irregular or unpredictable food (O'Connor 1978). Stanback (1991) considered this and other

hypotheses for the functional significance of the hatching asynchrony facilitating brood reduction in Acorn Woodpeckers, but concluded that there was little support for any of them. Thus, the selective advantages of hatching asynchrony and brood reduction in Acorn Woodpeckers, if any, remain unknown, despite being a significant factor limiting reproductive success.

How do birds detect reproductive vacancies?

Reproductive vacancies, formed when all breeders of one sex die or disappear, are often followed by intense, prolonged fights among same-sex coalitions of helpers termed 'power struggles' for the opportunity to fill the vacancy and become breeders in the new territory (Koenig 1981). Power struggles can be initiated very rapidly when a vacancy arises, involving dozens of birds, a great deal of vocalising and fighting, and are generally won by the largest participating sibling coalition (Hannon et al. 1985). In some cases, vacancies may be filled in less than an hour: we have observed cases of power struggles initiating within 30 min of dawn after temporary detention of the only breeder of one sex in a group and Hannon et al. (1985) reported one experimental removal in which replacement occurred within 20 min. If helpers of the same sex as the breeding vacancy remain in the group, however, these helpers will often prevent new breeders from joining the group and result in a significant delay in filling the vacancy (Hannon et al. 1985, Koenig et al. 1999).

How do birds detect vacancies so quickly? Hannon et al. (1985) suggested that birds still in the group may advertise for new mates, supporting this hypothesis with evidence that *karrit-cut* calls, a common display often given in conjunction with head-bobbing in response to a variety of stimuli (MacRoberts & MacRoberts 1976), increased on experimental territories following removals. This hypothesis seems unlikely to explain the ability of birds to detect and initiate power struggles within such a short time frame, however, since there would be little opportunity for residents, much less intruders, to assess and respond to a newly-created vacancy within minutes of a bird being removed. We do know that helpers regularly foray off their home territory in search of vacancies (Koenig et al. 1996), and we suspect that they know the birds present on many nearby territories individually and are thus able to quickly assess and detect when a key bird is no longer present and a vacancy may therefore exist.

Once a bird detects a vacancy, his or her best option would presumably be to fill it as quietly as possible before other potential competitors discover and contest it, thereby avoiding a power struggle. We have no way of knowing how frequently this happens, although anecdotally it appears possible that some birds discover that a replacement has taken place — and thus that it is worth contesting a newly-established breeder — even several days after a vacancy has otherwise been filled. One such case involved a singleton female that had filled a vacancy, apparently successfully, without initiating a power struggle, but was then forced out by a coalition of three sisters four days later in a power struggle initiated by the coalition. The singleton female subsequently returned home to her natal group, recruited a sister, returned to the territory with the vacancy, and succeeded in displacing the coalition of three females in collaboration with her sister (Hannon et al. 1985).

This example supports the hypothesis that birds may recognise individuals within groups to the extent that they can tell when a vacancy has been filled and initiate power struggles as a means of contesting a new recruit that is not yet entirely settled. Alternatively, it is possible that birds detecting a vacancy may, at least in some cases, initiate a power struggle as a means of ensuring that the established breeder has indeed disappeared and that a vacancy actually exists. As a third possibility, the remaining breeders may advertise the vacancy, as suggested by Hannon et al. (1985), as a means of inciting competition among potential replacements (Cox & Le Boeuf 1977). Regardless of which mechanism is involved, the detection of vacancies and the initiation of power struggles involve intriguing behaviours worthy of additional attention.

Does cavity limitation drive cooperative breeding?

There is considerable variability among woodpeckers in the degree to which they excavate new cavities vs. reuse old cavities (Martin 1993), a difference that has a variety of potential fitness consequences in terms of predation rates, parasitism, and the time and energy required to construct a new cavity (Wiebe et al. 2007). As mentioned above, Acorn Woodpeckers frequently (> 50% of the time) reuse old nest cavities and are thus on the 'weak-excavator' side of this continuum. Although this is consistent with the hypothesis that cavities play an important role in limiting the life-history of this species, populations of at least

five other species of woodpeckers have approximately equivalent or higher rates of nest reuse, and thus are presumably even weaker excavators, but only one of these — the Red-cockaded Woodpecker — is a cooperative breeder (Wiebe et al. 2006).

As discussed previously, experimental work indicates that cavities play a key role in limiting territory establishment. Why this limitation apparently drives the unusual social behaviour of this species remains unclear, however. In contrast to the special resin-coated cavities used by Red-cockaded Woodpeckers that have been shown to play a key role in the evolution of delayed dispersal and cooperative breeding in that species (Walters et al. 1992), there is no obvious feature of cavities produced by Acorn Woodpeckers that distinguishes them in any special way (Hooge et al. 1999). Differences in the propensity of various species to excavate cavities in different habitats could certainly play a role in social evolution, but has only begun to be investigated either by examining species life histories (Wiebe et al. 2006, 2007) or by comparing different habitats and communities (Cornelius et al. 2008, Cockle et al. 2011).

How did caching behaviour evolve and how is it related to social behaviour?

The California range of Acorn Woodpeckers experiences a Mediterranean climate with generally dry summers and cool, wet winters. In such areas, it makes sense to cache acorns individually in small holes in a way that allows them to dry out despite wet, but typically above-freezing, conditions that would otherwise leave them vulnerable to rot or mould. The range of this species extends as far south as Colombia (Koenig et al. 1995b), however, with the center of its geographic distribution being in the highlands of southern Mexico (Honey-Escandón et al. 2008) where the diversity of oaks is particularly rich (Nixon 1993). In these more tropical regions, the phenology of oaks is likely to be considerably more variable than in temperate regions (Koenig & Williams 1979) and the environmental conditions during the non-breeding season are likely very different from the Mediterranean climate of California. Nonetheless, acorn storage in these regions has been observed, but appears to be neither universal nor necessarily correlated with group living (Dickey & Van Rossem 1938, Miller 1963, Skutch 1969, Koenig & Williams 1979, Ridgely & Gaulin 1980, Kattan 1988). Thus, it is unclear not only how or where

the unique caching behaviour of this species evolved, but also the relationship of acorn storage to its complex social organisation. Studies of other social *Melanerpes* species, yet to be conducted, may help address these questions.

What drives the ecological effects of male and female helpers?

Analysis of the fitness benefits of helpers indicates that female helpers have a non-significantly positive effect on the number of young fledged that does not vary with ecological conditions (i.e. the acorn crop) while that of male helpers is linearly related to the acorn crop, being highly positive when the crop is good and slightly negative when poor (Koenig et al. 2011; Figs. 3A,B). These differences are difficult to explain at any level of analysis. Functionally, they beg the question of why most helpers are tolerated by breeders, with the exception of male helpers when the acorn crop is large and conditions are good. Mechanistically, there appears to be no correlation between the fitness effects of helpers and their respective provisioning rates (Figs. 3C,D), and thus it is unclear what mechanism accounts for this positive male helper effect on group reproductive success.

It is possible that the fitness effects of helpers are due to behaviours besides provisioning, although to the extent that such data are available, they similarly fail to parallel the fitness effects of helpers (Mumme & de Queiroz 1985). Clearly there is much to be learned about both the fitness effects of helpers and the proximate mechanisms driving those effects in Acorn Woodpeckers, as well as most other cooperative breeding species.

How important is female mate choice in determining paternity?

We have already discussed the secretive manner in which Acorn Woodpeckers mate, with copulations being rarely observed. Consequently, we have no direct data on whether, or how, females discriminate among potential mates, despite there being high reproductive skew with a single male often siring all the young within a brood (Haydock & Koenig 2002, 2003). We are currently attempting to obtain data on the identity of sperm present on the perivitelline membrane of eggs (Carter et al. 2000) as a proxy for which males have copulated with females, but much remains to be done regarding the role of mate choice and sperm competition in this species.

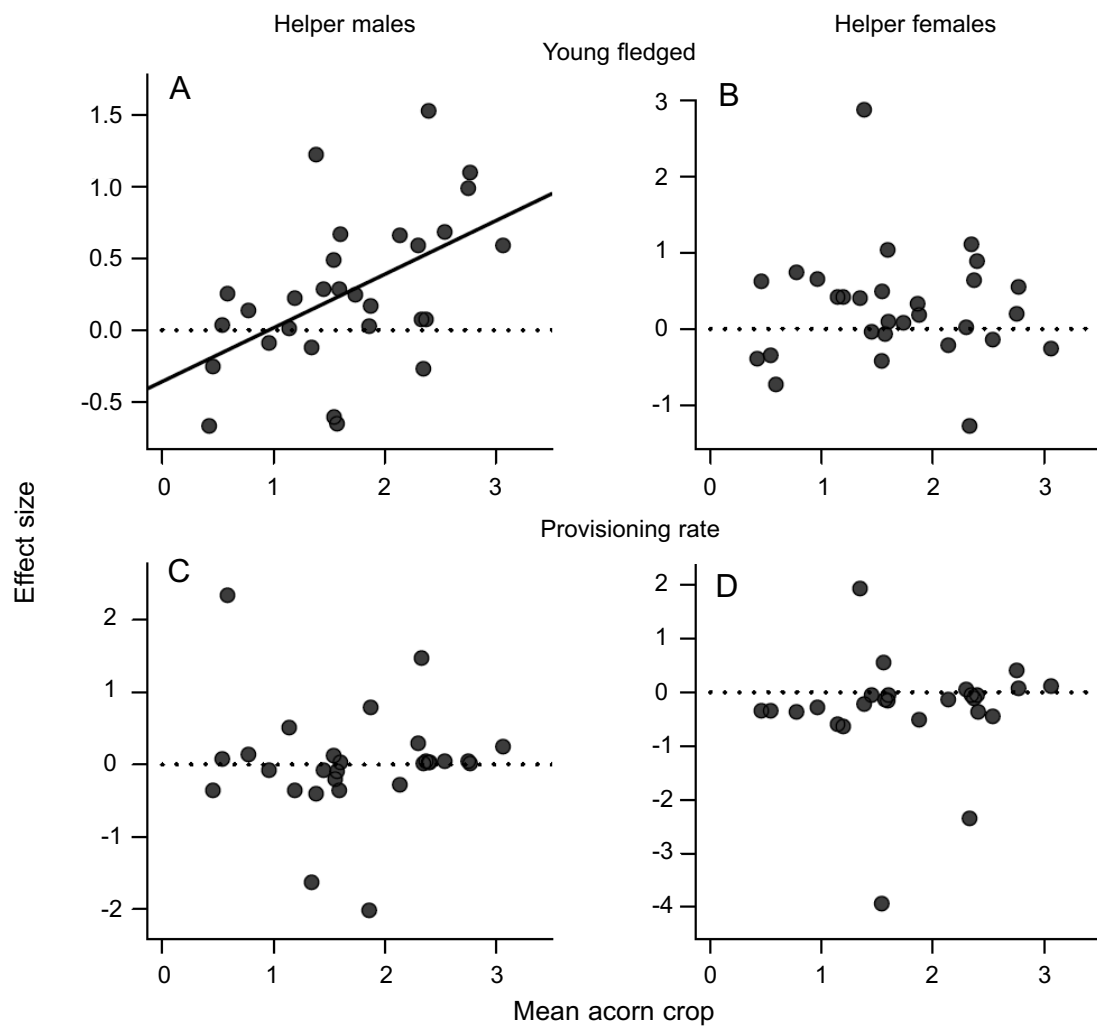


Fig. 3. Top: the indirect fitness benefits (estimated by the number of young fledged) attributable to a single (A) helper male and (B) helper female plotted against the mean size of the acorn crop (Koenig et al. 2011). Bottom: the provisioning rate (standardised for brood size and nestling age) of (C) helper males and (D) helper females plotted against the acorn crop. In all plots, each point is the mean for a year. Only (A) is significant ($r = 0.49$; $n = 29$ years; $p = 0.007$): the fitness effects of a helper male increases with the size of the acorn crop and is slightly negative when the crop is small, whereas the fitness effects of a helper female are non-significant and unrelated to the acorn crop. Provisioning rates are unrelated to the acorn crop for both helper males and females.

Why do females nest jointly?

Typically females will reciprocally destroy each other's eggs, forcing them to nest jointly in order for either to be successful (Koenig et al. 1995a). In 2012, however, we discovered, for the first time, a group whose females apparently nested separately within the territory, with both females provisioning at both nests (E. Walters & W. Koenig, unpublished data). Thus, plural breeding can occur, although it is apparently rare. More generally, however, we do not understand why females generally nest jointly rather than separately. Joint-nesting ensures both synchrony and shared maternity within nests, but entails considerable wasted effort in terms of egg destruction

that could potentially be avoided by plural nesting. On the other hand, joint-nesting eliminates the necessity for group members to choose among nests at which to provision, which may ultimately benefit a subordinate female that would otherwise be outcompeted by her joint-nesting relative.

A dominant female could conceivably keep a subordinate from laying eggs entirely within a group if she could recognise her own eggs, but such egg recognition apparently does not occur. Presumably the all-white, relatively indistinguishable eggs of this species are a constraint making it difficult for birds to evolve egg recognition, although additional study is, once again, called for. In any case, we understand very little about

why females nest jointly. Geographic variation in this behaviour, although difficult to assess, could potentially shed light on the ecological basis of this problem.

DISCUSSION

There are many more questions to be answered than there is time, energy, or funds to address in a complex species like the Acorn Woodpecker. We suspect that a similar list of questions could be made for almost any species, although no doubt several of the unique aspects of Acorn Woodpeckers make this task particularly easy in our case. Indeed, we believe that some of the most important benefits of long-term studies — in addition to the demographic data that can be acquired and the quantification of otherwise difficult-to-study factors such as lifetime fitness and linkage across generations (Fitzpatrick & Woolfenden 1981) — are the opportunity to observe responses to environmental changes, the ability to discover and observe phenomena that may initially appear to be rare but illustrate unexpected behavioural plasticity, and the chance to digest the potential significance of behaviours whose function is not immediately obvious. Long-term population studies are difficult to fund and maintain (Birkhead 2014), but provide unique opportunities to test hypotheses for the adaptive significance of many behaviours and to gain perspective of a sort that cannot be achieved in short time-frames or by alternatives such as space-for-time investigations (Clutton-Brock & Sheldon 2010).

There are, of course, pitfalls to studying the same population for an extended period of time. As pointed out by Cohen (1976), there is always the possibility that we are chasing 'nondegenerate limit random variables' that converge over time, but to an arbitrary value with no ecological or functional significance. If we were to start a second study of a population of Acorn Woodpeckers in a parallel universe that was identical to the one we've studied at Hastings Reservation, would we generate comparable demographic data, come to similar conclusions, and have the same set of unanswered questions? Our guess is probably not, although we suspect that we would generate equally interesting sets of conclusions and questions, just as studies of the same species have frequently revealed intraspecific differences, both in Acorn Woodpeckers (Koenig & Stacey 1990) and in vertebrates generally (Lott 1991).

The bottom line is that there is much to be gained by in-depth, long-term studies, not just in terms of answering the questions one might have had initially, but by generating questions that could not possibly have been asked when the study was started. For example, we have observed enormous changes in molecular methods over the past four decades, allowing questions of relatedness to be asked today that were impossible to address in the 1970s. Some of these new questions will potentially lead to novel ideas that will likely alter our prior perspectives. Indeed, a unique advantage of a long-term study is that it provides one with the opportunity to revise one's thoughts about the factors that are important to the population as one has the opportunity to observe and study it under differing ecological conditions and using newly developed techniques.

In the case of the Acorn Woodpecker, we offer the above list as a starting point for a future woodpecker student (or more generally of animal behaviour) looking for interesting unanswered questions to study. We trust they will answer at least some of them, no doubt generating their own list of even more perplexing questions in the process.

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STRESZCZENIE

[Czego jeszcze nie wiemy o gniazdującym kooperatywnie dzięciole — dzieciurze żółędziowym]

Dzięciur żółędziowy jest jednym z niewielu gatunków dzięciołów, u którego stwierdzono lęgi kooperatywne. Żyje on w grupach składających się z maksymalnie 15 osobników obu płci i charakteryzuje się dość skomplikowanym systemem rozrodczym. Wiedza o tym gatunku jest dość rozległa, głównie dzięki ponad 40 letnim badaniom prowadzonym w Kalifornii, jednak nadal jest wiele niezbadanych aspektów jego biologii. W pracy wiele z takich zagadnień jest omówionych w szerszym kontekście, wraz z sugestiami przyszłych badań. Przedstawione zagadnienia są pogrupowane od relatywnie szczegółowych pytań interesujących z punktu widzenia gatunku, takich jak dlaczego ptaki dorosłe mają jasne tęczówki lub dlaczego młode osobniki przypominają upierzeniem dorosłe samce (Fig. 1), aż do problemów bardziej ogólnych, jak związek dostępności miejsc gniazdowych z ewolucją specyficznych zachowań socjalnych, czy adaptacyjne znaczenie redukcji lęgu u gatunku z pomocnikami gniazdowymi. W tym ostatnim kontekście interesujące są pytania o wpływ dostępności pożywienia (zmagazynowanych żółędzi) na liczbę piskląt (Fig. 2), czy zależności pomiędzy płcią pomocników lęgowych a liczbą wyprowadzanych piskląt przez grupę dzięciurów (Fig. 3).

Autorzy podkreślają, że szczególnie wartościowe są badania długoterminowe, które nie tylko dają nam możliwość odpowiedzi na wiele ciekawych pytań, ale co ważniejsze — generują kolejne pytania, które mogłyby być przeoczone bez szczegółowej wiedzy o biologii badanego gatunku.

A minimally invasive method for sampling nest and roost cavities for fungi: a novel approach to identify the fungi associated with cavity-nesting birds

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Abstract. Relationships among cavity-nesting birds, trees, and wood decay fungi pose interesting management challenges and research questions in many systems. Ornithologists need to understand the relationships between cavity-nesting birds and fungi in order to understand the habitat requirements of these birds. Typically, researchers rely on fruiting body surveys to identify the fungal players in these relationships. Fruiting body surveys enable nondestructive sampling, but vastly underestimate fungal presence and diversity and may miss species of critical importance to cavity-nesting birds; thus new methods for such analyses are necessary. Here we present a novel technique to nondestructively sample the wood inside tree cavities, which produces samples that can be processed using DNA-based methods to identify fungi. We tested our method on Red-cockaded Woodpecker *Picoides borealis* excavations, half of which were from trees with *Porodaedalea pini* fruiting bodies. Using our new approach, we detected *P. pini* in 90% of the excavations in trees with fruiting bodies, but also in 60% of the excavations in trees without fruiting bodies and identified nine additional taxa of wood decay fungi that did not have fruiting bodies present. Our approach offers improved detection of fungi through non-destructive sampling of excavated cavities and we developed an improved primer specific to the fungal phylum that contains most wood decay fungi (Basidiomycota), thus providing managers and researchers a critical tool to better determine which fungi are important to cavity-nesting birds.

Key words: Basidiomycota specific primer, cavity-excavating birds, cavity-nesting birds, excavators, fungi, hole-nesting birds, ITS4b-21, *Picoides borealis*, *Porodaedalea pini*, Red-cockaded Woodpecker, wood decay fungi

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INTRODUCTION

Primary and secondary cavity-nesting birds rely heavily upon tree cavities. Heartwood infecting fungi help create suitable excavation habitat for cavity-excavating birds by softening the wood surrounding excavation sites (Conner et al. 1976, Jackson & Jackson 2004, Witt 2010, Cockle et al. 2012, Zahner et al. 2012). Fungi also create non-excavated or “naturally formed” cavities which are used by cavity-nesters in many systems (Cornelius et al. 2008, Cockle et al. 2011,

Wesołowski 2012). However, very little is known about which fungi actually inhabit the wood surrounding excavated and non-excavated cavities. A better understanding of the fungal inhabitants of excavation sites and sites of naturally occurring cavities is necessary in order to better understand cavity formation processes and the dynamics of cavity-nesting communities and to inform forest management affecting these species.

Some studies have implicated specific wood decay fungi to be associated with cavity-excavating birds. For example, Red-cockaded

Woodpeckers *Picoides borealis* have long been thought to have an association with *Porodaedalea pini* (previously *Phellinus pini*), a fungus that infects the heartwood of the living pine trees in which the birds excavate (Ligon 1970, Conner et al. 1976, Jackson & Jackson 2004). Cockle et al. (2012) recently suggested that fungi in the family Polyporaceae facilitate cavity excavation for woodpeckers in Argentina. *Fomitopsis pinicola* has been linked to Piced excavations in northwestern USA (Huss et al. 2002). Many others have noted that *Phellinus tremulae*, one of the most common causes of decay in live aspen, may be important for cavity-excavating birds in aspen-dominated systems (Hart & Hart 2001, Savignac & Machtans 2006, Witt 2010).

Traditionally, correlations between cavity-excavating birds and wood decay fungi have been based on surveys of external fruiting bodies observed on trees that birds choose for excavation. However, fruiting body surveys are biased to the fungal species fruiting at the time of sampling and thus, a limited fungal community is observable with this method (Blanc & Martin 2012, Cockle et al. 2012). Moreover, reliance on visual surveys could cause important fungal species that rarely produce fruiting bodies or produce microscopic or cryptic fruiting bodies to be overlooked completely. Even among those species producing visible fruiting bodies, while the presence of a fruiting body indicates a tree is infected by a fungal species, the absence thereof is not indicative of the absence of fungi. Fungal mycelia can be present within the heartwood of a tree for years, even decades before producing a fruiting body and hence, fruiting body surveys drastically underestimate the prevalence of fungi (Lindner et al. 2011b), as well as the diversity of fungi inhabiting individual trees. Rather, fruiting bodies provide information about which of the fungi present in a tree happen to be fruiting at the time of the survey (Boddy 2001). Furthermore, the presence of a fruiting body on the trunk of a tree may represent a localized fungal infection and does not demonstrate that the entire tree, including the cavity excavation location, has been affected. The columns of decay above and below fruiting bodies are highly variable across host and fungal species (Silverborg 1954). Some heartwood decaying fungi can be responsible for decay in other areas of a tree (e.g. the sapwood) and thus are not necessarily affecting the excavation site. Similarly, fruiting bodies of fungi that are known as agents of heart rot are not always reliable indicators of

the presence of heart rot — for example, *Ganoderma applanatum* can be an agent of both heart and butt rot (Ostry et al. 2011). Thus, fruiting body surveys tell us little about which fungal species are actually in the wood surrounding a cavity that has been excavated.

Reliance on fruiting body surveys to examine the relationships between cavity-nesting birds and wood decay fungi results in management guidelines that promote the preservation of trees with existing cavities and visible signs of decay. While it is important to preserve trees with existing cavities and visible symptoms of decay, infected trees that do not have visible signs of decay (i.e. apparently sound trees) may be equally or even more important to cavity-nesting birds (Blanc & Martin 2012). Some bird species, including Red-cockaded Woodpeckers, make their excavations in living trees and continue to use their excavations for many years. For these species, living trees without visible signs of decay may be more suitable for excavation than living trees with visible signs of decay because cavities in the former will endure longer, this may hold true for dead trees in some systems as well. While most cavity excavators complete excavation in dead trees in a relatively short amount of time and only utilize their cavities for one breeding season, it is important that they select trees that are sound and will withstand natural stochastic events, trees with some internal decay but without fruiting bodies fit this description. Furthermore, when a tree with a cavity remains on the landscape for multiple years, it is beneficial to the non-excavating community of cavity users as well as excavating species (Blanc & Walters 2008). Birds often select trees without visible signs of decay for excavation, perhaps purposefully selecting trees that do not have fruiting bodies and thus have not yet entered an advanced stage of decay.

Currently, several methods exist to detect the presence of internal decay in living trees, such as increment coring, destructive sampling (large-scale dissection), the use of Resistographs and sonic and electrical impedance tomography (Brazee et al. 2011). In most cases, these methods only measure the soundness of wood, either visually (coring and destructive sampling) or via resistance (Resistographs). None of these methods allow researchers to determine the identities of the actual agents of decay, and thus like fruiting body surveys, are limited in their utility in documenting fungal communities. Culture-based work is one method that does allow for accurate species

identification, under the proper conditions, but the time and effort required frequently makes large-scale culture-based community studies impractical for managers and researchers alike.

The Red-cockaded Woodpecker is an endangered, cooperatively breeding bird that is an important cavity excavator in the longleaf pine ecosystem of the southeastern United States (Ligon 1970, Walters et al. 1988). Red-cockaded Woodpeckers may have a particularly interesting relationship with heartwood infecting fungi due to their excavation behavior. Uniquely, Red-cockaded Woodpeckers solely excavate their cavities through the sapwood and into the heartwood of living pine trees, and the time to complete this process can range from less than one year to over 15 years (Harding & Walters 2004). Populations of these birds can be limited by the availability of cavities and therefore understanding their excavation behavior is an aspect that continues to be critical to successful management efforts of these endangered birds (Walters 1991).

In an effort to better understand Red-cockaded Woodpecker habitat requirements and help inform forest management decisions based on these requirements, we designed a tool to collect samples of fungi from the wood surrounding Red-cockaded Woodpecker cavities in a non-destructive, minimally invasive manner. These samples were processed with molecular methods using a known fungal specific forward primer (ITS1F; Gardes & Bruns, 1993) and a newly designed reverse primer (ITS4b-21; described herein) specific for the phylum Basidiomycota, the group that contains most wood decay fungi. Our new, non-destructive sampling tool, primer, and method not only aid in determining whether or not a tree selected for excavation is decayed, but also allow for the identification of the main agents of decay within the excavation site. This novel approach can be used to uncover ecological linkages between excavators and fungi and to help guide future management decisions that focus on the preservation of trees suitable for excavation, not only for Red-cockaded Woodpeckers but also for other avian species in other systems.

METHODS

Study site

We conducted this research on Marine Corps Base Camp Lejeune (MCBCL), in Onslow County, on the central coastline of North Carolina, USA. This

military installation consists of 110,000 acres of land and 26,000 acres of water. Of the pine stands on MCBCL that are not heavily mixed with hardwoods, 64% are dominated by Loblolly Pine *Pinus taeda*, 24% by Longleaf Pine *Pinus palustris* and 11% by Pond Pine *Pinus serotina* (Walters 2004). The only heart rot fungus we observed fruiting on living pine trees on MCBCL was *Porodaedalea pini* s.l. (Southeastern clade), hereafter referred to as *P. pini* SE. Fruiting body surveys of this close relative of *Porodaedalea pini* s.s. (see description of *Porodaedalea* sp. 1 in Brazee & Lindner 2013) would suggest that this species is not found in abundance on MCBCL. Over 4 years of intermittent but intense visual surveying of our study site, we located only 24 *P. pini* SE fruiting bodies in Red-cockaded Woodpecker habitat on MCBCL. Approximately 2% of the trees housing complete or incomplete, human-made (drilled) or Red-cockaded Woodpecker-made excavations had *P. pini* SE fruiting bodies. The proportion of pine trees in similar habitat with *P. pini* SE fruiting bodies and without excavations is less than 1% (M. A. Jusino unpublished data).

Sampling tool

To collect wood from the interior of Red-cockaded Woodpecker cavities, we designed a specialized tool that can scrape and capture wood shavings from within a cavity without causing destruction of the cavity itself. This tool can be sterilized and easily used at cavity height. Our sampling tool, hereafter called "the sharpened spoon", was designed with ease of sampling in mind. By design, the spoon is less arduous to use for wood collection at cavity height than other tools such as increment borers, chisels or drills. The sharpened spoon enables the collection of wood samples from the interior of cavities or cavity starts and causes much less damage to the tree or the interior of the cavity than drills, chisels, and increment borers.

The prototype of our sampling tool consisted of a 20 gauge stainless steel ½ teaspoon measuring spoon, a 0.33 meter long M6 x 1.0 (¼"-20) threaded steel rod and a M6 x 1.0 steel hex nut (Fig. 1A). We cut the handle of the spoon to a length of 5 centimeters. A 5 centimeter long slot was created in one end of the rod with a grinding wheel affixed to a rotary Dremel tool. The spoon was test fitted into the rod and its width adjusted to allow fitting of the M6 x 1.0 hex nut over the spoon handle. After test fitting, the pieces were disassembled and a sufficient amount of paste flux was applied

to the slot within the rod and the spoon handle to allow for a clean solder connection. The pieces were re-assembled and the M6 x 1.0 nut was threaded onto the rod, locking the spoon handle into place. To ensure the pieces would not loosen over time, we soldered the spoon handle into the rod with a flux-core solder and a propane torch. Finally, we sharpened the outer rim and the inside edge of the spoon with a small grinding stone affixed to the Dremel tool and metal files. Sharpening the inside edge allowed the spoon to scrape the target wood more efficiently (Fig. 1B). Field trials suggest the spoon may need to be re-sharpened after sampling about 100 trees. A 0.3 centimeter hole was drilled through the rod opposite the spoon end, allowing a 2.5 centimeter metal key ring to be added for attaching the tool to a belt for field use (Fig. 2).

Sample collection

We tested our collection tool against two other methods of decay detection, visual fruiting body surveys and core samples at cavity height, using 20 trees on MCBCL with Red-cockaded Woodpecker excavations. Of the 20 trees selected, 10 trees had fruiting bodies of *P. pini* SE and 10 trees did not have fruiting bodies. We photographed and aseptically sampled fruiting bodies, but did not collect them because they are very rare on our study site. One of us (MAJ) climbed each selected tree with Swedish climbing ladders, a climbing harness and a tree strap. Once cavity height was reached, the sharpened spoon was flame sterilized with 70% ethanol. We collected samples from two to three locations within the cavity

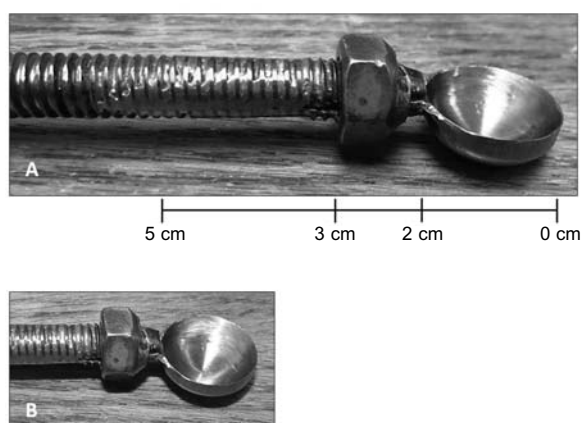


Fig. 1. The design of our sampling tool, which is made of a sharpened measuring spoon, a steel rod and a hex nut. A — side view, with a size reference, B — top view of the inside of the spoon.

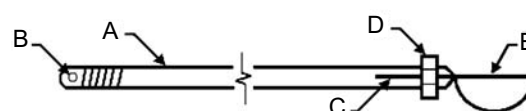


Fig. 2. An outline of our sampling tool with the components labeled. A — the threaded steel rod; B — key ring hold; C — five centimeter long slot; D — hex nut; E — sharpened measuring spoon.

depending on whether the tree housed a fully excavated cavity or a cavity start (i.e. incomplete excavation; Fig. 3). We flame sterilized the spoon between each sampling location.

The sampling locations within the cavity were determined by how accessible they were with the spoon (Fig. 3). Sampling location A refers to the entrance tunnel of the cavity, and represents the sapwood of the tree. Location B refers to the dome (or roof) of the cavity and consists of heartwood. Location C refers to the back wall of the cavity, and consists of heartwood. Location E refers to the front of a cavity start and is sapwood whereas location D refers to the back of a cavity start and is typically heartwood. If a start was not advanced enough to have reached the heartwood, we collected E, but not D.

We used the sharpened spoon to scrape wood shavings from each sampling location. Some force was used to effectively scrape the wood and gather the shavings in the bottom of the spoon. After each scrape, the sharpened spoon was extracted from the cavity and the sample was transferred from the spoon into a sterile 1.5 mL tube. Though each scrape could be considered a separate sample, our data are pooled for this analysis because our goal is to show that the sharpened spoon can be used to identify agents of decay in the wood surrounding Red-cockaded Woodpecker excavations. After attaining cavity height, the total time to sterily sample all locations in one excavation with the spoon ranged from 5 to 10 minutes.

Additionally, the cavity starts in our sample were aseptically cored approximately 20 cm above the cavity entrance using a sterilized borer (Fig. 3F). The heartwood of these cores was kept, the sapwood portion was re-inserted into the core site to prevent the introduction of pathogenic organisms. Completed cavities were not cored at cavity height because it is possible to introduce a fissure in the dome of a cavity when coring, which would allow resin to drip into the body of the cavity and cause harm to the cavity occupant(s). There was

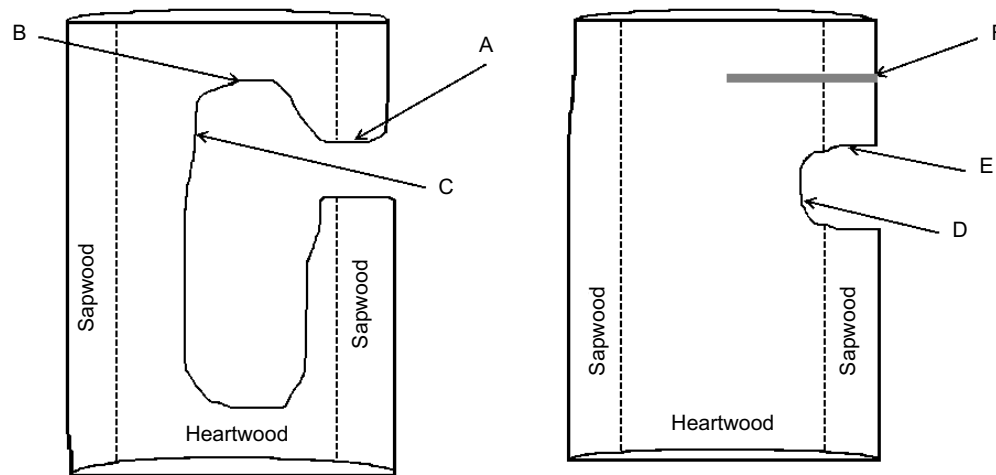


Fig. 3. Cross sections of a complete cavity (left), and a cavity start (right), showing approximate sampling locations as well as approximate heartwood and sapwood dimensions. A-E — scrape samples: A & E — in the sapwood, B, C & D — in the heartwood, F — the approximate coring site.

no such danger for cavity starts. The total time to properly clean a borer and collect a core sample at cavity height ranged from 30 to 40 minutes, not including climbing time.

DNA extraction, PCR, cloning and sequencing

Scraped wood samples and fruiting body samples were stored in 200 μ L of filter-sterilized CTAB cell lysis solution (see Lindner and Banik 2009 for solution protocol) and frozen at -80°C . DNA extraction followed the protocol described by Brazee & Lindner (2013). Increment core samples were placed in 30 mL of filter-sterilized CTAB cell lysis solution (Lindner & Banik 2009) and ground using a sterilized immersion hand blender. After the cores were ground, they were frozen at -80°C for at least 24 hours. Subsequent extraction of DNA from cores followed a modified version of the protocol described by Brazee & Lindner (2013). Frozen samples were placed in a 65°C water bath for 3 hours. Then one mL of supernatant was transferred to a 1.5 mL tube and centrifuged at 10,000 rcf for 10 minutes and 100 μ L of supernatant was transferred to a new strip tube. Negative controls were included for both extraction protocols, and these extractions served as our negative controls for each downstream step.

We tested standard PCR, cloning and sequencing protocols on *Porodaedalea pini* SE fruiting body DNA using a primer pair that is reportedly specific for fungi in the phylum Basidiomycota, ITS1F and ITS4b (Gardes & Bruns 1993). We had limited success directly sequencing or cloning and sequencing *Porodaedalea pini* SE DNA using this

primer pair, even after significant manipulation of variables such as annealing temperature, number of PCR cycles, etc. To ensure we successfully extracted *Porodaedalea pini* SE DNA, we performed PCR, cloning and sequencing using the general fungal primer pair ITS1F and ITS4 (Gardes & Bruns 1993), and had no issues obtaining sequences using these primers. Because we wanted to ensure detection of fungi from the phylum Basidiomycota, and especially fungi in the Hymenochaetoid clade, we performed an analysis of mismatches between known sequences from the Hymenochaetoid clade and the primer ITS4b. Based on this analysis, we designed a new primer specific for Basidiomycota, ITS4b-21 (CAGGA-GACTTGACACGGTCC), which is derived from ITS4b (Gardes & Bruns 1993) and which had fewer mismatches for members of the Hymenochaetoid clade. Preliminary testing determined that ITS4b-21 amplifies members of the Hymenochaetoid clade of fungi, including *Porodaedalea pini* SE, that are not amplified by ITS4b (M. A. Jusino and D. L. Lindner own data). Many important white-rot fungi belong to the Hymenochaetoid clade, and therefore their detection is vital to studies of fungi associated with cavity excavation.

We performed PCR on all samples taken with the sharpened spoon and the increment borer using ITS1F and ITS4b-21. Our PCR protocol was similar to the protocol for ITS1F and ITS4 used by Lindner & Banik (2009), however, the thermocycler conditions differed (see below). We diluted the 5x green GoTaq reaction buffer to a 1x working

concentration and we used 0.04 units of GoTaq DNA Polymerase per microliter of reaction volume. We also added 0.13 μ L of 3% polyvinylpyrrolidone (PVP) per microliter of each PCR reaction. All other PCR component concentrations can be found in Lindner and Banik (2009). Our thermocycler conditions were as follows: initial denaturing at 95 °C for 5 minutes; 15 cycles of denaturing at 94 °C for 30 seconds, annealing at 55 °C for 45 seconds and extension at 72 °C for 1 minute; 25 cycles of denaturing at 94 °C for 30 seconds, annealing at 52 °C for 45 seconds and extension at 72 °C for 1 minute; a final extension at 72 °C for 10 minutes.

After amplification, we ran the PCR products on a 1.5% agarose gel stained with ethidium bromide (hereafter, gel). Reactions with visible amplification products were cloned and sequenced following the protocol described by Lindner & Banik (2009) and the sequencing protocols described by Lindner et al. (2011a). We did not sequence in both directions, ITS4 was used for all sequencing reactions. We edited our sequences with Sequencher 4.9 (GeneCodes Corp.). Sequences were assigned identities based on BLAST comparisons to GenBank (NCBI) sequences.

RESULTS

Fungal prevalence was determined by successful PCR amplification which was confirmed via gel electrophoresis for 18 of the 20 trees sampled (90%), with varying rates of success achieved by sampling method (scrapes or cores) and presence of fungal fruiting bodies. Specifically, 18 of the 20 trees (90%) sampled with the sharpened spoon (scrapes) and 6 of the 13 (46%) that were cored produced PCR products that could be visualized on a gel. Of the 10 trees that had fruiting bodies, 9 of the 10 (90%) that were scraped and 5 of the 7 (71%) that were cored produced PCR products that could be visualized on a gel. Of the ten trees without fruiting bodies, 8 of the 10 (80%) that were scraped and 1 of the 6 (17%) that were cored produced PCR products that could be visualized on a gel. None of the negative controls produced PCR products that could be visualized on a gel.

PCR products were ligated and cloned regardless of whether they could be visualized on a gel, although the only samples that produced viable bacterial colonies were those that could be visualized. The most prevalent wood decay fungus we identified in our samples was *P. pini* SE, which we

successfully cloned and sequenced from 16 of the 20 (80%) excavations that we sampled with spoon scrapes, and in 6 of the 13 (46%) of the cores (Table 1). We also identified 9 other wood decay fungi from spoon scrapes from 8 of the 20 (40%) trees sampled: *Agaricomycetes* sp. 1, *Atheliaceae* sp. 2, *Atheliales* sp. 3, *Peniophora cinerea*, *Peniophora* sp. 4, *Phlebia brevispora*, *Postia sericeomollis*, *Stereum* sp. 4, and *Trametes versicolor* (Table 1). *Porodaedalea pini* SE was the only fungus detected from the core samples.

Among trees with *P. pini* SE fruiting bodies (i.e. trees that are known to be infected with a wood decay fungus), we were able to detect *P. pini* SE in 9 of the 10 (90%) excavations that were sampled in such trees with the sharpened spoon and in 5 of the 7 (71%) core samples. We detected *P. pini* SE in 1 of the 6 (17%) core samples from above excavations in trees without fruiting bodies. However, when these same excavations were scraped, we detected wood decay fungi in 8 out of 10 (80%) excavations, including 6 detections of *P. pini* SE. We did not detect any fungi in cores or scrapes from 2 of the 10 (20%) trees with excavations but without fruiting bodies (Table 1).

DISCUSSION

Our novel protocol provides a considerable improvement over traditional methods for detecting fungi associated with excavating and non-excavating cavity-nesting birds. Our method can be used to identify fungi that would otherwise be undocumented because of the absence of fruiting bodies and the failure of other methods to detect these fungi. When combined with molecular methods and the primer we designed (ITS4b-21), our collection tool can be used to help determine the incidence and identity of decay fungi as well as the other fungal species (lacking fruiting bodies) present within the wood surrounding an excavation site. By identifying the fungi present we can determine which fungi are associated with excavating and non-excavating cavity-nesters. This information can be used to inform habitat management for cavity-nesting species.

We found the sharpened spoon to be more effective in detecting fungi than the increment borer in both complete and incomplete Red-cockaded Woodpecker excavations (Table 1). We also found that molecular methods can be used to detect fungi from both types of samples. However, we detected far less Basidiomycota diversity in the

Table 1. Cavity type (complete cavity or cavity start), presence of a *Porodaedalea pini* SE fruiting body, the total number of fungal taxa cloned from the scrape and core samples, and the identities of the wood decay fungi detected from scrape and core samples collected from Red-cockaded Woodpecker excavations, and the closest Genbank BLAST hits of the decay fungi detected, with accession numbers and % identity match to those hits. NA denotes not applicable as not all completed cavities used in this analysis were cored. Taxa indicated with (*) may be associated with processes other than the decay of heartwood.

<i>P. pini</i> SE fruiting body	Excavation type	Scrapes # fungal taxa	Decay fungi	Nearest GenBank match (accession number, identity match)	# fungal taxa	Cores	Decay fungi
Present	Complete	6	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	1		<i>Porodaedalea pini</i> SE
			<i>Atheliales</i> sp. 3*	JN943909.1; 92%			
	Complete	5	<i>Agaricomycetes</i> sp. 1*	EF694649.1; 99%	NA		
			<i>Porodaedalea pini</i> SE	JX110039.1; 100%			
			<i>Peniophora</i> sp. 4	EF672293.1; 99%			
	Complete	3	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	NA		
	Complete	2	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	NA		
	Start	5	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	1		<i>Porodaedalea pini</i> SE
	Start	2	<i>Phlebia brevispora</i>	AB084616.1; 99%	0		
			<i>Porodaedalea pini</i> SE	JX110039.1; 100%			
	Start	2	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	1		<i>Porodaedalea pini</i> SE
	Start	2	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	0		
			<i>Trametes versicolor</i>	KC176344.1; 99%			
	Start	1	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	1		<i>Porodaedalea pini</i> SE
	Start	0			1		<i>Porodaedalea pini</i> SE
Absent	Complete	6	<i>Phlebia brevispora</i>	AB084616.1; 99%	NA		
			<i>Postia sericeomollis</i>	KC585367.1; 98%			
	Complete	5	<i>Phlebia brevispora</i>	AB084616.1; 99%	NA		
	Complete	4	<i>Atheliaceae</i> sp. 2	GU187502.1; 96%	NA		
			<i>Peniophora cinerea</i>	GU062269.1; 99%			
			<i>Porodaedalea pini</i> SE	JX110039.1; 100%			
			<i>Trametes versicolor</i>	KC176344.1; 99%			
	Complete	1	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	NA		
	Start	2	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	0		
			<i>Stereum</i> sp. 4	JX460856.1; 98%			
	Start	1	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	0		
	Start	1	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	1		<i>Porodaedalea pini</i> SE
	Start	1	<i>Porodaedalea pini</i> SE	JX110039.1; 100%	0		
	Start	0			0		
	Start	0			0		

cores (1 taxon overall) than in the samples taken with the sharpened spoon (24 taxa overall, 10 of which were decay fungi). Analysis of samples taken with the sharpened spoon confirmed the presence of multiple species of fungi that were not externally apparent and that were not observed with the core samples. Furthermore, the sharpened spoon can be used to collect samples from within an excavation, and thus can be used to examine the fungi associated with the cavity occupant.

We were able to sample within the actual cavity or cavity start with the spoon and safely sample the heartwood of completed cavities without the risk of creating a fissure in the top of the cavity, which is one potential problem with heartwood cores at cavity height. Creating a fissure in the dome of a cavity would allow resin to leak into the cavity, thus introducing a possible risk to any bird using the cavity. Additionally, samples taken with the sharpened spoon require much less time for collection and processing compared to samples taken with the increment borer. Based on this study, we found that an experienced climber can sample more than sixteen excavations in an eight-hour field day with the sharpened spoon, twice as many as when an increment borer is used. Sampling with the sharpened spoon also required less lab processing time than cores. Unlike the fine scrapings collected with the sharpened spoon, cores collected by an increment borer require a vigorous sterile grinding step prior to DNA extraction. Even though our implementation of an immersion blender required less time than traditional core grinding methods, processing cores was still much more laborious and time consuming than processing spoon-collected samples.

For this study, our principal objective was accurate detection and species identification of the fungi collected using various sampling techniques. Therefore, we choose traditional Sanger sequencing methods over newer next-generation techniques because Sanger methods provide longer read lengths and more accurate sequence identification than most cost-comparable next-generation sequencing methods. We detected multiple fungal taxa in 12 of the 20 trees we tested and may have detected even more taxa if we had used a more general primer pair capable of capturing more than one fungal phylum, such as ITS1F and ITS4 (Gardes & Bruns 1993). We did not use a more general fungal primer pair for our PCR reactions because we were specifically interested in determining if the samples collected with the

sharpened spoon could be used to detect wood decay fungi. Fungi from the phylum Ascomycota are very common and tend to dominate samples (based on preliminary data using general primers; Jusino et al. unpublished data), and while some fungi from this phylum can be important contributors to wood decay, most known decay fungi are in the phylum Basidiomycota. Wood decay fungi from the phylum Basidiomycota would have been amplified with a more general primer pair, but we increased our chances of successfully detecting such species by using a more specific primer pair. By using our modified primer, ITS4b-21, we were able to detect wood decay fungi in the Hymenochaetoid clade that otherwise would have been missed.

While the presence of a fungal fruiting body indicates that a fungus is present in a tree, it does not indicate that the fungus has spread throughout the entire stem of a tree. Thus, when sampling Red-cockaded Woodpecker excavations in trees with *P. pini* SE fruiting bodies, one should not always expect to find *P. pini* SE in the wood surrounding the cavity. This may explain the instances in which either the sharpened spoon or increment borer failed to detect *P. pini* SE in trees with fruiting bodies. However, that *P. pini* SE was detected in the core sample taken near the cavity in one of these instances, and in the spoon sample but not the core sample in the other two instances, suggests that we did not always detect every heart rot species present in the trees we sampled with our methods. We note that all of these detection failures were associated with incomplete rather than complete excavations. Nevertheless, we have demonstrated that the absence of a fruiting body does not imply the absence of a fungus given that we successfully detected *P. pini* SE from 6 of the 10 (60%) trees without fruiting bodies as well as six other wood decay fungi, from four such trees.

Recently, it has been suggested that cavity excavators use fungal fruiting bodies as visual cues to select trees suitable for excavation (Hart & Hart 2001, Witt 2010). This hypothesis has only been tested once, by Rudolph et al. (1995), who found no support for this idea related to Red-cockaded Woodpeckers. Rudolph et al. (1995) attached *Porodaedalea pini* fruiting bodies to 40 trees within 10 active Red-cockaded Woodpecker territories, using 40 other trees within those territories as controls. After three years, none of the trees with fruiting bodies were used by Red-cockaded Woodpeckers, though the birds excavated a cavity start in one control tree.

Some researchers have suggested that cavity excavators use acoustic cues to detect decay in a tree (e.g. Zahner et al. 2012). Specifically, some birds may assess the density of wood acoustically, although this would be difficult to test for most cavity excavators. There are multiple other cues and cue combinations that primary cavity excavators can use to determine trees and locations on trees suitable for excavation, including olfactory signals. The use of our new method will help researchers determine if cavity excavators select excavation sites based on the presence or absence of certain fungal species. If they do, the mechanism behind excavation site selection can be tested.

Our results indicate that trees without visible signs of decay may harbor wood-decaying fungi and thus be a potentially important resource for cavity-nesting birds. For researchers, internal detection of rot via acoustic methods is an improvement over visual surveys, however the information gained from these methods is based on the density of wood. One does not learn the identity of important hidden players in a fungal community by simply examining a substrate visually or acoustically. To understand whether specific fungi or specific groups of fungi are important to cavity-excavating and cavity-nesting birds, it is necessary to determine which fungal groups are associated with the nest and roost cavities of these birds. Our novel approach allows us to more robustly determine the fungi present in the wood surrounding excavations, a critical first step in resolving the relationships between cavity users and fungi so that forests can be managed effectively for cavity-nesters and cavity excavators.

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STRESZCZENIE

[Nowa metoda pobierania prób w dziuplach w celu identyfikacji występujących w nich grzybów]

Zależności pomiędzy dziuplakami, drzewami i grzybami rozkładającymi drewno stanowią ważne zagadnienie zarówno z punktu widzenia ochrony przyrody, jak i interesujące pytanie badawcze. W tym drugim przypadku poznanie zależności między dziuplakami i występującymi w dziuplach grzybami może mieć istotne znaczenie dla zrozumienia wymagań siedliskowych wielu gatunków ptaków.

Dotychczas w celu określenia obecności i gatunków grzybów występujących w danym drzewie analizowano owocniki tych grzybów. Badanie owocników należy do nieinwazyjnych sposobów

pobierania prób, jednak wiąże się z dużym niedoszacowaniem częstości występowania i różnorodności grzybów, a także pomijaniem gatunków, które mogą mieć kluczowe znaczenie dla gatunków gnieźdzących się w dziuplach. Dlatego rozwój metod mających na celu identyfikację grzybów rozkładających drewno, szczególnie tych obecnych w miejscach powstania lub wykuwania dziupli, jest bardzo ważny.

W pracy przedstawiono nową, nieinwazyjną technikę pobierania z wnętrza dziupli prób drewna, które następnie wykorzystywane są do określania obecności i taksonów grzybów na podstawie metod molekularnych. Do pobierania prób z wnętrza dziupli zastosowano nowe narzędzie — stalową „łyżeczkę” umieszczoną na metalowym pręcie (Fig. 1, 2). Krawędzie tej łyżeczki zostały zastrzone tak, aby możliwe było zdrapywanie drewna z wnętrza dziupli. Taka konstrukcja jest wygodna do używania w przypadku pobierania prób na wysokości, pozwala także na łatwą sterylizację narzędzia przed każdym pobraniem próby. Zebrane wióry analizowane były następnie metodami molekularnymi — autorzy zaprojektowali nowy starter specyficzny dla podstawczaków z grupy zawierającej grzyby rozkładające drewno.

Nową metodę pobierania prób oraz analiz molekularnych przetestowano na dziuplach dziecięcia skromnego. Wybrano drzewa, z których połowa miała widoczne owocniki grzyba z grupy *Porodaedalea pini*. Wióry z wnętrza dziupli pobierano w trzech miejscach, tak, aby zebrać próby dla obu rodzajów drewna — zarówno bieli, jak i twardej (Fig. 3). W przypadku zaczątków dziupli dodatkowo wykonywano nawiercenie w celu pobrania do badań rdzenia (Fig. 3).

Używając nowej metody pobierania prób z wnętrza dziupli oraz nowego protokołu do analiz molekularnych stwierdzono obecność grzybów w 90% dziupli w drzewach z widocznymi owocnikami, oraz w 60% dziupli w drzewach, na których nie było owocników (Tab. 1). Dodatkowo, w próbach zebranych przy pomocy nowego narzędzia stwierdzono 9 dodatkowych taksonów grzybów rozkładających drewno, żaden z nich nie został stwierdzony w próbach pobranych z wywierconych rdzeni (Tab. 1).

Wypracowana metoda pobierania prób i ich analizy pozwala na dokładniejsze identyfikowanie grzybów występujących dokładnie w miejscu wykucia dziupli przez dziecięć, co pozwala na dalsze badania dotyczące powiązań pomiędzy grzybami rozkładającymi drewno a dziuplakami.

Habitat determinants of woodpecker abundance and species richness in sub-Himalayan dipterocarp forests of north-west India

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Abstract. Ecological impacts of habitat change on woodpeckers remain largely unstudied in regions other than Europe and North America. The sub-Himalayan sal *Shorea robusta* forests of northwest India have 17 woodpecker species, and a history of management-induced habitat modification. We studied how habitat parameters affect woodpeckers at a community level (viz. total abundance and species richness) as well as at individual species level. We assessed woodpecker abundance, species richness and described habitat features at 8 sites representing a gradient of structure and composition in a sal-dominated landscape. We surveyed each site in 2-km-long transects 20 times over breeding and non-breeding seasons and evaluated habitat characteristics in 10 circular and belt plots. We analysed woodpecker abundance, species richness, and abundance of individual species as functions of habitat variables and season. Woodpecker encounter rates and mean species richness, respectively, ranged from 1.5 to 10.0 birds/km and 1.7 to 6.9 species per survey at individual sites. Distance-based estimates of densities for the most frequently-observed species were also obtained. Basal area (large trees) and density of snags positively influenced total woodpecker abundance and species richness, with snags being more important during breeding season. Basal area was important for Greater Flameback *Chrysocolaptes lucidus*, Grey-faced Woodpecker *Picus canus*, Fulvous-breasted Woodpecker *Dendrocopos macei* and Lesser Yellownape *Picus chlorolophus*. Snags, tree density, tree diameter and termitarium density appeared to affect Grey-capped Pygmy Woodpecker *Dendrocopos canicapillus*, Black-rumped Flameback *Dinopium benghalense*, Himalayan Flameback *Dinopium shorii* and Streak-throated Woodpecker *Picus xanthopygaeus*. Hence, for the conservation of native woodpecker communities in sal forests, it is necessary to retain large trees and standing dead wood.

Key words: bird communities, forest management, Picidae, seasonality, *Shorea robusta*, sub-Himalayas, vegetation structure, selective logging

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INTRODUCTION

In bird communities, the densities of individual species as well as the number of species in a given habitat is influenced by resource availability. Resources, in turn, are largely dependent on vegetation structure, which defines the suite of foraging opportunities in a habitat (Gill 2006). Avifaunal communities are highly sensitive to changes in habitat caused by human activity. This includes alteration of structural attributes such as tree density, tree size heterogeneity, abundance of old trees and snags (Mac Nally 1990, Raman et al. 1998, Jayapal et al. 2009) and tree species composition (Fleishman et al. 2003, Lee & Rotenberry

2005), which may translate into alteration in quality and quantity of forage available.

Woodpeckers (family Picidae) are considered keystone species and particularly important for conservation because of their ability to create cavities that are crucial for many other organisms (Martin & Eadie 1999). Diversity of woodpeckers is a reliable predictor of the general avifaunal diversity both at the stand level (Drever et al. 2008, Kumar et al. 2011) and at the landscape scale (Mikusinski et al. 2001). Hence, picids are useful in assessing the status of bird diversity and ecological health of a forest (Drever & Martin 2010). Woodpeckers tend to have very specific habitat requirements, such as abundance of large trees

and trees with decay, as shown by studies in Europe (Wiklander et al. 2001, Melletti & Penteriani 2003, Pasinelli 2007, Robles et al. 2007, Roberge et al. 2008) and North America (Block 1991, Setterington et al. 2000, Bevis & Martin 2002). Being strongly tied to wooded areas, woodpeckers are particularly sensitive to forest degradation and modification by forestry operations that alter the natural structure and composition, usually through removal of larger trees, establishment of exotic plantations (Thompson et al. 2003, Mikusinski 2006) and extraction of dead wood (Lindenmayer & Noss 2006). Woodpeckers are also important targets for conservation as several large or specialized species are facing population declines, and some have even become critically endangered or possibly extinct (Mikusinski 2006).

While tropical and subtropical forests of Asia have high picid diversity, not much is known about the ecology of woodpeckers there (Mikusinski 2006). These forests are undergoing rapid changes in land use, the ecological impacts of which, particularly on woodpeckers, remain largely unstudied. An example of one such region is the sub-Himalayan region of northwest India, which is covered by tropical moist deciduous dipterocarp forests dominated by Sal *Shorea robusta* trees. This region has both a rich woodpecker assemblage with 17 species, as well as a diverse array of forest stands that have been structurally and compositionally manipulated through a long history of forest management.

In an earlier study based on the same data as the present paper it was found that stands of unmanaged sal had a significantly higher abundance and species richness of woodpeckers compared to managed sal and that this difference was greater in the breeding season (Kumar et al. 2011). While this previous study described the patterns of woodpecker abundance and diversity in relation to forest management, it was necessary to identify the habitat characteristics that influence woodpecker abundance and diversity.

Community-level response to habitat features is, to a large extent, the collective result of different species' responses to habitat characteristics. Within the community individual species are expected to respond differently to habitat characteristics depending upon their disparate foraging, breeding and other ecological niches. Therefore, it is important that key habitat determinants for individual species are identified. Such information is vital for conservation of native woodpecker assemblages in tropical forests, a large propor-

tion of which have been modified by silvicultural management (Putz et al. 2001).

With this background, our main objective in the present study was to identify the specific habitat features that influence total abundance, species richness, and community composition of woodpeckers in the sal forest landscape. We also assessed the effect of season on the relationship between woodpecker communities and habitat characteristics.

METHODS

Study area

The sub-Himalayan foothills, which form the southernmost range of the Himalayan mountain system, are covered by tropical moist deciduous forests dominated by dipterocarp Sal trees *Shorea robusta*. Uttarakhand state in northwest India has c. 3100 km² under sal forests (Uttarakhand Forest Department 2008). While some sal-bearing tracts of Uttarakhand are protected for biodiversity conservation, most of these are 'reserved forests', which were formerly managed for timber under shelterwood silviculture with a 120–150 year rotation period. These managed stands were at various stages of silvicultural operations until the 1980s when large-scale harvesting of timber was stopped because of a change in policy. However, selective removal of standing dead trees has been continuing on a limited scale in these stands since the 1980s. The present structure of vegetation in these forests has therefore been heavily influenced by past management, resulting in stands with a variety of age-class profiles. Also, over 6% of sal-bearing areas in the state have been converted (largely since the 1960s) to plantations of Teak *Tectona grandis* that is exotic to this region (Uttarakhand Forest Department 2008).

Although classified as moist deciduous, Sal is never completely leafless (Stewart & Brandis 1874); the foliage is scanty a short time towards the end of winter (Troup 1921). Teak usually sheds leaves in middle or late winter and sprouts new leaves between April and June (Troup 1921).

In sub-Himalayan Uttarakhand we selected the Corbett–Ramnagar landscape (1775 km²) as study area (Fig. 1). This tract consists of Corbett Tiger Reserve — a strictly protected area and Ramnagar Forest Division, which has managed stands of Sal as well as Teak plantations. The area lies at 200–900 m elevation and receives c. 2000

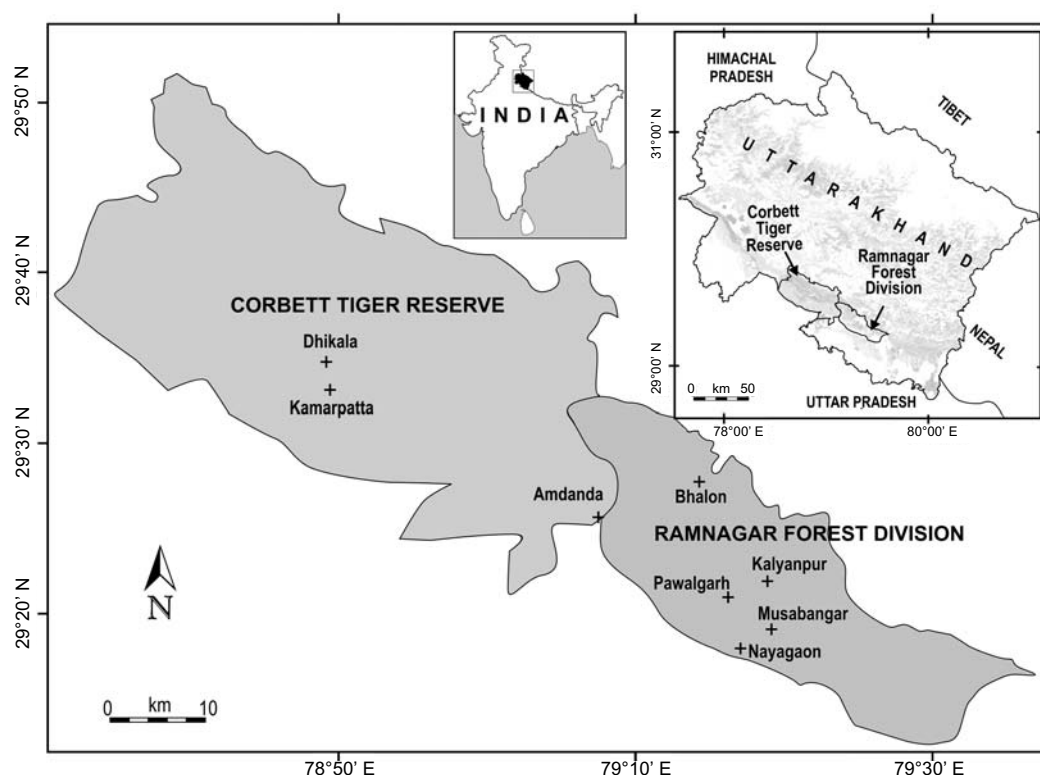


Fig. 1. Map of study area with location of sites.

mm rainfall annually. It is an important region for conservation of large mammals such as Tiger *Panthera tigris* and Asian Elephant *Elephas maximus*, and supports more than 500 species of birds including 17 woodpecker species (Mohan & Sinha 2003).

We consulted management plans of sal forests in the Corbett-Ramnagar landscape and identified stands that represented the range of structural and compositional complexity resulting from management operations. Eight forest stands with areas ranging from 93 ha to 351 ha were selected as study sites. Of these, two represented protected, unlogged stands and contained trees of all size classes (categorized as 'Natural sal'), two had mature overwood with regenerating understorey ('Old managed sal'), two had a nearly uniform size profile dominated by pole-sized trees regenerated since the last harvest ('Young managed sal'), and the final two sites were *Tectona grandis* plantations established c. 50 years ago ('Teak plantation'). While the first two were free from any silvicultural operations, in the remaining six sites standing dead trees were still being removed as part of management prescriptions at the time of the study.

At each site we marked transects of 2.0 km length along existing trails, inspection paths or fire-lines that had continuous canopy. The transects were roughly linear with no acute-angle turns, and were more than 100 m from the stand edge.

Habitat measurements

We enumerated the habitat at each site from ten circular plots of 10 m radius at 150 m intervals along the transect. In each plot we counted the numbers of live trees and snags (i.e. standing dead trees), and measured their girth at breast height (GBH) and species identity of all trees >20 cm GBH. Canopy cover was estimated using a densiometer. These data were used to calculate total basal area, tree density per unit area, density of large trees (>157 cm GBH) per unit area, density of snags per unit area, mean tree diameter and tree diameter diversity. Tree diameter diversity was computed as a Shannon Diversity Index (H') that was calculated as: $H' = -\sum p_i \ln p_i$, where p_i is proportion of trees in diameter class i , with classes being 10–20 cm, 20–30 cm, and so on. Values of habitat variables for each transect were calculated as means of the 10 constituent plots. As

woodpeckers are also known to feed on termites (which are available in the study area in both winter and summer), density of termite mounds at each site was evaluated by surveying a 100 m-wide strip (50 m on either side) along the 2-km length of the transect. Description of habitat was carried out in February–March 2008.

Woodpecker surveys

Surveys for woodpeckers were done by two observers traversing the marked transects on foot at a steady pace of 1–2 km/h. The observers recorded all woodpeckers (detected visually or by listening to their calls or tapping) and noted the numbers and species identities. Whenever the species identity was doubtful, one of the observers temporarily left the transect to locate and identify the bird. Surveys were carried out on clear days between 08:00–16:00 as we found no significant change in the activity and detections of woodpeckers in this period (Kumar & Singh 2010). We surveyed each site 20 times covering breeding (March–May) and non-breeding (November–February) seasons during 2006–2008. All surveys were carried out by the same two observers. For every survey we thus had the total numbers as well as species-wise break-up of woodpeckers encountered, which we assumed to represent abundances.

We additionally measured perpendicular distances of all woodpeckers encountered using a laser range finder to enable us to carry out distance analysis to estimate densities. Although densities were not used in analyses, they were estimated and presented, as there is very little baseline information about woodpecker densities for Asia.

DATA ANALYSIS

Modelling woodpecker abundance and species richness

For model analyses we used encounter rates as a measure of abundance (Kumar et al. 2011) because the latter information was available at a higher level of information (i.e. per survey), thus capturing temporal variability in detection of woodpeckers. Based on the general natural history of woodpeckers (Ali & Ripley 1983, Winkler et al. 1995), from our set of habitat variables we hypothesized six (viz. basal area, mean tree diameter, tree density, density of large trees (>50 cm DBH), snag density and termitarium density) that were related to the quantum of resources available and thus influenced woodpecker abundance (see Appendix 1).

Similarly, we identified six variables (viz. basal area, mean tree diameter, tree density, density of large trees, snag density and tree diameter diversity) that represented the diversity of resources available, which potentially determine woodpecker species richness. As basal area was found to be highly correlated with density of large trees ($r = 0.98$, $p < 0.001$) as well as tree diameter diversity ($r = 0.84$, $p < 0.01$) the last two variables were omitted from model definitions. Additionally, we included season as a categorical variable, as in an earlier study we had found differences in woodpecker abundance between breeding and non-breeding seasons (Kumar et al. 2011).

We used generalized linear mixed-effects model (GLMM) analysis for two reasons. Firstly, our study had a multi-level design that involved surveying each site multiple times. By using GLMMs we could account for temporal replication as random effects and thereby address the concerns of pseudoreplication (Bolker et al. 2009). Secondly, GLMMs are suited for modelling count data that are non-normally distributed (Bolker et al. 2009).

Habitat variables were centered and scaled to have zero means and unit standard deviations to make the variables mutually comparable. We built a set of a priori candidate models representing combinations of up to two habitat variables and their interactions with season as explanatory variables, and total number of woodpeckers detected as the response variable. As ours was an observational study replicated across sites with multiple repeat surveys, we included site and survey (nested within site) as random effects in the GLMM. We assumed Poisson error structure and log link function for the models.

Using Akaike information criterion (AIC) we identified a confidence set of ranked models that cumulatively contributed at least 0.95 to the weight of evidence (Burnham & Anderson 2002). Habitat factors that were important for explaining overall woodpecker abundance were inferred by evaluating model-averaged estimates of coefficients from the above set (Johnson & Omland 2004). Model 'fit' was assessed by examining the correlation between model-predicted values of woodpecker abundance with the corresponding observed values (Zheng & Agresti 2000). Factors affecting woodpecker species richness were also estimated using the same analytical approach as above. For this particular set of GLMMs we used the number of woodpecker species recorded on each survey as the response variable. In order to

assess individual species' responses to habitat characteristics we also conducted separate GLMM analyses with encounters of individual species as response variable. All analyses were done in statistical software R version 2.11.1 (R Development Core Team 2005) with the aid of the 'lme4' package (Bates & Maechler 2009).

Estimating woodpecker densities

Woodpecker observations were analysed using program Distance v. 5.0 (Thomas et al. 2010) to estimate densities of species with adequate detections for the eight sites, separately for breeding and non-breeding seasons. Densities were calculated using separate detection curves for individual species. A few species, for which we had too few detections to construct detection curves, were assumed to have detection curves similar to those of species closest to them in body size (see Table 1 for details). Final detection curves were selected from candidate curves on the basis of minimum AIC values and were subsequently used to estimate densities.

RESULTS

Woodpecker densities

Woodpecker densities at individual sites varied from 13.8 km⁻² to 74.5 km⁻². *Picus canus*, *Dendrocopos canicapillus* and *Dinopium shorii* showed highest densities among individual species, while the least abundant species were *Picumnus innominatus*, *Dendrocopos auriceps*, *Micropternus brachyurus* and *Chrysocolaptes festivus*. Details are presented in Table 1.

Habitat characteristics

Our eight study sites showed a broad range of values in basal area, tree diameter diversity, mean tree diameter and snag density (Table 2). Most of these structural differences can be attributed to the history of logging according to the four management-based categories (Kumar et al. 2011). Other habitat variables e.g. termitarium density and tree density did not show any patterns that could be attributed to management.

Woodpecker abundance and species richness

During our surveys we had 1425 detections of woodpeckers (679 and 746 in breeding- and non-breeding seasons, respectively), belonging to 15 species. Five species — Grey-capped Pygmy Woodpecker *Dendrocopos canicapillus*, Grey-faced

Woodpecker *Picus canus*, Himalayan Flameback *Dinopium shorii*, Black-rumped Flameback *Dinopium benghalense* and Fulvous-breasted Woodpecker *Dendrocopos macei* — constituted more than 70% of the community (Table 1). Woodpecker abundances (i.e. encounter rates) at individual sites had mean values ranging from 1.5 km⁻¹ to 10.0 km⁻¹; and the number of woodpecker species detected per survey also showed variability between sites, spanning mean values of 1.7 to 6.9.

Although woodpecker abundance for the study area as a whole did not change much between seasons, individual sites showed marked inter-seasonal differences (Fig. 2; Appendix 2). The two sites representing natural sal had higher densities in breeding season than in non-breeding season. However, most other sites showed a reverse pattern and showed greater woodpecker abundances during the non-breeding season. A similar seasonal trend was observed for mean woodpecker species richness (Fig. 2).

Factors influencing overall woodpecker abundance and species richness

We compared candidate GLMMs for overall woodpecker abundance as a function of habitat variables and season. Two models showed particularly high likelihood, given the data (Table 3). Both of these included basal area, snag density and interactions with season. The rest of the models had low Akaike weights ($w_i < 0.04$) and were hence highly improbable. An examination of the model-weighted parameter estimates showed that basal area, snag density, season and the snag density×season interaction were the important factors influencing total woodpecker abundance (Table 4). Coefficients of other variables had very low estimated values with confidence intervals that included zero. Random effects (i.e. site ID and survey number ID) were found to contribute little to the overall model variance and were therefore negligible compared to the main effects.

Out of the candidate models for woodpecker species richness, two models had appreciable support. These models included basal area, season, snag density and interaction with season (Table 4). Other models contributed very little evidence, having $w_i < 0.01$. Model-weighted parameter estimates showed basal area, snag density, season and snag density×season interaction were the main factors influencing woodpecker species richness (Table 4). Random effects were found to be unimportant compared to main effects.

Table 1. Densities (in km^{-2}) (%CV) of individual woodpecker species as estimated from distance analysis along with detection function (DF) and effective strip width (ESW) in breeding (B) and non-breeding (NB) seasons. Species codes: MUPU — *Mulleripicus puberulentus*, CHLU — *Chrysocolaptes lucidus*, PIFL — *Picus flavinucha*, CHFE — *Chrysocolaptes festinus*, PICA — *Picus canus*, DISH — *Dinopium shortii*, PIXA — *Picus xanthopygus*, DIBE — *Dinopium benghalense*, PICH — *Picus chlorolophus*, MIBR — *Micropternus brachyurus*, DEAU — *Dendrocopos auriceps*, DEMA — *Dendrocopos macei*, DECA — *Dendrocopos canicapillus*, DENA — *Dendrocopos nanus*, UI — Unidentified. Site codes: 1 — Dhikala, 2 — Kamarpata, 3 — Musbangar, 4 — Pawalgarh, 5 — Bhalon, 6 — Kalyanpur, 7 — Amdanda, 8 — Nayagaon. DF — Function codes: H/H — Half-normal/Hermite, U/P — Uniform/Polynomial, H/P — Hazard/Polynomial, H/C — Half-normal/Cosine.

Species	Detections	DF	DF Group	ESW (m)	Season	Sites							
						Natural sal		Old managed sal		Young managed sal		Teak plantation	
						1	2	3	4	5	6	7	8
MUPU	6	H/H	CHLU	87	B	1.0 (71)	0.9 (71)	-	-	-	-	-	-
					NB	0.5 (100)	-	-	-	-	-	-	0.5 (100)
CHLU	91	H/H	CHLU	87	B	8.1 (26)	6.9 (27)	1.5 (58)	2.8 (41)	1.5 (58)	-	-	-
					NB	5.1 (32)	1.4 (58)	5.8 (30)	5.1 (31)	3.4 (39)	1.8 (51)	-	0.5 (100)
PIFL	40	H/H	CHLU	87	B	4.6 (34)	3.2 (39)	-	-	0.5 (100)	-	-	-
					NB	6.1 (30)	2.8 (41)	0.5 (100)	-	1.5 (58)	0.5 (100)	-	-
CHFE	2	H/H	CHLU	87	B	-	-	-	-	-	-	-	-
					NB	-	-	-	-	-	-	1.0 (71)	-
PICA	213	U/P	PICA	85	B	28.8 (15)	34.0 (14)	-	0.8 (71)	3.7 (35)	-	-	-
					NB	8.6 (24)	5.8 (27)	1.2 (58)	-	3.7 (35)	-	-	-
DISH	129	H/P	DISH	63	B	6.1 (34)	9.2 (27)	2.6 (51)	13.4 (23)	1.3 (71)	6.7 (31)	2.7 (51)	2.2 (58)
					NB	4.1 (41)	2.4 (51)	3.9 (41)	9.2 (27)	5.1 (36)	9.8 (26)	2.0 (58)	0.7 (100)
PIXA	41	H/P	DISH	63	B	2.7 (51)	1.2 (71)	-	7.9 (29)	-	1.2 (71)	2.0 (58)	-
					NB	0.7 (100)	-	-	4.9 (36)	-	4.9 (36)	-	-
DIBE	109	H/P	DIBE	70	B	3.4 (42)	4.1 (37)	0.5 (101)	6.1 (31)	1.6 (59)	3.1 (42)	7.3 (30)	4.8 (37)
					NB	4.0 (39)	1.0 (72)	-	8.6 (27)	2.7 (46)	3.1 (42)	5.1 (35)	3.6 (42)
PICH	74	H/C	PICH	58	B	4.8 (61)	3.2 (64)	0.6 (112)	1.6 (76)	-	-	-	0.6 (112)
					NB	8.4 (56)	7.5 (56)	3.4 (64)	3.2 (64)	6.8 (57)	1.6 (76)	-	-
MIBR	4	H/C	PICH	58	B	1.2 (86)	-	-	0.5 (112)	-	-	-	-
					NB	0.6 (112)	-	-	-	-	-	-	-
DEAU	2	H/C	DEMA	47	B	-	-	-	-	-	-	-	-
					NB	-	-	0.7 (101)	-	0.7 (101)	-	-	-
DEMA	95	H/C	DEMA	47	B	5.6 (37)	8.8 (29)	1.3 (71)	1.3 (71)	-	-	-	-
					NB	11.9 (26)	9.4 (28)	5.3 (37)	5.7 (35)	7.3 (32)	2.5 (51)	0.7 (101)	3.0 (51)
DECA	224	H/P	DECA	46	B	14.2 (26)	15.9 (24)	8.4 (33)	3.2 (51)	10.9 (29)	5.6 (39)	14.2 (26)	1.9 (71)
					NB	12.4 (28)	19.1 (22)	15.9 (24)	13.6 (25)	24.3 (20)	12.0 (27)	8.9 (33)	9.4 (33)
DENA	2	H/P	DECA	46	B	-	-	-	-	-	-	>0.1 (na)	-
					NB	-	-	-	-	-	-	-	-
UI	46	H/C	UI	71	B	2.0 (46)	3.5 (33)	0.7 (71)	0.4 (100)	0.4 (100)	0.7 (71)	-	0.4 (100)
					NB	4.3 (31)	2.5 (39)	0.7 (71)	1.1 (58)	-	0.4 (100)	-	-

Table 2. Mean (standard error) values of habitat variables for the eight study sites.

Habitat variables	Sites							
	Natural sal		Old managed sal		Young managed sal		Teak plantation	
	Dhikala	Kamarpata	Musbangar	Pawalgarh	Bhalon	Kalyanpur	Amdanda	Nayagaon
Number of trees	14.3 (0.7)	22.1 (1.8)	17.8 (1.6)	9.3 (0.8)	15.5 (1.1)	13.5 (1)	12.3 (1.0)	12.1 (0.5)
Number of large trees (> 50 cm DBH)	3.0 (0.6)	2.9 (0.5)	1.4 (0.4)	2.6 (0.7)	0.8 (0.3)	0.3 (0.2)	0.1 (0.1)	0.3 (0.2)
Canopy cover %	67.3 (3.7)	80.0 (3.1)	73.5 (3.7)	71.3 (3.6)	71.3 (3.8)	79.3 (3.1)	68.3 (3.8)	70.5 (3.4)
Basal area (m ²)	1.6 (0.2)	1.7 (0.2)	1.3 (0.1)	1.4 (0.2)	1.1 (0.0)	1.0 (0.1)	0.6 (0.0)	0.8 (0.1)
Number of snags	2.8 (0.7)	3.3 (0.5)	0.5 (0.3)	0.3 (0.2)	0.3 (0.2)	0.2 (0.2)	1.4 (0.5)	0.4 (0.2)
Mean tree diameter (cm)	33.8 (2.7)	24.4 (1.7)	28.2 (2.6)	37.6 (4.1)	28.9 (1.1)	30.4 (0.9)	23.8 (0.9)	27.6 (1.2)
Tree diameter diversity (H')	1.7 (0.1)	1.6 (0.1)	1.6 (0.0)	1.3 (0.1)	1.4 (0.1)	1.1 (0.1)	1.0 (0.1)	1.3 (0.1)
Number of termitaria (ha ⁻¹)	4.9	1.9	5.1	3.5	1.3	4.6	1.4	2.1

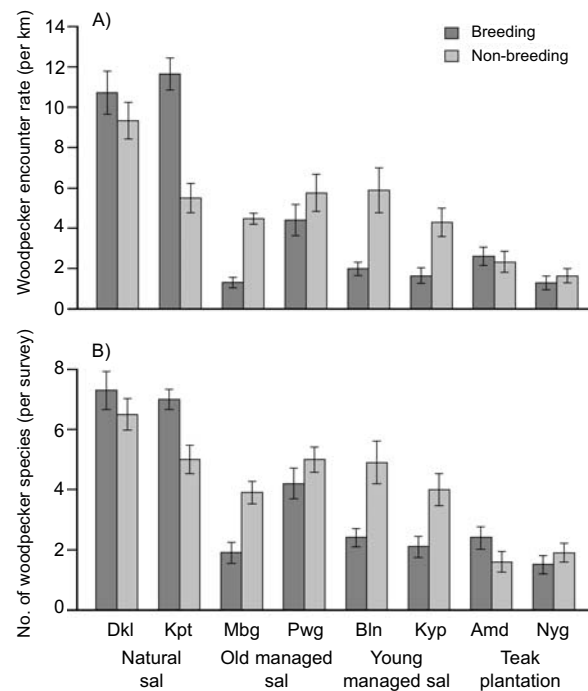


Fig. 2. Seasonal variation in (A) mean species richness, and (B) mean encounter rates of woodpeckers at individual study sites. Error bars depict SE. Site abbreviations: Dkl — Dhikala, Kpt — Kamarpata, Mbg — Musbangar, Pwg — Pawalgarh, Bln — Bhalon, Kyp — Kalyanpur, Amd — Amdanda, Nyg — Nayagaon.

The model-predicted values of both total abundance and species richness showed a very high correlation with their respective observed values, signifying reasonably good model 'fits' (Table 4).

Factors affecting abundance of particular woodpecker species

GLMM analysis on abundances of nine individual species was carried out. Models for all these species had sufficiently high 'fits' except the one for Greater Yellownappe *Picus flavinucha*. Model-weighted parameter estimates for four species — Greater Flameback *Chrysocolaptes lucidus*, Grey-faced Woodpecker, Fulvous-breasted Woodpecker and Lesser Yellownappe *Picus chlorolophus* — showed basal area as an important variable (Table 5). Model coefficients for the first three of the above species also had a significant basal area×season interaction, implying that basal area was a more important factor in the breeding season. Density of snags was a major factor for Grey-capped Pygmy Woodpecker with the snags×season interaction implying that snags were more important during the breeding season. The termitarium density emerged as a significant factor for

Table 3. Generalized linear mixed-effects models for total woodpecker abundance and number of woodpecker species detected. Models that cumulatively contribute > 0.95 to weight of evidence w_i have been presented. ^a — Indicates relative variance (proportion to residual variance of model).

Model	AIC	Δ AIC	w_i	Random effects ^a	
				Survey ID	Site ID
Total woodpecker abundance					
Basal area + Snag density + Season + Basal area×Season + Snag density×Season	205.2	0.0	0.71	< 0.01	0.08
Basal area + Snag density + Season + Snag density×Season	207.2	2.0	0.26	0.09	0.04
Number of woodpecker species					
Basal area + Snag density + Season + Basal area×Season + Snag density×Season	123.4	0.0	0.71	< 0.01	0.08
Basal area + Snag density + Season + Snag density×Season	125.4	2.0	0.26	0.09	0.04

two species (positive for Streak-throated Woodpecker *Picus xanthopygaeus*, negative for Grey-faced Woodpecker). Similarly, tree density appeared significant for Black-rumped Flameback (negatively) and Grey-capped Pygmy (positively). For the Himalayan Flameback the only significant factor was mean tree diameter.

Detections of other species viz. Great Slaty Woodpecker *Mulleripicus pulverulentus*, White-naped Woodpecker *Chrysocolaptes festivus*, Rufous Woodpecker *Microptrenus brachyurus*, Brown-fronted Woodpecker *Dendrocopos auriceps*, and Brown-capped Pygmy Woodpecker *Dendrocopos nanus*, as well as Speckled Piculet *Picumnus innotatus*, were insufficient to carry out any modelling analysis.

DISCUSSION

Patterns of woodpecker abundance and species richness

With 15 species observed during the present study, the assemblage of woodpeckers in sub-Himalayan sal forests is comparable to the richest regions in the world, such as Pasoh in peninsular Malaysia with 15 species (Styring & Ickes 2001)

and Gunung Palung in western Borneo with 14 species (Lammertink 2004), and exceeds the richness for a typical tropical/subtropical moist broad-leaved forest (Mikusinski 2006). In abundance too, undisturbed sal forests match woodpecker densities observed in unlogged forests of Sungai Lalang Reserve, Malaysia (Styring & Zakaria 2004), which underscores the conservation importance of sub-Himalayan forests.

While the overall abundance did not change from breeding to non-breeding seasons, individual sites showed marked inter-seasonal differences in abundance and species richness. This suggests that woodpeckers in the sal forest landscape migrate locally in order to track resources for foraging or breeding, depending on what is more critical in a particular season (Kumar et al. 2011). However, this needs to be confirmed by studying their movement in greater detail.

Sites that had the lowest abundance and richness of woodpeckers happened to be teak plantations. This observation is in agreement with reports of a relatively lower usage of exotic plantations by woodpeckers in Borneo (Mitra & Sheldon 1993, Sheldon et al. 2010). Lower densities in teak are possibly due to lower availability of rough-barked trees that potentially affect forage

Table 4. Summary of generalized linear mixed-effects model analyses for woodpecker abundance and number of woodpecker species. Figures indicate model-averaged coefficient estimates (SE in brackets). Estimates with values greater than two standard errors shown in bold. Since variables have been scaled and centred, predictors are expressed in unit standard deviations.

Variable	Woodpecker abundance	Number of woodpecker species
(Intercept)	1.23 (0.43)	1.14 (0.32)
Basal area	0.49 (0.19)	0.35 (0.11)
Snag density	0.33 (0.08)	0.23 (0.07)
Season- Non-breeding	0.30 (0.12)	0.21 (0.08)
Basal area $\times$ Season	-0.17 (0.27)	-0.01 (0.18)
Snag density $\times$ Season	-0.25 (0.10)	-0.23 (0.11)
Correlation (r) between predicted and observed values	0.90	0.91

Table 5. Summary of generalized linear mixed-effects model analyses for abundance of individual species. Figures indicate model-averaged coefficient estimates (SE in brackets). As variables have been scaled and centred, predictors are expressed in unit standard deviations. Estimates with values greater than two standard errors shown in bold. Correlations significant at $p = 0.01$ given in bold.

Variable	<i>Chrysocolaptes lucidus</i>	<i>Picus flavinucha</i>	<i>Picus canus</i>	<i>Dinopium shorii</i>	<i>Dinopium benghalense</i>	<i>Picus xanthopygaeus</i>	<i>Picus chlorolophus</i>	<i>Dendrocopos macei</i>	<i>Dendrocopos canicapillus</i>
(Intercept)	-2.22 (0.70)	-3.67 (1.96)	-3.67 (1.85)	-0.54 (0.22)	-0.81 (0.20)	-2.78 (1.03)	-2.80 (0.80)	-3.52 (0.99)	-0.43 (0.29)
Basal area	1.30 (0.35)	1.86 (1.06)	4.43 (0.70)	0.09 (0.05)	-0.01 (0.01)	0.01 (0.02)	0.88 (0.30)	2.62 (0.75)	0.01 (0.01)
Mean tree DBH	0.86 (0.71)	0.06 (0.10)	<0.01 (<0.01)	0.39 (0.17)	-0.03 (0.02)	0.04 (0.02)	0.49 (0.29)	-0.01 (0.03)	-0.07 (0.43)
Tree density	0.86 (0.70)	0.11 (0.13)	<0.01 (<0.01)	0.14 (0.12)	-0.67 (0.19)	-1.64 (0.89)	0.35 (0.38)	0.01 (0.03)	0.29 (0.10)
Snag density	<0.01 (0.08)	0.46 (0.13)	<0.01 (<0.01)	0.01 (0.02)	0.04 (0.03)	<0.01 (<0.01)	0.02 (0.02)	0.03 (0.03)	0.25 (0.10)
Termitaria	<0.01 (0.03)	-0.60 (0.31)	-1.92 (0.40)	<0.01 (0.01)	-0.07 (0.04)	0.99 (0.50)	-0.01 (0.17)	0.03 (0.06)	-0.01 (0.01)
Season- Non-breeding	0.98 (0.58)	0.33 (1.00)	0.11 (0.65)	0.06 (0.17)	-0.05 (0.17)	-0.82 (1.18)	1.39 (0.54)	2.89 (0.99)	0.65 (0.23)
Basal area × Season	-0.59 (0.26)	-0.14 (0.16)	-1.38 (0.45)	-0.03 (0.02)	<0.01 (<0.01)	<0.01 (<0.01)	-0.10 (0.29)	-2.17 (0.76)	-0.01 (0.01)
Mean tree DBH × Season	-0.56 (0.44)	<0.01 (<0.01)	<0.01 (<0.01)	0.05 (0.06)	0.01 (0.01)	<0.01 (0.01)	0.06 (0.14)	-0.01 (0.01)	0.05 (0.03)
Tree density × Season	-0.64 (0.40)	-0.01 (0.01)	<0.01 (<0.01)	-0.03 (0.03)	-0.09 (0.07)	-0.17 (0.45)	0.04 (0.03)	<0.01 (<0.01)	-0.05 (0.12)
Snag density × Season	-0.25 (0.16)	-0.03 (0.04)	<0.01 (<0.01)	-0.02 (0.01)	<0.01 (0.01)	<0.01 (<0.01)	-0.01 (0.01)	-0.01 (0.02)	-0.31 (0.12)
Termitaria × Season	0.03 (0.02)	<0.01 (0.04)	0.50 (0.23)	0.01 (0.01)	0.01 (0.02)	0.61 (0.74)	-0.17 (0.13)	-0.05 (0.04)	<0.01 (0.01)
Correlated & observed values	0.70	0.40	0.72	0.73	0.91	0.94	0.70	0.91	0.75

abundance, as observed for Great and Middle Spotted Woodpeckers *Dendrocopos major*, *D. medius* in Europe (Kosinski & Kempa 2007). Whether teak trees are less preferred sites for building cavities also needs to be investigated.

Factors influencing overall woodpecker abundance and species richness

Among the factors that determined overall woodpecker abundance, basal area (which is strongly influenced by large trees) and snag density emerged as key habitat characteristics. Dependence of picid abundances on the above habitat variables has been reported by several previous studies. For example, the abundance of cavity-nesters was related to tree maturity in eastern Europe (Nikolov 2009) and snag density (Bevis & Martin 2002, Drever & Martin 2010). In our study these factors were important across seasons, with snag density being more critical during the breeding season.

The density of trees, however, did not affect woodpecker abundance. Stand maturity has been found to be more important than stand density in determining habitat use by Red-cockaded Woodpeckers *Picoides borealis* in North America (de Lotelle et al. 1987) and the same may hold true for several species in sal forests. Thus sites that have a greater number of large trees and have good availability of snags could be offering better resources for the requirements of woodpeckers.

With regards to woodpecker species richness, our study demonstrates that like overall abundance, the number of species encountered per survey also increases appreciably with basal area and snag density, as also reported by Drapeau et al. (2002) for Canadian boreal forests. Importantly, snag density was less important a determinant of woodpecker richness during the non-breeding season.

Large diameter trees, which contribute substantially to basal area, contain a greater diversity of microhabitats such as cavities, cracks and bark features that favour biodiversity (Vuidot et al. 2011). Hence, a high density of large diameter trees represents more resources, which can support a greater abundance of woodpeckers.

Considering the correlation between habitat variables in our study, basal area is also a surrogate for other correlated habitat variables like diversity of tree sizes. Hence, the variable 'basal area' in our case also represents the complexity of vegetation structure, which translates into

the number of niches available to accommodate different picid species, and may thus determine woodpecker species richness. The effect of basal area remained consistent between seasons. Hence, it can be inferred that the inherent capacity of a forest to harbour woodpeckers and their diversity is primarily determined by the number of large trees, or vegetation complexity.

The second determinant of woodpecker abundance and richness — snag density — was more important during the breeding season. This suggests that several species of sal forest woodpeckers may be preferentially selecting snag-rich areas for nesting, as is prevalent among picids in many parts of the world (Winkler et al. 1995). Therefore, snags could offer resources for nesting, the perceived importance of which changes according to season, depending on whether foraging or breeding is priority.

Factors affecting abundance of individual woodpecker species

Four species i.e. *Chrysocolaptes lucidus*, *Picus canus*, *Dendrocopos macei* and *Picus chlorolophus* chose stands with higher basal area (or density of large trees). This factor was more important during the breeding season for the first three species, with *Picus canus* displaying the strongest response. These four species have been identified as indicators of undisturbed sal forests (Kumar et al. 2011). Earlier studies in other parts of the world have also highlighted the importance of large trees for woodpeckers, e.g. Great Slaty Woodpecker *Mulleripicus pulverulentus* (Lammertink et al. 2009), Middle Spotted Woodpecker *Dendrocopos medius* (Roberge et al. 2008), Pileated Woodpecker *Dryocopus pileatus* (Newell et al. 2009) and Black-backed Woodpecker *Picoides arcticus* (Settlington et al. 2000),

Picus xanthopygaeus needed forest stands that were abundant in termite mounds. We occasionally observed this species feeding on termites on the ground. However, *Picus canus*, a congener, had a negative association with termitarium abundance, although this species was also often seen foraging on the ground.

Density of snags affected the abundance of *Picus flavinucha*, one of the larger species, as well as *Dendrocopos canicapillus*, the smallest, although for the latter snags appeared more important during breeding season. This adds to the evidence of deadwood removal as an important factor that affects woodpeckers, for instance, as observed in studies done in the Canary Islands (Garcia-del-

Rey et al. 2009) and Bulgaria (Nikolov 2009) and Poland (Wesołowski et al. 2005).

Dendrocopos canicapillus was associated with high tree density. Being a smaller bodied species, the number of trees rather than tree size, is perceived as foraging resource. On the other hand, *Dinopium benghalense* had a strong negative association with tree density, suggesting that the species avoided dense stands and preferred open areas. This may be explained by the fact that it is a generalist with possibly less specialized habitat requirements. Lastly, *Dinopium shorii* appeared to require a different suite of habitat conditions. Since this species responded positively to only one factor i.e. mean tree diameter, this suggests that it may prefer areas with mature trees.

Our study demonstrates that community-level responses to management-modified habitat are driven by the differential responses of individual species to various habitat characteristics. The habitat factor that appears to be important for most species is total basal area, a variable that is strongly dependent on the abundance of large trees.

While we did not have adequate sample size to build models for *Mulleripicus pulverulentus*, it is notable that this globally vulnerable species of conservation importance (BirdLife International 2014) was observed only in undisturbed natural sal, which has been documented in a more recent study (Kumar & Shahabuddin 2012). The species is known to occur in old growth forests at low densities throughout its range (Lammertink et al. 2009).

Conservation importance

While managed forests apparently are able to support woodpeckers in the non-breeding season, large trees and snags could well be crucial factors that affect breeding and thereby enable populations of various picid species to survive. Stands having these features are predominantly located in unmanaged forests. Therefore, if the native picid community of sal forests is to be conserved, managers should encourage practices that retain large trees and standing deadwood in managed stands, or at least ensure that managed areas are physically connected to unmanaged forests that provide these resources.

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STRESZCZENIE

[Czynniki siedliskowe wpływające na liczebność i bogactwo gatunkowe dzięciołów w wilgotnych lasach monsunowych u podnóża Himalajów (północno-wschodnie Indie)]

Wpływ zmian zachodzących w środowisku wywołanych gospodarką leśną na dzięcioły w zasadzie nie jest badany na terenach innych niż Europa i Ameryka Północna.

W wilgotnych lasach na południowych zboczach Himalajów, których podstawowym składnikiem jest damarzyk mocny (drzewo sal), występuje 17 gatunków dzięciołów. W lasach tych prowadzona była gospodarka leśna, mająca na celu pozyskanie drewna, wycinanie martwych drzew, oraz zamianę obszarów porośniętych przez damarzyka w plantacje drzewa tekowego. Na terenie północnych Indii wybrano 8 powierzchni różniących się stopniem przekształcenia drzewostanu damarzykowego związanym z gospodarką leśną — po dwa: w lasach uznawanych za naturalne, nie poddanych gospodarce, w starych lasach, w których dochodzi do regeneracji piętra podrośtu, w młodym lesie, oraz w lesie przekształconym w plantacje drzewa tekowego (Fig. 1).

W pracy analizowano wpływ charakterystyki środowiska na dzięcioły — zarówno na poziomie całego zespołu tych ptaków (łączna liczebność, czy bogactwo gatunkowe), jak również na liczebność poszczególnych gatunków. W każdym z badanych terenów wyznaczono transekt o długości 2 km, na którym przeprowadzono łącznie 20 kontroli, zarówno w sezonie lęgowym (marzec–maj), jak i pozalęgowym (listopad–luty). Dane dotyczące siedliska zbierano w 10 okręgach o promieniu 10 m na każdym z transektów. Opisywano gatunki i liczbę żywych i martwych drzew, mierzono ich obwody, określano zwarcie koron. Na podstawie tych danych określano powierzchnię poprzecznego przekroju drzew (basal area), zagęszczenie drzew, zagęszczenie dużych drzew (> 157 cm obwodu) oraz różnorodność klas pierśnic (przy pomocy współczynnika Shannona). Jako, że dzięcioły mogą żywić się termitami, na całej długości transektu określano zagęszczenie gniazd termitów.

W analizach na poziomie całego zespołu brano pod uwagę te czynniki siedliskowe, które mogą być związane z dostępnością miejsc do gniazdowania oraz pokarmu (Apendyks 1), a także sezon prowadzenia badań. Na podstawie odległości obserwowanego osobnika od transektu,

biorąc także pod uwagę możliwość detekcji osobników danego gatunku, wyliczono zagęszczenia dla poszczególnych gatunków, dla każdego z badanych terenów i sezonu lęgowego i pozalęgowego (Tab. 1).

Badane tereny różniły się charakterystykami siedliska, co wiąże się z przekształceniami związanymi z użytkowaniem przez człowieka. Tylko zagęszczenie termitier nie układało się w gradient zmian związanych z gospodarką leśną (Tab. 2).

Częstość stwierdzenia przedstawicieli zespołu dzięciołów wahała się od 1,5 do 10 ptaków na 1 km transektu, zaś średnie bogactwo gatunkowe — od 1,7 do 6,9 gatunku na kontrolę/powierzchnię. Dzięcioł zielonosiwy, dzięcioł drobny oraz sułtan himalański osiągały najwyższe zagęszczenia, zaś najrzadziej stwierdzano dzięcioła nepalskiego, dzięciolnika himalańskiego, sułtana białogrzbietego oraz mohuna wielkiego (Apendyks 2).

Stwierdzono, że powierzchnia poprzecznego przekroju drzewostanu (powiązana z występowaniem dużych drzew) oraz zagęszczenie martwych drzew pozytywnie wpływały na liczebność całkowitą zespołu dzięciołów oraz

bogactwo gatunkowe, przy czym zagęszczenie martwych drzew miało większe znaczenie w okresie lęgowym (Tab. 3, 4). Zarówno bogactwo gatunkowe dzięciołów, jak i ich liczebność różniły się pomiędzy badanymi sezonami (Fig. 2, Tab. 3, Apendyks 2).

Analizy czynników wpływających na liczebność poszczególnych gatunków przeprowadzono dla 9 najczęściej spotykanych gatunków. W przypadku sułtana złotogrzbietego, dzięcioła zielonosiwego, dzięcioła żółtoczubego oraz dzięcioła płowego największy wpływ na ich liczebność miał poprzeczny przekrój drzewostanu, szczególnie w sezonie lęgowym, w przypadku dzięcioła drobnego — zagęszczenie martwych drzew, zaś w przypadku dzięcioła białobrowego i dzięcioła zielonosiwego — zagęszczenie termitier, odpowiednio pozytywny i negatywny (Tab. 5).

Autorzy konkludują, że w celu zachowania dużego bogactwa zespołu dzięciołów konieczne jest zachowanie dużych, starych drzew oraz nie usuwanie z lasów damarzykowych drzew martwych.

Appendix 1. Habitat variables considered a priori to potentially influence woodpecker community features, and the rationale for their inclusion in candidate models.

Woodpecker community attributes potentially affected	Variable	Rationale for consideration
Abundance and richness	Tree density	More trees per unit area signify a greater concentration of resources for foraging and nesting
	Basal area	High basal area translates into broader resource base that can accommodate more individuals and more species
	Mean tree diameter	Older stands have relatively greater surface area and volume of wood, offering more foraging and nesting opportunities, which can support more individuals and more species
	Mean tree diameter	Larger trees contain more crevices that harbour more insects, and have relatively more branches that can provide more nesting sites. Mature trees offer nesting/foraging sites of various dimensions and thus may support greater diversity of woodpeckers
	Large tree density	Larger trees have greater bark area, more wood volume, which can provide more forage/nesting resources. Larger trees contain a greater diversity of substrate sizes, and can thus potentially support more species.
	Snag density	Decaying wood has wood-boring insects and is easier to excavate nests in. Therefore, snags have high resource value for forage and nesting.
Abundance Richness	Termitarium density	Termites are an important food resource for woodpeckers
	Tree diameter diversity	A greater diversity of tree sizes offers a larger number of foraging niches, and therefore can support more species

Appendix 2. Encounter rates (km^{-1}) of individual woodpecker species for the breeding (B) and non-breeding (NB) season at individual sites.

Species	Season	Natural sal		Old managed sal		Young managed sal		Teak plantation	
		Dhikala	Kamarpata	Musbangar	Pawalgarh	Bhalon	Kalyanpur	Amdanda	Nayagaon
<i>Mulleripicus pulverulentus</i>	B	0.39	0.45	-	-	-	-	-	-
	NB	0.11	-	-	-	-	-	-	0.06
<i>Chrysocolaptes lucidus</i>	B	1.39	0.90	0.16	0.35	0.21	-	-	-
	NB	0.89	0.20	0.89	0.60	0.42	0.25	-	0.12
<i>Picus flavinucha</i>	B	0.72	0.40	-	-	0.11	-	-	-
	NB	1.11	0.45	0.05	-	0.21	0.05	-	-
<i>Picus canus</i>	B	4.22	5.20	-	0.10	0.58	-	-	-
	NB	1.72	0.85	0.16	-	0.58	-	-	-
<i>Dinopium shorii</i>	B	0.56	1.05	0.26	1.45	0.11	0.60	0.28	0.35
	NB	0.67	0.30	0.58	1.45	0.63	1.50	0.17	0.06
<i>Chrysocolaptes festivus</i>	B	-	-	-	-	-	-	-	-
	NB	-	-	-	-	-	-	0.17	-
<i>Dinopium benghalense</i>	B	0.33	0.50	0.05	0.90	0.21	0.40	0.94	0.65
	NB	0.50	0.10	-	1.15	0.42	0.50	0.78	0.47
<i>Picus xanthopygaeus</i>	B	0.28	0.10	-	1.00	-	0.20	0.17	-
	NB	0.06	-	-	0.60	-	0.40	-	-
<i>Picus chlorolophus</i>	B	0.50	0.30	0.05	0.15	-	-	-	0.12
	NB	1.33	0.80	0.47	0.35	0.74	0.15	-	-
<i>Micropternus brachyurus</i>	B	0.17	-	-	0.10	-	-	-	-
	NB	0.06	-	-	-	-	-	-	-
<i>Dendrocopos auriceps</i>	B	-	-	-	-	-	-	-	-
	NB	-	-	0.05	-	0.05	-	-	-
<i>Dendrocopos macei</i>	B	0.56	0.95	0.11	0.10	-	-	-	-
	NB	1.00	0.85	0.47	0.45	0.58	0.35	0.06	0.24
<i>Dendrocopos canicapillus</i>	B	1.28	1.30	0.58	0.20	0.74	0.35	1.00	0.12
	NB	1.28	1.60	1.68	1.00	2.26	1.05	1.17	0.71
<i>Dendrocopos nanus</i>	B	-	-	-	-	-	-	0.22	-
	NB	-	-	-	-	-	-	-	-
<i>Picumnus innominatus</i>	B	0.06	-	-	-	-	-	-	-
	NB	-	-	-	-	-	-	-	-
Unidentified	B	0.28	0.50	0.11	0.05	0.05	0.10	-	0.06
	NB	0.61	0.35	0.11	0.15	-	0.05	-	-

Global trends in woodpecker cavity entrance orientation: latitudinal and continental effects suggest regional climate influence

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Abstract. Animal constructions represent an extension of the individual phenotype upon which selection may act to create discernable population level patterns. Here we explore global patterns in woodpecker cavity entrance orientation to infer underlying selective forces that shape cavity construction. We performed a comprehensive systematic meta-analysis of woodpecker cavity entrance orientation from 80 populations of 23 species of woodpeckers and other picids throughout the Northern Hemisphere. We show that woodpecker cavity entrance orientation is typically non-random, suggesting that selection acts on cavity entrance orientation. The proportion of studies in which significant results were found increased significantly with sample size, and we estimated that more than half of the studies with a sample size of at least 100 showed non-random cavity entrance orientation. Populations occurring at higher latitudes preferred a more southerly orientation, indicating that temperature or something related thereto may be driving cavity entrance orientation. Differences between Eurasia and North America in orientation are consistent with this hypothesis. Taxonomic relationships were not a significant predictor of the strength of orientation and thus unrelated woodpecker populations respond similarly to regional environmental drivers. Our results demonstrate latitudinal and continental patterns that strongly suggest regional climate as a selective force on cavity entrance orientation. Further work utilizing available long-term data sets throughout the world promises to uncover possible fitness consequences of cavity orientation on woodpeckers.

Key words: animal architecture, building alignment, primary excavators, Picidae, nest site selection, cavity entrance orientation, nest holes

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INTRODUCTION

A variety of animals act as architects by modifying their environment to create structures to provide food or shelter, or attract mates (Hansell 2005). Well-known examples of animal architecture include termite mounds (Korb & Linsenmair 1999), fish nests (Kawase et al. 2013), rodent burrows (Dawson et al. 1988) and bird nests (Hansell 2000). Construction of animal architecture has impacts that expand beyond the architects themselves because the built structures provide habitat and resources for a variety of other taxa (Coleman & Williams 2002). Therefore, animal architects can be considered to be ecosystem engineers (Jones et al. 1996) and the selective forces that act on architects and guide the structure and function of their

constructions may have community-level implications (Wright & Jones 2004). For instance, in certain cases, woodpeckers create new niches through excavation in systems where naturally formed cavities are not abundant, thereby providing habitats for a variety of secondary cavity nesters (Aubry & Raley 2002, Saab et al. 2004, Blanc & Walters 2008). While there are numerous studies that investigate the structure and function of insect buildings or mammalian tunnel-systems and nests, bird architecture is much less understood (Hansell 2000).

The alignment of animal constructions can influence their function and provide evidence of the underlying selective forces and environmental cues that guide animal architecture. Animal buildings represent an extended phenotypic trait

(Dawkins 1982), meaning that selection acts on the structure and function of an animal's buildings, as on other phenotypic traits of the animal. Selection on extended phenotypes can be expected to be strong if the individual invests considerable time and energy in their construction. The geographic alignment of a structure is one potentially important facet of animal construction upon which selection may act. Building alignment can be defined either as the direction of the longest axis of a structure or, in cases of open nests, as the direction towards the open area (e.g. when a nest is leaning against a tree, or a wall). Alignment can have effects on the microclimate of a structure via convection by wind and exposure to solar radiation (Hansell 2005). For instance, observed patterns of alignment in termite mounds may represent a trade-off between thermoregulation and gas exchange (Korb & Linsenmair 1999). Thus, selection may favor individuals who align their construction in directions that increase their fitness, creating non-random alignment patterns at the population level (Goodenough et al. 2008).

Woodpeckers all over the world construct and/or use tree cavities for nesting and roosting. In many cases cavity entrance directions show non-random orientation patterns in various woodpecker populations (Inouye et al. 1981, Locke & Conner 1983, Wan et al. 2008), suggesting that selection favors individuals within these populations that align their cavities to a particular direction. Selective cavity entrance orientation may be advantageous for woodpeckers in at least two ways: the effort required for excavation may be reduced and breeding success could be increased with certain alignments. Both mechanisms have been discussed previously (Conner 1975, Wiebe 2001), though previous studies have been largely limited to single localities or single woodpecker taxa. Case studies provide valuable insights to the taxon-specific and local habitat variables that may account for observed patterns in cavity entrance orientation, but leave one wanting a more general understanding of the importance of cavity entrance orientation to woodpecker biology. Cavity entrance orientation is often recorded in the field and several long-term study sites of cavity-nesters exist around the world, providing an excellent basis for a synthetic analysis of the causes and consequences of non-random cavity entrance orientation in woodpeckers.

Our goal is to highlight the widespread ubiquity of non-random woodpecker cavity entrance orientation and stimulate future scientific inquiry

into its causes and consequences. Here we survey the literature to address questions concerning the general importance of cavity entrance orientation to woodpecker biology. First we ask if non-random cavity entrance orientation is commonplace among woodpecker populations of multiple species and across a broad range of geographic locations. Second, we ask if there are geographical, ecological, or phylogenetic patterns in the direction of alignment that may suggest underlying causative mechanisms. We also provide recommendations to guide appropriate future studies of woodpecker cavity entrance orientation. A better understanding of cavity entrance orientation and its significance to the success of cavity excavators may be of great value to evolutionary studies of cavity-nesting communities and may inform conservation efforts by providing a better understanding the nest site requirements of these ecosystem engineers.

METHODS

Do woodpeckers have a preferred cavity entrance orientation direction?

To determine if non-random cavity entrance orientation is a general phenomenon among woodpecker populations, we performed a re-analysis of published data. In a first step data were obtained from a systematic literature search using Google Scholar® and the English search terms "[common name] cavity orientation" and "[scientific name] cavity orientation". Google Scholar® is a freely accessible and comprehensive global scientific search engine, which allows for an efficient and systematic literature search available to everyone. Using current species checklists for the 5 continents on which woodpeckers and other picids exist, we searched over 200 Picidae species names from North, Central, and South America, Eurasia, and Africa. In order to capture more representatives of European species, we also conducted searches for European species in German language, and likewise we conducted additional searches in Spanish in order to capture more Central and South American species. In addition to our systematic search we also opportunistically included papers that were mentioned and made available to us by other researchers.

From the studies found through our systematic and opportunistic search, we include here only those that provided sufficient data in the original manuscript for re-analysis using standardized

methods. We excluded studies in which the species associated with cavities could not be determined unambiguously, and studies examining artificial cavities such as nest boxes or human-made tree-holes. In some cases where tabular data were not provided in the original manuscript, data were inferred visually from graphical representations. We also included studies that reported orientation statistics but did not provide data in tabular or graphical form, if the results of appropriate analyses were reported in the original manuscript. Using these criteria we found 46 studies from North America, 30 studies from Europe, and 4 studies from Asia from 53 publications (some publications contain studies of more than one species) to include in our analyses, representing 1–12 studies per each of 23 Picidae species (Appendix 1). Because Europe and Asia represent a single landmass and the separation is founded on cultural rather than scientific reasons, and we recovered relatively few Asian studies, European and Asian studies were combined as 'Eurasia'.

To determine the prevalence, geographic, and phylogenetic patterns of cavity orientation in Picidae populations, we re-analyzed all available data sets using a standardized method to allow for cross-study comparisons. Data from each report were analyzed using the Rayleigh-test (Batschelet 1981) to test for a significant deviation from a random distribution ($\alpha = 0.05$) and strength of orientation. The strength of the deviation from random is represented by r , which ranges from 0 to 1, 0 indicating a perfectly random distribution and 1 representing perfect alignment. The Rayleigh-test is the most common statistical test used to analyze circular data for significant unimodal orientation and it is a standard statistical function in all circular statistic software packages (e.g. Oriana; Kovach 2011, or the R-packages 'circular'; Lund & Agostinelli 2011, and 'CircStat'; Lund & Agostinelli 2009). In this meta-analysis, we used the circular statistic software package Oriana 4.0 for all circular re-analyses.

Because the studies surveyed varied greatly in total sample size ($n = 3$ to 437), and sample size has a large influence on statistical power, we correlated the binary response variable of significance (1) versus non-significant (0) results with study sample size to estimate the degree to which published non-significant findings were due to under-sampling. This binary response analysis allowed us to make an estimate of sufficient sample sizes for determining non-random cavity orientations in woodpecker populations. We used a

generalized linear model (GLM; function `glm`, R base package v 2.15.1) to estimate the proportion of studies that found significance as a function of sample size, assuming a binomial error distribution.

Global patterns of woodpecker cavity orientation

Using the published datasets described above, we investigated global patterns in woodpecker population cavity orientation to determine if orientation varies predictably with geographic location by examining the effect of latitude and continent (North America and Eurasia) on the mean direction of picid cavity orientation. For this analysis, we only included studies that provided evidence of significant non-random orientation according to our re-analyses ($\alpha = 0.05$, $n = 31$). We used generalized linear models (GLM; function `glm`, R base package v 2.15.1, family = gaussian) to model the singular effects of latitude and continent, and the interaction of latitude and continent, on deviation of the population mean vector from north. Angular deviation from north was used to linearize circular data, i.e. an orientation towards south would have the maximum value of 180, a northward orientation the minimum value 0. However, orientation towards east or west would both be 90. Model fit was assessed visually and non-significant predictors and interactions were sequentially dropped during model selection.

RESULTS

Do woodpeckers have a preferred cavity entrance orientation direction?

Of 80 studies, 39% (31 studies) showed a significant cavity entrance orientation preference (Appendix 1). Sixteen of the 23 species considered (70%) had a significant orientation in at least one study. The proportion of studies in which significant results were found increased significantly with sample size ($z = 3.636$, $p = 0.0003$, Fig. 1). By using a GLM approach, we estimated that more than half of the studies with a sample size of at least 100 showed non-random cavity entrance orientation (Fig. 1). All studies for the 7 species for which we found no evidence of non-random cavity entrance orientation had relatively small sample sizes (max = 47, mean = 26 ± 14 SD). Those seven species were: White-headed Woodpecker *Picoides albolarvatus*, Syrian woodpecker *Dendrocopos syriacus*, Red-headed Woodpecker *Melanerpes erythrocephalus*, Red-bellied

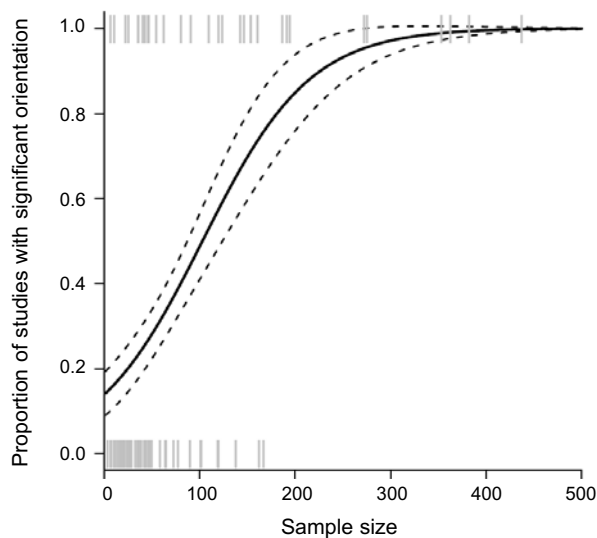


Fig. 1. The proportion of studies in which a significantly non-random cavity entrance orientation was found in relation to increasing sample size. Solid black line shows GLM model fit, $\pm$ standard error (dotted lines). Data are represented by grey “|” symbols.

Woodpecker *Melanerpes carolinus*, Red-breasted Sapsucker *Sphyrapicus ruber*, Lesser Spotted Woodpecker *Dendrocopos minor* and Downy Woodpecker *Picoides pubescens*.

In order to compare the mean strength of orientation (the mean vector length ‘ r ’, used in the Rayleigh’s test) among genera of Picidae we used

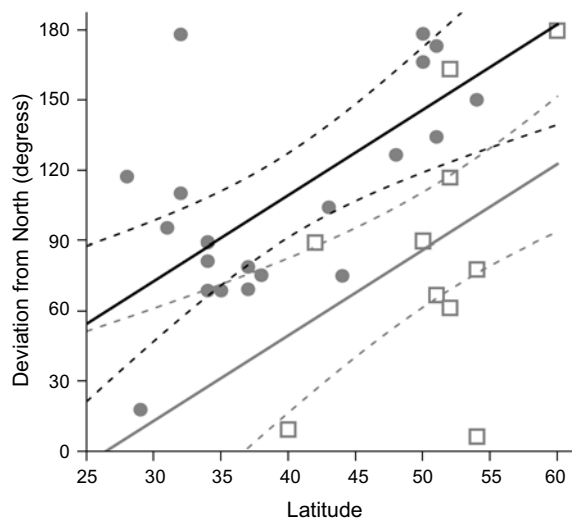


Fig. 2. Relationship between latitude of study site and angular deviation of study population mean vector from North for all studies from which a mean orientation vector could be extracted ($n = 31$). North American studies — black lines $\pm$ 95% CI and closed symbols; Eurasian studies — gray lines $\pm$ 95% CI and open symbols.

a one-way ANOVA. We only included genera for which sample size was greater than four studies, thus excluding *Picus* ($n = 2$). There was no detectable difference in strength of orientation across genera (one-way ANOVA, $F = 1.816$, $p = 0.12$, $df = 5$).

Global patterns of woodpecker cavity orientation

There was a highly significant global relationship between population latitude and the mean deviation from north in cavity entrance orientation ($t = 3.746$, $p = 0.0008$; Fig. 2). Interestingly, the mean deviations differ significantly between North America and Eurasia, showing a more southerly alignment in North America compared to Eurasia in relation to latitude ($t = 3.074$, $p = 0.005$; Fig. 2).

DISCUSSION

Do woodpeckers have a preferred cavity entrance orientation direction?

Though woodpecker cavity entrance orientations are often recorded, many reports include no or inappropriate statistical analyses, and instead provide only qualitative descriptions of the observed cavity orientation data. In other cases, proper analyses reveal non-random alignments but interpretation of the findings is restricted to anecdotes. Some have argued for random cavity entrance orientation in birds (Blume 1961). Others have recognized non-random cavity entrance orientations, but dismissed them as “largely a statistical phenomenon” (Kerpez & Smith 1990), arguing that because high amounts of dispersion typical to cavity orientation data require large sample sizes to detect non-random patterns, a significantly non-random mean direction would not be biologically meaningful. Although large sample sizes do increase the power of an analysis to detect non-random patterns, we emphasize that they *do not* increase the likelihood of false positive results. Proper statistical tools and analytical methods for circular data provide robust tests for non-random patterns in orientation data (Batschelet 1981, Fisher 1995). Ecological and behavioral data are often plagued by high variance, but dismissing significant patterns as merely statistical phenomena may cause researchers to overlook potentially important natural processes such as natural selection on cavity entrance orientation.

The lack of a difference in the strength of orientation between genera suggests that cavity

entrance orientation preferences are ubiquitous among woodpecker taxa and not limited to any particular subset of genera. Our results also suggest that the main reason for the lack of significant cavity entrance orientation in some studies is due to undersampling and not due to a lack of orientation. We suspect that more rigorous sampling of populations of picid species will uncover more non-random patterns in cavity entrance orientation. Together, our results show that non-random cavity entrance orientation is commonplace among woodpecker populations and therefore likely to be an important facet of the biology of this group.

Global patterns of woodpecker cavity orientation

Considering the hypothesis that yearly mean temperatures influence cavity entrance orientation of woodpeckers (Wiebe 2001), one would expect northern populations to orient their cavity entrances more towards the south than southern populations, as more northern populations would benefit more from the warmer cavity temperatures provided by a southerly exposure. Indeed, our results overwhelmingly demonstrate the expected effect: cavity entrance orientations are highly significantly more southern oriented with increasing latitudes. Furthermore, we found that the orientation of North American populations were on average more southerly oriented than Eurasian populations of similar latitudes. If cavity temperatures are driving cavity orientation, such a difference is expected, as European climates are generally warmer than the North American climates of similar latitude due to warming influences such as the Gulf Stream. For instance, in January parts of Western Europe can be as much as 15 °C to 20 °C warmer than the same latitudes in North America (Seager et al. 2002). Therefore, these findings together provide a strong case for temperature as the major driver of global cavity entrance alignment direction in picids. Thus our results are congruent with other studies indicating population-level variation in bird constructions is related to thermal factors, such as those showing local temperature effects on the nest mass of Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* (Deeming et al. 2012).

While our work emphasizes that regional temperature shapes average population-level cavity orientation on a global scale, factors such as wind and microclimate may have effects at smaller, regional or local scales. Such effects could account for the frequently observed high

degree of individual variation in cavity entrance orientation within many populations, such as those noted by Kerpez & Smith (1990). An interesting topic for future research could be to investigate different cavity entrance orientations at different time points during the breeding season, such as comparing alignments of first nests to those for second nesting attempts and any subsequent breeding attempts. For instance, Cactus Wrens *Campylorhynchus brunneicapillus* build closed nests facing away from the prevalent wind direction during the cool part of their breeding season (March and April) and towards the wind during the hotter portion of their breeding season (May and June; Ricklefs & Hainsworth 1969). In contrast to other bird species, woodpeckers and other picids have rather permanent constructions, and for certain species with longer excavation times, such as the Red-cockaded Woodpecker *Picoides borealis* and the Black Woodpecker *Dryocopus martius*, it may not be feasible to construct a new breeding cavity in order to change the orientation of a nest during the breeding season. Instead, woodpeckers that live in territories with multiple cavities could choose a different available cavity with a different cavity entrance orientation for a second breeding attempt than that used in their first attempt.

Does cavity orientation affect Picid fitness?

Our review uncovered a paucity of efforts to relate cavity construction to individual fitness. One study of Northern Flickers related cavity orientation to the fitness consequences of nesting site selection (Wiebe 2001), focusing on the relationship between cavity microclimate and hatching and fledging success. Cavity entrance orientation in the study population was indeed oriented towards south (210°), and Wiebe (2001) showed that southerly-aligned cavities yielded warmer cavity temperatures than more northerly-aligned cavities. However, a relationship between cavity temperature and fledging success was not found, suggesting that something other than directional effects on fledgling success caused the observed southerly orientation. One potential alternative explanation is that excavation is facilitated in certain directions due to regional variation in the directional growth of decay fungi. Most decay fungi present within excavation sites are not initially noticeable with visual observation (Jusino et al. in press) and many excavation sites with decayed wood do not exhibit external signs of decay (Zahner et al. 2012); thus uneven decay

within trees housing excavation sites would be difficult to visually assess in standing trees. Decay fungi are thought to facilitate cavity excavation (Conner et al. 1976, Jackson & Jackson 2004, Witt 2010, Cockle et al. 2012, Zahner et al. 2012, Jusino et al. in press), consequently a fitness advantage of cavity orientation could come from conserved energy during the excavation process rather than increased survival of offspring.

Furthermore, in this review we observed that data collected for woodpecker excavations often do not distinguish excavations based on their usage, such as roosting versus nesting or between cavity orientations on different tree species. However, at least the latter parameter could have important effects on cavity entrance orientation, as it was indicated in a study by Mazgajski (1998). Nonetheless, several efforts from researchers studying non-excavating species give promise that orientation and nesting success may be linked. In Black Kites *Milvus migrans*, rainfall and prevailing winds appear to affect nest orientation. Nests which aligned to the east, which was also the preferred direction, were less exposed to rain and wind and were more successful (Viñuela & Sunyer 1992). Additionally, Cactus Wrens were found to have higher breeding success when their nests are aligned towards the predominant wind direction (southwest) in the late breeding season (Austin 1974).

We suspect that future comprehensive studies analyzing fitness effects of cavity entrance alignment direction will uncover the biological significance of alignment of woodpecker nest cavities and that this topic will provide a fruitful avenue of future research (Goodenough et al. 2008). Woodpeckers spend considerable amounts of energy during cavity excavation, thus this behavior likely is subject to strong selection. Surprisingly, cavity entrance orientation has not gotten the scientific attention that other variables in nest site selection and cavity construction have: for instance, a search on Google Scholar® comparing the search term “woodpecker cavity orientation” with “woodpecker cavity height” revealed 3,410 and 10,200 hits, respectively (Google Scholar® search on Oct 7 2014). We suggest two possible reasons for this imbalance of investigation. First, large sample sizes are often needed to detect fitness effects and in the case of cavity entrance orientation the actual benefit might be small. However, because orientation mechanisms are well developed in birds, choosing a certain direction for excavation might not require any

substantial cost. Therefore, cavity orientation could very likely provide net fitness benefits, but these benefits might be difficult to detect with low sample sizes. Second, cavity orientation data are circular. Circular statistics remain a specialized field and the development of rigorous analytical tools for relating circular predictors to non-circular response variables, such as reproductive success, is a persistent and largely unresolved challenge. We are optimistic that these challenges will soon be met as more research is directed towards orientation studies, circular analytical tools become better developed and more available, and wide-spread fascination for the selective advantages of directional orientation unites specialists from the organismal biology and analytical realms.

CONCLUSIONS

This review is the first attempt to summarize woodpecker cavity entrance orientation data on a global scale and investigate the underlying factors governing orientation of cavities. Our reanalysis of published orientation data clearly shows that most woodpecker populations for which sufficient orientation data are available show significantly non-random cavity orientations. These results strongly suggest that selection acts on individual cavity entrance orientation, but the magnitude and precise nature of such selective forces remain unknown. Quantification and characterization of the effect of cavity entrance orientation on individual woodpecker fitness will provide fruitful future work to advance our understanding of woodpecker biology, the evolution of cavity excavation, and the interface between animal extended phenotypes and the natural environment. Furthermore, entire communities of secondary cavity users depend on the excavations of woodpeckers and different taxa may be differently affected by cavity entrance orientation. Therefore, selection on excavation orientation in woodpeckers may have effects that extend to entire communities of cavity inhabitants, and thus the selective forces that act directly on excavators may act indirectly to shape diversity in communities of organisms, which depend on woodpecker excavations. Cavity directionality is a standard measurement for field protocols, but rarely do researchers invest time for a thorough analysis of this cavity feature. However, long-term data sets, with sample sizes above 100 cavities, could be

easily used to explore some of the questions we raised in this review, including the question of fitness consequences of cavity entrance orientation. Although we attempted to create an inclusive data set on a global scale, there is an apparent lack of searchable published accounts from Central and South America, Asia, Africa, and southern parts of Europe. We hope that this review initiates discussion, data collection in under-represented regions, and further comprehensive analyses of woodpecker cavity entrance orientation in order to gain a better understanding of woodpecker excavation biology and the evolutionary interplay between environment and the extended phenotype.

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STRESZCZENIE

[Ekspozycja otworu wejściowego dziupli dzięciołów — związek z szerokością geograficzną i różnice między kontynentami]

W celu określenia potencjalnych czynników selekcyjnych wpływających na wykuwanie dziupli, zbadano ekspozycję otworów wejściowych

do dziupli dzięciołów. Przeszukano literaturę dotyczącą dzięciołów wybierając prace, z których możliwe było wyselekcjonowanie danych, które mogłyby być użyte do analiz. Do meta-analizy użyto danych dla 80 populacji 23 gatunków dzięciołów (appendix 1) gniazdujących na półkuli północnej.

Stwierdzono, że rozkład kierunków otworów wejściowych do dziupli nie jest losowy, a proporcja prac wykazujących preferencje dzięciołów do wybierania kierunków świata rośnie wraz z wielkością próby. Co najmniej połowa prac z liczbą po najmniej 100 analizowanych dziupli wykazywała rozkład nielosowy (Fig. 1). Populacje gniazdujące w wyższych szerokościach geograficznych zamieszkują dziuple o otworach skierowanych bardziej na południe (Fig. 2), co może wskazywać na związek z temperaturą lub innymi czynnikami z nią związanymi. Podobnie można tłumaczyć różnice pomiędzy Europą, a Ameryką Północną (Fig. 2). Nie stwierdzono, aby powiązania filogenetyczne, analizowane na poziomie rodzajów, wpływały na uzyskane wyniki.

Appendix 1. Data summary of all publications that were included in the meta-analysis. Data are sorted by the mean latitude of species and by latitude of study sites. Cav. Ori. = Cavity entrance orientation, N = north, NE = north-east, ENE = east-north-east, E = east, ESE = east-southeast, SE = south-east, SSE = south-southeast, S = south, SSW = south-southwest, SW = south-west, WSW = west-southwest, W = west, WNW = west-northwest, NNW = north-northwest, n — sample size, r — strength of the deviation from random distribution (see Methods).

Species	Location	Cav. Ori.	Reference	n	r	p
Grey-headed Woodpecker <i>Picus canus</i>	Norway, South Norway	S	Hågvar et al. 1989	10	0.56	0.04
Lesser Spotted Woodpecker <i>Dendrocopos minor</i>	Finland, North Karelia	Random	Pynnönen 1939	19	0.2	0.47
	Norway, South Norway	Random	Hågvar et al. 1989	47	0.06	0.83
	Poland, Białowieża National Park	Random	Wesołowski 1989	26	0.19	0.39
Green Woodpecker <i>Picus viridis</i>	Sweden, Central Sweden	SSE	Aulén 1988	153	0.19	< 0.01
	Norway, South Norway	Random	Hågvar et al. 1989	63	0.17	0.17
White-backed Woodpecker <i>Dendrocopos leucotos</i>	Norway, South Norway	Random	Hågvar et al. 1989	10	0.48	0.1
	Great Britain	N	Marples 1936	123	0.33	< 0.01
	Italy, Latium/Abruzzi	W	Melletti & Penteriani 2003	40	0.41	< 0.01
Red-breasted Sapsucker <i>Sphyrapicus ruber</i>	Canada, British Columbia	Random	Joy 2000	32	0.3	0.05
Black Woodpecker <i>Dryocopus martius</i>	Finland, North Karelia	Random	Pynnönen 1939	15	0.26	0.38
	Norway, South Norway	Random	Hågvar et al. 1989	101	0.11	0.31
	Poland, Greater Poland	Random	Kosiński & Kempa 2007	13	0.25	0.46
	Germany, Brandenburg	Random	Schmidt 1970	47	0.24	0.06
	Germany, Berlin	ENE	Viebig 1935	146	0.35	< 0.01
	Germany, Hesse	WNW	Hoffmann 2005	353	0.13	< 0.01
	Czech Republic, Central Bohemian Region	E	Loos 1910	80	0.35	< 0.01
	Japan, Sounkyo Area, Central Hokkaido	Random	Iso & Fujimaki 1990	16	0.36	0.12
	Japan, Hakodate, Hokkaido	Random	Sumita et al. 1990	3	0.96	0.05

Continue on the next page

Species	Location	Cav. Ori.	Reference	n	r	p
Great Spotted Woodpecker <i>Dendrocopos major</i>	Finland, North Karelia	Random	Pynnönen 1939	38	0.02	0.99
	Sweden, Central Sweden	Random	Aulén 1988	72	0.02	0.97
	Estonia, western Saaremaa	Random	Volke et al. 2010	19	0.25	0.31
	Great Britain	ENE	Tracy 1938	35	0.39	< 0.01
	Poland, Greater Poland	Random	Kosiński & Kempa 2007	166	0.06	0.55
	Poland, Warsaw	Random	Mazgajski 1998	100	0.09	0.48
	Poland, Białowieża National Park	Random	Wesołowski & Tomiałojć 1986	119	0.09	0.41
	Poland, 'various parts'	Random	Hebda 2009	137	0.125	0.12
	France, Orient Forest Region.	Random	Fauvel et al. 2001	77	0.124	0.31
	Natural Park					
	Croatia, NW Croatia	Random	Cikovic et al. 2014	41	0.1	0.64
	Italy, Bosco della Fontana	Random	Hardersen et al. 2004	23	0.306	0.12
	China, Inner Mongolia	N	Wan et al. 2008	153	0.39	< 0.01
Middle Spotted Woodpecker <i>Dendrocopos medius</i>	Poland, Greater Poland	ESE	Kosiński & Kempa 2007	45	0.26	< 0.05
	Poland, Białowieża National Park	SSW	Wesołowski & Tomiałojć 1986	62	0.22	0.04
	France, Orient Forest Region.	Random	Fauvel et al. 2001	58	0.02	0.97
	Natural Park					
Yellow-bellied Sapsucker <i>Sphyrapicus varius</i>	Canada, Ontario	S	Lawrence 1967	42	0.44	< 0.01
White-headed Woodpecker <i>Picoides albolarvatus</i>	USA, Colorado	Random	Inouye 1976	36	0.22	0.18
Red-naped Sapsucker <i>Sphyrapicus nuchalis</i>	USA, Washington State	Random	Kozma et al. 2009	41	0.2	0.2
	USA, Colorado	SSE	Losin et al. 2006	272	0.41	< 0.01
	USA, Oregon	Random	Dobkin et al. 1995	25	0.17	0.49
	USA, Idaho	Random	Sadoti & Vierling 2010	34	0.16	0.42
	USA, Nevada	Random	Butcher et al. 2002	89	0.18	0.06
Downy Woodpecker <i>Picoides pubescens</i>	Canada, Ontario	Random	Lawrence 1967	11	0.46	0.1
	USA, Virginia	Random	Connor 1975	19	0.28	0.22
Lewis's Woodpecker <i>Melanerpes lewis</i>	USA, Black Hills	WNW	Vierling et al. 2009	46	0.28	0.03
	USA, Wyoming	ESE	Linder 1994	35	0.32	0.03
Northern Flicker <i>Colaptes auratus</i>	Canada, British Columbia	S	Wiebe 2001	160	0.19	< 0.01
	Canada, Ontario	SE	Lawrence 1967	25	0.61	< 0.01
	USA, Colorado	S	Inouye 1976	6	0.75	0.03
	USA, Wisconsin	Random	Burkett 1989	17	0.33	0.16
	USA, Oregon	Random	Dobkin et al. 1995	21	0.3	0.15
	USA, Massachusetts	Random	Dennis 1969	118	0.12	0.17
	USA, Ohio	Random	Ingold 1994	44	0.09	0.7
	USA, Virginia	NE	Connor 1975	22	0.44	0.01
	USA, New Mexico	Random	Arsenault 2004	27	0.1	0.76
	USA, Arizona	Random	Kerpez & Smith 1990	28	0.16	0.49
Hairy Woodpecker <i>Picoides villosus</i>	USA, Washington State	SE	Kozma et al. 2009	54	0.34	< 0.01
	USA, Virginia	Random	Connor 1975	10	0.14	0.83
Red-bellied Woodpecker <i>Melanerpes carolinus</i>	USA, Illinois	Random	Reller 1972	7	0.48	0.21
	USA, Ohio	Random	Ingold 1994	46	0.18	0.23
Red-headed Woodpecker <i>Melanerpes erythrocephalus</i>	USA, Black Hills	Random	Vierling et al. 2009	36	0.25	0.1
	USA, Illinois	Random	Reller 1972	10	0.47	0.11
	USA, Ohio	Random	Ingold 1994	26	0.07	0.88
	USA, Virginia	Random	Connor 1975	6	0.67	0.06
Pileated Woodpecker <i>Dryocopus pileatus</i>	USA, Montana	Random	McClellan & McClelland 1999	162	0.13	0.08
	USA, Virginia	Random	Connor 1975	18	0.11	0.81
	USA, Texas	S	Dennis 1964	142	0.27	< 0.01
Acorn Woodpecker <i>Melanerpes formicivorus</i>	USA, California	ENE	Hooge et al. 1999	194	0.16	0.01
	USA, New Mexico	Random	Arsenault 2004	15	0.05	0.96
Gila Woodpecker <i>Melanerpes uropygialis</i>	USA, Arizona	Random	Kerpez & Smith 1990	64	0.02	0.1
	USA, Arizona	Random	Inouye et al. 1981	49	0.24	0.06
	USA, Arizona	WNW	Korol & Hutto 1984	191	0.24	< 0.01
Red-cockaded Woodpecker <i>Picoides borealis</i>	USA, Kentucky	WNW	Kalisz & Boettcher 1991	90	0.28	< 0.01
	USA, Oklahoma	WNW	Wood 1983	275	0.45	< 0.01
	USA, South Carolina	W	Dennis 1971	362	0.55	< 0.01
	USA, South Carolina	W	Hopkins & Lynn 1971	382	0.34	< 0.01
	USA, Georgia	WSW	Jones & Ott 1973	119	0.54	< 0.01
	USA, Texas	W	Lay 1973	437	0.29	< 0.01
	USA, Florida	SW	Baker 1971	186	0.39	< 0.01
Syrian Woodpecker <i>Dendrocopos syriacus</i>	Israel, Tel Aviv	Random	Ar et al. 2004	19	0.08	0.9
Gilded Flicker <i>Colaptes chrysoides</i>	Mexico, Sonora	NNW	Zwartjes & Nordell 1998	109	0.37	< 0.01

Mates exhibit similar brightness of carotenoid red caps in Middle Spotted Woodpeckers *Dendrocopos medius*

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Abstract. Most bird species display sexually dimorphic traits. In contrast to this general rule, both males and females of the Middle Spotted Woodpecker present a carotenoid red cap, which constitutes mutual ornamentation. In our study we investigated whether pair members are matched in terms of the brightness of this ornament. We also examined the similarity between mates in red cap size as well as biometric parameters, such as weight and the length of the wing, beak and tarsus. We found that males and females within pairs were positively assortatively mated with respect to the red cap brightness as well as body weight. We found no similarity between pair members neither in red cap size nor the length of wing, beak or tarsus. We discuss our findings in the light of mutual mate choice, social competitions and other factors that may account for the similarity in expression of the red cap in the studied species.

Key words: mutual ornamentation, assortative mating, carotenoid ornaments, Middle Spotted Woodpecker

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INTRODUCTION

Most studies of sexual selection in birds have concentrated on species with sexually dimorphic traits, in which males are characterized by elaborated ornaments. After the years of research it has been well documented that male ornamentation evolved due to selective pressures of male-male competition and/or female choice (Andersson 1994). Relatively less research has been devoted to the evolution and function of female ornamentation, despite the fact that in many species both sexes display the same kind of ornaments, which is defined as mutual ornamentation (Kraaijeveld et al. 2004).

Mutual ornamentation may be explained by genetic correlation between males and females (Hill 1993, Cuervo et al. 1996, Roulin et al. 2001) or social competition over non-sexual resources, for example food or winter territories (Kraaijeveld & Dickinson 2001). This kind of selection may lead to evolution of badges of status in males and females signaling their position in hierarchy (Zahavi 1991). Alternatively, mutual ornamentation may result from sexual selection acting on both males and females. The first documented case of mutual mate choice in birds reported on the Crested Auklets

Aethla cristatella, a species in which both males and females showed strong preferences towards opposite-sex individuals with accentuated ornaments (Jones & Hunter 1993). Since then growing numbers of studies have demonstrated mutual sexual selection in avian taxa (reviewed in Kraaijeveld et al. 2007).

In its theoretical frames mutual sexual selection may be expected if (a) individuals differ in quality, (b) both sexes display ornaments reflecting their individual quality, (c) reproduction is particularly costly for both sexes and (d) both sexes invest equally in rearing offspring. According to above premises, the studies that confirmed mutual sexual selection in birds concerned monogamous species of biparental care of nestlings (e.g. Monaghan et al. 1996, Hunt et al. 1999, Faivre et al. 2001, Romero-Pujante et al. 2002). In a number of studied species the expression of mutual ornaments was related to individual quality (Kraaijeveld et al. 2007). If mutual ornamentation results from mutual mate choice, one may expect positive assortative mating, in which highly ornamented individuals would choose highly ornamented partners, leaving less ornamented individuals to pair among themselves (e.g. Johnstone 1997). A

number of studies supported this assumption (reviewed in Kraaijeveld et al. 2007 but see Van Rooij & Griffith 2012 for the opposite). Despite the growing evidence on the evolution of mutual ornamentation due to mutual sexual selection in many avian taxa, relatively few studies have looked for assortative mating with respect to plumage colouration (reviewed in Kraaijeveld et al. 2007) and no such study has been reported on woodpeckers so far.

Thus, to fill this gap, the aim of our paper is to test for the relation between the expression of carotenoid-based ornament (a red cap) of pair members in the Middle Spotted Woodpecker *Dendrocopos medius*. The Middle Spotted Woodpecker is a medium-sized bird (20–22 cm long) which inhabits deciduous forest regions, especially areas with old oaks, hornbeams and elms as well as a patchwork of clearings, pasture and dense woodland of the western Palearctic (Pasinelli 2003). It is sedentary, socially monogamous (Michalek & Winkler 2001) and territorial in spring (Pasinelli et al. 2001). Both parents share breeding duties (Michalek & Winkler 2001). Each year they build a new cavity and raise a single brood (Pasinelli 2001, 2003).

The upperparts of Middle Spotted Woodpeckers are predominantly black with white oval wing patches and white barring on the wings. The underparts are white with reddish area under a tail. A relatively large red crown is characteristic for both males and females. Adults undergo a complete moult after the breeding season in the late summer (Pasinelli 2003) and ingested carotenoids can be deposited in feathers only during this period.

In our present study we investigated the mating patterns in breeding pairs with respect to the brightness of the red cap, as in a previous study we demonstrated that this feature has the potential to reflect individual quality in woodpeckers (Leniowski & Węgrzyn 2013). Beside the expression of the red cap colour in pair members we also tested for assortative mating with respect to red cap size as well as physical traits of mates, such as body weight and the length of the wing, beak and tarsus.

METHODS

Study area

The study was conducted in the riverine forest of Warta river valley situated in central Poland near

Czeszewo (17°31'E, 52°09'N) in years 2009–2011. The study plot consists of 222 ha of *Quercus-Fraxinus-Ulmus* (Fraxino-Ulmetum) woodland in the flooded parts, *Quercus-Carpinus* (Stellario-carpinetum) forest on higher grounds and old river-beds and meadows. The whole study area, of which about 40% is covered by mature, near-natural forest stands, is protected as a nature reserve “Czeszewski Las” since 2004.

Territory mapping

Each year before breeding season (March to April) the whole study area was inspected three times in search of territorial pairs (Kosiński et al. 2004). To make the inspections more efficient we used a playback of the Middle Spotted Woodpecker calls. All territories were mapped and confirmed during subsequent controls. Nesting holes were searched for within mapped territories since mid-April to the beginning of June. Next, pair members were caught at the nest hole in order to conduct the spectrophotometric measurements of the red cap of male and female. For more details on territory mapping see Leniowski & Węgrzyn (2013).

Biometric and cap colour measurements

We mist-netted, ringed and took measurements of biometry and a red cap size and colour of 20 individuals (10 pairs). Each bird was caught only once during breeding season at the late stage of incubation or up to five days since nestlings hatched. Birds nesting in low cavities (up to 4 m above the ground) were caught with a regular mist-net spread near a hole. For pairs nesting in higher places were used a trap made of mist-net spread over a metal ring fixed on a telescopic aluminum pole. With the latter device (and a ladder) we were able to reach holes up to 20 m high. None of mist-netted individuals deserted its clutch. Each individual was measured and analyzed only once during the whole study so our paper presents data on 10 different pairs of the Middle Spotted Woodpecker. All individuals were colour banded. None of the pairs re-mated in the subsequent season — we observed at least one pair member from each pair with a new partner in a successive season. Only one male of all analyzed woodpeckers (20) occupied the same territory on the following year.

Each individual was weighted using Pesola balance to the nearest 0.5 g. The length of a tarsus and a beak was measured using a caliper to the nearest 0.1 mm and a wing was measured with

a ruler to the nearest 1 mm. Measurements of all birds were taken by the same person.

The length and width of a red cap was measured with a caliper to the nearest 0.1 mm. Colour of the ornament was estimated using measurements of the reflectance spectra (400–700 nm) obtained from a Photon Control SPM-002 portable spectrophotometer connected to a SPL-1DH deuterium-halogen lamp, a SPA-200U reflectance probe and Spectrosoft Pro v. 2.3.1. software. Colour measurements were conducted directly on ornaments of mist-netted birds. The colour was measured on three randomly selected areas in the central part of the cap. Each area was measured five times and the mean values were used in further analyses. The spectrophotometer covers the reflectance spectrum from 300 to 800 nm in intervals of 1 nm. Reflectances were measured with the probe placed at a constant distance (2 mm) and reaching feathers at 90°. Measurements were relative and referred to a standard white reference and to the dark, both calibrated before the measurement of each ornament. The index of ornament brightness was calculated as the sum of reflectances for each nanometer in red spectral region (580–700 nm) divided by the number of nanometers (120).

Statistical analysis

To preliminary test assortative mating by carotenoid-based plumage colour we calculated a Spearman correlation (r_s) between the brightness of a red cap of males and females in real and randomly arranged pairs. To create randomly arranged pairs we numbered each male and female. Next, for each male we drew blindly one ticket with the female. We did not return the tickets so each male got different female. Spearman correlation was also used to test the relation between cap size of males and females as well as the relation between biometric parameters (weight and the length of wing, beak and tarsus) of both sexes.

Next, we tested whether differences in cap brightness between pairs were greater than these between pair members using Linear Mixed Model (LMM) analysis with cap brightness of an individual as a dependent variable and pair number as a fixed factor. As the study was conducted in 3 seasons, we controlled for the effect of year by including variable „year” as a random factor.

The analyses were conducted in SPSS 16 software (SPSS Inc., Chicago, USA).

RESULTS

We found a strong and significant correlation between cap brightness of males and females in real pairs ($r_s = 0.85$, $p = 0.001$, $n = 10$ pairs; Fig. 1) and no such correlation between males and females arranged in random pairs ($r_s = -0.015$, $p = 0.97$, $n = 10$ pairs).

Linear Mixed Model analysis demonstrated that, after controlling for the year effect by including year as a random term, the differences in cap brightness between pairs were significantly larger than the differences in cap brightness between pair members ($F = 27.73$, $df = 9$, $p = 0.006$).

By contrast, there was no significant correlation between male and female cap width ($r_s = 0.58$, $p = 0.082$, $n = 10$ pairs) or length ($r_s = 0.16$, $p = 0.65$, $n = 10$ pairs). Values of male and female cap width and length and biometry are given in Table 1.

Weight of males and females within a pair was significantly correlated ($r_s = 0.66$, $p = 0.037$, $n = 10$ pairs; Fig. 2). However, there was no correlation between pair members in tarsus, wing and beak length ($r_s = -0.48$, $p = 0.16$, $r_s = 0.29$, $p = 0.41$ and $r_s = -0.007$, $p = 0.85$ respectively, $n = 10$ pairs).

DISCUSSION

Our study showed that Middle Spotted Woodpeckers were positively assortatively mated with

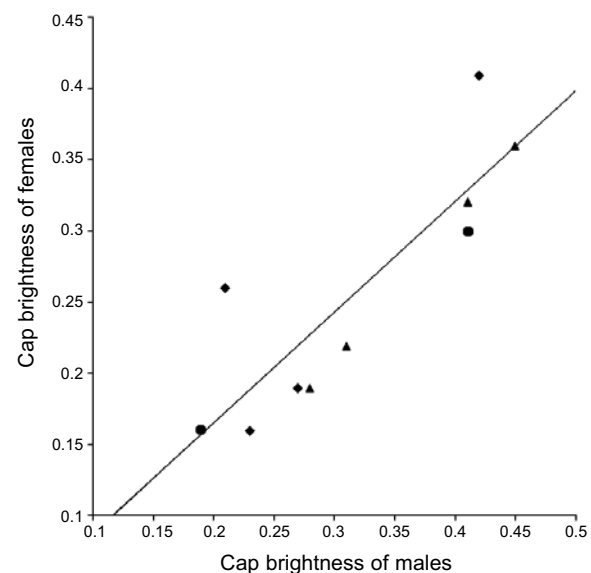


Fig. 1. Relation between the index of cap brightness of mates in the Middle Spotted Woodpecker ($n = 10$ pairs). ● — pairs captured in year 2009, ▲ — pairs captured in year 2010, ◆ — pairs captured in year 2011.

Table 1. Male and female cap characteristics and biometry in Middle Spotted Woodpecker.

	Female (N = 10)		Male (N = 10)	
	mean $\pm$ SD	min–max	mean $\pm$ SD	min–max
Cap width (cm)	1.86 $\pm$ 0.24	1.55–2.35	2.21 $\pm$ 0.35	1.73–2.91
Cap length (cm)	2.76 $\pm$ 0.36	2.28–3.40	3.37 $\pm$ 0.22	3.09–3.78
Beak length [cm]	2.52 $\pm$ 0.17	2.16–2.70	2.69 $\pm$ 0.12	2.50–2.88
Tarsus length [cm]	2.44 $\pm$ 0.05	2.40–2.95	2.56 $\pm$ 0.15	2.40–2.95
Wing length [cm]	12.62 $\pm$ 0.19	12.30–12.90	12.65 $\pm$ 0.32	12.20–13.10

respect to the brightness of a red cap, which means that both pair members have similar expression of this carotenoid trait, and this similarity was greater within pair members than between different pairs. The Middle Spotted Woodpecker is the only true woodpecker species in the Western Palearctic in which males and females are mutually ornamented with a carotenoid red cap and our recent study demonstrated that the brightness of the cap has the potential to reflect the quality of individuals in both sexes (Leniowski & Węgrzyn 2013). Thus it is possible that the individuals use this feature to assess the reproductive value of a potential partner during pair formation.

Theoretically, mutual ornamentation in the woodpeckers may be the result of strong competition of both sexes over non-sexual resources as the species is sedentary and restricted to certain food (Pasinelli 2003). Thus both males and females

may benefit from badges of status in the form of accentuated red caps. The species also meets some important requirements for mutual sexual selection: (i) it is monogamous, (ii) both parents care for nestlings and (iii) males invest highly in incubation and feeding the young. Thus both sexes would benefit from mating with a high quality partner and males, similarly to females, have the interest to be choosy (Johnstone et al. 1996). It has been well documented so far that carotenoid ornaments signal individual quality and health in many bird species (Olson & Owens 1998) including woodpeckers (Leniowski & Węgrzyn 2013), and that they are the subject of preference in mate choice (Hill 1991, 1999).

Similar level of expression of the red cap brightness within pair-members of Middle Spotted Woodpeckers suggests that the evolution of this mutual ornamentation may be driven by mutual mate choice with respect to the carotenoid ornament. Although similarity in mates cap colour could also result from sharing the same territory, and thus feeding on the resources of the same carotenoid content, this is rather not the case of our study. Ingested carotenoids can be deposited in feathers only during the feather growth. Middle Spotted Woodpeckers undergo a complete moult after the breeding season (Pasinelli 2003). So, if cap colour depends on the quality of a territory, it is not the current territory, but the territory from the previous year where the individual foraged just before moult. Only one out of 10 studied males occupied the same territory in the subsequent year and none of the studied females did so. In such scenario the only situation in which cap colour similarity between pair members may result from sharing the same food resources would occur if given pair members re-mated in the following year (because they had shared the same food resources before moult in the preceding year). None of the woodpeckers in our study re-mated with the same partner in the subsequent year. This shows that changing a territory and a partner in a succeeding season seems to

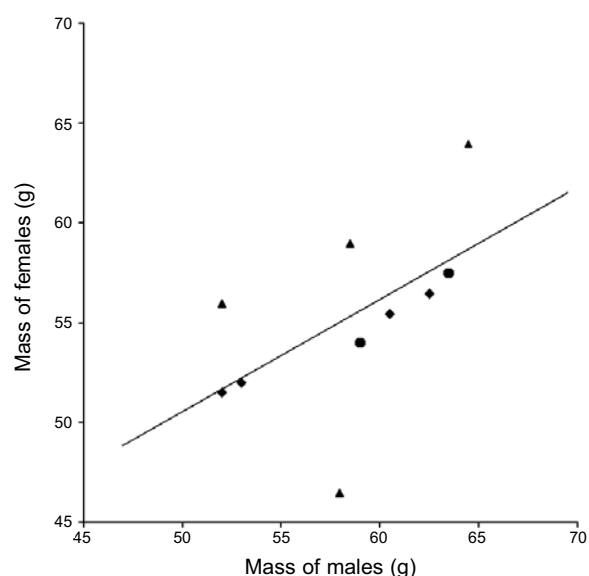


Fig. 2. Relation between the mass of mates in the Middle Spotted Woodpecker ($n = 10$ pairs). • — pairs captured in year 2009, ▲ — pairs captured in year 2010, ♦ — pairs captured in year 2011.

be a general pattern in the studied population. Thus it seems rather unlikely that pair-members that displayed similar ornaments in our study had been mated with each other in the preceding year. Consequently, we do not suppose that similarity in cap brightness of mates results from sharing food resources. However, we cannot fully reject such possibility as we did not monitor studied birds in the year preceding colour measurements.

Our previous study revealed that woodpeckers in better condition, which was expressed by a brighter red cap, produced more offspring (Leniowski & Węgrzyn 2013). Thus mating with highly ornamented individual could be an evolutionary force towards mutual sexual selection. However, social competition and sexual selection do not have to be mutually exclusive as the mechanisms of mutual ornamentation in Middle Spotted Woodpeckers. Mutual ornamentation may have originated from social competition over limited food resources in winter but later it might have been used and strengthened by mutual mate choice.

Interestingly, we did not find significant similarity between cap size (width and length) of mates, and our previous study showed that cap size was not related to individual quality in the Middle Spotted Woodpecker (Leniowski & Węgrzyn 2013). This supports the assumption that woodpeckers may use the features linked to their body condition during pair formation while ignoring those not advertising individual quality.

We also demonstrated significant positive correlation between mate body mass. This may result either from similar intrinsic quality of mated individuals or sharing the same territory during the current breeding season or both factors interacting. Thus, without additional data (for example from translocation experiments) the observed similarity in mates body mass is difficult to explicit interpretation.

Our finding that pair members in Middle Spotted Woodpeckers exhibit similar brightness of red caps, which have the potential to advertise individual quality, sheds some light on possible mechanisms of mating in the studied species. However, we admit that our research is descriptive and thus, an experimental study is required to confirm our assumptions.

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STRESZCZENIE

[Samce i samice dzięcioła średniego są dobrane w obrębie pary pod względem jaskrawości czerwonej czapeczki]

U większości gatunków ptaków występuje dymorfizm płciowy w ubarwieniu samca i samicy. W przeciwieństwie do tej ogólnej zasady, zarówno samce jak też samice dzięcioła średniego posiadają karotenoidową czerwoną czapeczkę, która stanowi u badanego gatunku ornament mutualny. Mutualne ornamenty u ptaków mogą wynikać z (i) korelacji genetycznej pomiędzy samcami i samicami, (ii) współzawodnictwa pomiędzy osobnikami o zasoby środowiska lub (iii) obustronny doboru płciowego. Jeśli mutualne ornamenty są skutkiem obustronnego doboru płciowego u danego gatunku można spodziewać się wybiórczego kojarzenia, w którym bardziej ornamentowane osobniki wybierają bardziej ornamentowanych partnerów, a mniej ornamentowane ptaki tworzą pary pomiędzy sobą. Pomimo rosnącej liczby dowodów na ewolucję mutualnych ornamentów u ptaków na skutek obustronnego doboru płciowego, stosunkowo niewiele badań dotyczy wybiórczego kojarzenia pod względem koloru upierzenia i żadne z nich nie było przeprowadzone na dzięciolach. Aby uzupełnić tę lukę, w naszych badaniach przeanalizowaliśmy zależność pomiędzy ekspresją karotenoidowego ornamentu (czerwonej czapeczki) osobników tworzących pary u dzięcioła średniego. Badaliśmy

również czy ptaki w obrębie pary są dobrane pod względem rozmiaru czapeczki jak również pod względem takich cech fizycznych jak masa ciała oraz długość skrzydła, dzioba i skoku.

Badania były prowadzone w Rezerwacie Czeszewski Las (17°31'E, 52°09'N), w latach 2009–2011. Dzięcioły (10 par) były chwytywane przy dziupli w celu przeprowadzenia spektrofotometrycznych pomiarów koloru czapeczki. Wszystkie osobniki zostały zaobrączkowane, dokonano też pomiarów biometrycznych.

Wykazaliśmy silną i istotną statystycznie korelację pomiędzy jaskrawością czapeczki samców i samic stanowiących rzeczywiste pary (Fig. 1) i brak takiej korelacji pomiędzy samcami i samicami połączonymi w pary losowo. Analiza wykazała, że różnice w jaskrawości czapeczki pomiędzy różnymi parami dzięcioła średniego były istotnie większe niż różnice pomiędzy członkami pary. Nie stwierdziliśmy natomiast istotnej statystycznie korelacji pomiędzy szerokością oraz długością czapek osobników tworzących pary. W zakresie analizowanych cech fizycznych stwierdziliśmy istotną korelację masy samców i samic w obrębie par (Fig. 2). Partnerzy nie byli jednak dobrani pod względem pozostałych cech biometrycznych (długość skrzydła, dzioba i skoku).

Uzyskane wyniki wskazują, że w obrębie badanych par dzięcioła średniego osobniki były wybiórczo skojarzone pod względem jaskrawości czerwonej czapeczki, czyli cechy, która jednocześnie wydaje się dobrze odzwierciedlać kondycję osobników u badanego gatunku. Możliwe zatem, że osobniki używają tej cechy aby ocenić reprodukcyjną wartość potencjalnego partnera podczas formowania pary. Podobna ekspresja czerwonej czapeczki u osobników w obrębie pary sugeruje, że ewolucja tego mutualnego ornamentu może być związana z obustronnym doбором płciowym. Tym niemniej, ze względu na opisowy charakter naszych badań, potwierdzenie powyższych wniosków wymaga przeprowadzenia odpowiednich eksperymentów.

Influence of old coniferous habitat on nestling growth of Black-backed Woodpeckers *Picoides arcticus*

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Abstract. Nest success is often used to evaluate the impact of environmental stressors on species, but nestling growth may also be indicative of subtle consequences on individual fitness. We monitored Black-backed Woodpecker *Picoides arcticus* nestling growth in unburned boreal forests under the influence of commercial logging. The objectives of our exploratory study were to estimate growth rate constants of weight and three morphometric measures (culmen length, tarsal length and wing length) in nestling Black-backed Woodpeckers and to determine how the amount of old coniferous habitat in home ranges may affect these rates. The amount of old coniferous habitat positively influenced weight gain in Black-backed Woodpecker nestlings but did not influence the three morphometric measures of growth rate. Our results suggest that Black-backed Woodpecker fitness may be affected by the reduction of old coniferous habitat in managed forest landscapes. We encourage further studies on the relationship between habitat quality and nestling growth as a potentially useful indicator of how habitat loss might influence individual fitness in these species.

Key words: cavity-nesting bird, fitness, forest management, nestling growth rate, unburned boreal forest, woodpecker

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INTRODUCTION

Nest success is often used to evaluate the impact of environmental stressors on species (Johnson 2004), but more subtle consequences on parental fitness may be evaluated by nestling growth (Starck & Ricklefs 1998). Slower growth at early life stages may negatively affect individuals through lowered post-fledging survival (Gebhardt-Heinrich & Richner 1998, McCarthy 2001) and even have long-term effects by decreasing the ability to obtain a breeding territory or a mate, or by lowering fecundity (Richner 1992). The growth rate of altricial bird species is thought to be constrained by the ability of nestlings to assimilate or process food, or by the rate at which tissues proliferate (Ricklefs et al. 1998). Furthermore, nestling growth may be affected by various external factors, including parental age and physical condition, choice of breeding habitat, hatching date,

clutch size, and environmental conditions (Ricklefs 1983). Many environmental constraints may affect nestling growth but most are related to food supply (Gebhardt-Heinrich & Richner 1998). Food availability (quantity and quality) or delivery rates may limit nestling development (Lack 1968) so that nestling growth patterns may reflect differences in nestling habitat quality (Duguay et al. 2000).

Species that rely on scarce or ephemeral resources for foraging may exhibit higher variability in their nestling growth rate. The Black-backed Woodpecker *Picoides arcticus* is a North American boreal habitat specialist that selects areas populated by xylophagous insects (especially members of the Cerambycidae, and Buprestidae). Many authors have associated the Black-backed Woodpecker with recently burned habitats (Hutto 1995, Murphy & Lehnhausen 1998, Hoyt & Hannon 2002) although the species breeds successfully in

unburned forests (Tremblay et al. 2009, Craig 2013). In recently burned habitats, Black-backed Woodpeckers feed predominantly on wood-boring larvae of Cerambycidae (Murphy & Lehnhausen 1998), mostly *Monochamus scutellatus* and *Acmaeops proteus* (Nappi & Drapeau 2009) but their diet in unburned forest stands is not well known. Based on foraging observations in unburned forest stands, Tremblay et al. (2010) suggested that Black-backed Woodpeckers mainly feed on wood-boring insect larvae obtained by excavation. Nests of Black-backed Woodpeckers in unburned forest stands may exhibit a lower productivity than those in burns (Tremblay 2009) and this habitat may be considered as sub-optimal, at least at the nest scale. Tremblay et al. (2009) indicated that foraging Black-backed Woodpeckers require 15 m³/ha of recently dead wood to breed successfully in unburned old coniferous forest stands. While dead wood resources are relatively scarce in Black Spruce *Picea mariana* forests of eastern Canada (Vaillancourt et al. 2008), the quantity of high-quality habitat (i.e. old coniferous forest stands) may be of high importance for sustaining Black-backed Woodpeckers in unburned boreal forests.

We monitored Black-backed Woodpecker nestling growth in unburned boreal forests under the influence of commercial logging and investigated the importance of old coniferous habitat on Black-backed Woodpecker nestling growth. The objectives of our exploratory study were to estimate growth rate constants in nestling Black-backed Woodpeckers and to determine how the amount of old coniferous habitat within home ranges may affect these growth rates. We hypothesized that an increase in the amount of old coniferous habitat within home ranges increases food availability and thus, increases parents' foraging efficiency and food provisioning of nestlings. As such, we predicted that there would be a positive relationship between the amount of old coniferous habitat within Black-backed Woodpecker home ranges and nestling weight gain and wing growth. We also tested the relationship between old coniferous habitat and nestling culmen and tarsus growth, but did not expect a relationship as these growth rates have been shown to be less sensitive to environmental constraints (sensu Alatalo et al. 1990) that influence energy acquisition and more to the availability of minerals such as calcium (Dawson & Bidwell 2005).

METHODS

Study area

Field work was conducted from May to July over two breeding seasons (2005–2006) within the black spruce-moss forest of the Canadian boreal forest ecological domain (Saucier et al. 1998) in central Quebec (50°34'N, 72°10'W). The stands were composed mainly of Black Spruce, or Black Spruce mixed with Jack Pine *Pinus banksiana*, Balsam Fir *Abies balsamea*, White Birch *Betula papyrifera*, Quaking Aspen *Populus tremuloides* and, occasionally, Tamarack *Larix laricina*. The topography was undulating and forest fires were the major natural forest perturbation. Commercial timber harvesting began in the last decade and the area was logged using mosaic harvesting, which favoured an interspersed of logged and residual forested blocks in the landscape. Even-aged management (cut with regeneration and soil protection, CRSP) was practiced in the southern part of the study area and uneven-aged management (cut with little merchantable tree protection, CLMTP) in the northern part.

Trapping and tracking

Birds were located with roadside surveys using playbacks of 20 min (or less if detection occurs) of calls and drumming of Black-backed Woodpeckers (Ibarzabal & Desmeules 2006). Woodpeckers were captured using mist nets and individuals showing signs of breeding (i.e., presence of a brood patch) were fitted with a radio-transmitter (2.3 g, Model PD-2, Holohil Systems Ltd.) attached at the base of the two central rectrices. Released birds were followed to locate their nests. The location of each nest was marked using flagging tape at a distance > 3 m from the nest tree. Nest location coordinates were recorded using a global positioning system (GPS Garmin Legend, Garmin Corporation). To obtain nestling growth data, an inspection hole was drilled approximately 5 to 8 cm below the cavity entrance using an 18 V wireless drill equipped with a 10 cm hole saw. This procedure allowed clear access to nestlings and the block of wood removed was used to create a weatherproof door (see Ibarzabal & Tremblay (2006) for further details). Only cavities at < 3 m height were opened.

Nestling growth

Where possible, nests were visited every two days from their discovery until nestlings fledged or the nest failed; any loss of eggs or nestlings was noted

(Table 1). Because of logistical difficulties, nest #2 was checked every three days. In addition, in 2005, a forest fire prevented nest visits for four days. Nestlings used for the biometric study were identified using a spot of nail varnish on one of the claws; this provided each individual with a unique colour code until it was large enough to be banded. Prior to this study, we developed an evolution chart of Black-backed Woodpecker nestlings based on nest histories and nestling observations from 37 nests (unpublished data) which enabled us to age nestlings precisely. We noted the order of the sequence in each nestling hatched as Black-backed Woodpecker nestlings hatch asynchronously (Dixon & Saab 2000). Four body traits were sampled during the three week nestling period: (1) body mass to the nearest 0.1 g, using a digital balance (Ohaus model CS200); (2) tarsus length and (3) culmen length to the nearest 0.01 mm, using a digital calliper (Mitutoyo model CD-6B); and (4) wing length (the distance from the anterior surface of the radiocarpal joint to the tip of the longest primary).

Only data from nestlings that survived to fledging were used for the analyses of nestling growth because inclusion of dead fledglings may bias results and no growth parameter can be calculated for nestlings that did not reach the asymptote. Only nest #5 had a dead nestling (found dead at day 16 after hatching, probably from food scarcity caused by the departure of the female during the nestling period). Nestlings were sampled at each visit providing a mixed longitudinal sample (Ricklefs 1983). Growth parameters were investigated using logistic, von Bertalanffy and Gompertz curves (Ricklefs 1967). We evaluated the best fit of the growth curve type by evaluating R^2 and selected curves with the highest values. We estimated the asymptotic size (A),

growth rate constant (K), and growth period between 10% and 90% of asymptotic size (T) of culmen, tarsus, weight, and wing length of each nestling.

Habitats

We estimated the amount of old coniferous habitat in the breeding home range of each Black-backed Woodpecker following Tremblay et al. (2009). Home ranges averaged about 150 ha (151.5 ± 18.8 ha; Tremblay et al. 2009) and we used this value to estimate the home range associated with a nest where the actual home range could not be measured (nest #2) by creating a buffer of 690 m-radii (149.6 ha). To determine the habitat composition of home ranges, we overlaid the home range area onto digitized habitat layers. ArcGIS Geoprocessing Wizard (ArcGIS 10.1, ESRI 2012) was used to clip habitat types within home range boundaries and calculate their proportions. Habitat types were established using 1:20 000 forest maps published by the Quebec Ministry of Natural Resources in 1992 and updated to incorporate disturbances (i.e., fires and logging). Predominant habitat types in the study area were barren lands, young (≤ 90 years old) and old (> 90 years old) coniferous stands, and recent (≤ 5 years old) and old (> 5 years old) cuts.

Statistical analysis

We limited our statistical analysis to growth rate constant (K), which is considered the most useful parameter for comparing growth rates (Starck & Ricklefs 1998). We fitted linear mixed effects models to examine the relationship between the growth rate constant of each body trait and the amount of old coniferous habitats within the home range, using the lme4 package (Bates 2010) in R version 2.15.1 (R Core Team 2013). We also

Table 1. Number of nestlings, day of nest discovery, first and last day of measurements and amount of old coniferous habitat in the home range for each nest. All days are reported relative to day of hatch with negative days prior to hatch (incubation) and positive days post-hatch. ^a — 3 nestlings hatched and one died from food scarcity caused by the departure of the female during the nestling period. We only included data from nestlings that survived to fledging in the analyses of nestling growth because inclusion of dead fledglings may bias results and no growth parameter can be calculated for nestlings that did not reach the asymptote.

Nest ID	Number of nestlings	Day of nest discovery	Day of first measurement	Day of last measurement	Old coniferous (ha)
1	2	-9	5	22	71.6
2	3	6	6	21	78.9
3	3	4	4	22	20.4
4	3	-9	2	22	25.8
5	2 ^a	-3	2	21	82.6

considered the hatching order of nestlings “hatch order” to account for possible inter-nestling competition (Hadow 1976) and assumed a linear change with increase in hatching order. We included “hatch order” and “amount of old coniferous habitat” (without interaction) as fixed-effects. Nest and year were initially considered as nested random effects (nest within year) but we were unable to include both due to the small sample size and therefore only considered nest, in which case the variance in the distribution might be broader to encompass annual variation. We used maximum likelihood to identify the model with the most supported fixed effects structure using Akaike’s Information Criterion for small samples (AICc, Burnham & Anderson 2002) and compared models with hatch order and amount of old coniferous forest to models that had only one of these variables and a model which contained only the random effect of nest. Model averaging was used to estimate the coefficient and standard error for the relationship between fixed effects and growth rates. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. Because of our small sample size relative to parameter number we also inspected the data for cases where outlier predictor values might have had a strong influence on the slope of the beta coefficient but there was little evidence for this and response values typically lay close to the regression line.

RESULTS

We measured growth parameters from hatching to fledging for 13 nestlings from 5 nests during the two years of the project. Amount of old coniferous forest in each home range varied from 20.4 to 82.6 ha (Table 1). All growth parameters were best described by logistic curves. Asymptotic sizes (A) varied little between nests whereas growth rate constants (K) and periods (T) were more variable between nests for each body trait. Tarsus and weight exhibited the highest coefficient of variation (Table 2). The amount of old coniferous habitat positively influenced weight gain of nestlings ($\beta = 0.0027 \pm 0.0008$ (SE); 95% CI: 0.0011, 0.0044; Table 3) but did not influence the growth rate constant for the three morphometric measures (Culmen: 0.00002 ± 0.0005 ; Tarsus: -0.0043 ± 0.0029 ; Wing: 0.0004 ± 0.0004). For each body trait, the coefficient for the order of hatching was

negative, indicating a declining growth rate for later hatched nestlings. However, the relationship was only significant for wing length ($\beta = -0.0219 \pm 0.0089$ (SE)) based on AICc model support (Table 3) and confidence intervals excluding zero (95% CI: -0.0394, -0.0045). The coefficient value and standard error for hatch order effects on the other three measures were as follows: culmen: -0.0083 ± 0.0128 , tarsus: -0.0208 ± 0.0737 , weight: -0.0158 ± 0.0267 .

DISCUSSION

Our results show that the amount of old coniferous habitat positively influences weight gain in Black-backed Woodpecker nestlings. Growth constants of others body traits were not influenced by the amount of old coniferous habitat which agrees with our predictions for culmen and tarsal growth, but not wing growth where we had predicted a positive effect. Old coniferous habitat contains $\geq 30\%$ more deadwood volume (m^3/ha)

Table 2. Mean $\pm$ SE and coefficient of variation (CV) of asymptotic size (A), growth rate constant (K), and growth period between 10% and 90% of asymptotic size (T in days), of culmen (mm), tarsus (mm), weight (g), and wing chord (mm) for each monitored nests of Black-backed Woodpeckers in unburned forest stands. All values were determined by logistic curves.

Variable	Nest ID	A	K	T
Culmen	1	22.3 ± 0.1	0.26 ± 0.00	16.8 ± 0.1
	2	22.0 ± 0.9	0.30 ± 0.06	15.2 ± 3.0
	3	22.8 ± 0.3	0.32 ± 0.02	14.1 ± 1.5
	4	23.1 ± 0.7	0.25 ± 0.00	17.8 ± 0.2
	5	21.0 ± 0.4	0.29 ± 0.01	15.2 ± 0.5
	CV	0.04	0.10	0.09
Tarsus	1	24.5 ± 0.5	0.36 ± 0.07	12.7 ± 2.6
	2	25.1 ± 0.2	0.95 ± 0.23	4.9 ± 1.2
	3	25.4 ± 0.3	0.54 ± 0.03	8.2 ± 0.5
	4	24.0 ± 0.3	0.84 ± 0.06	5.3 ± 0.3
	5	25.4 ± 0.6	0.53 ± 0.15	9.0 ± 2.6
	CV	0.02	0.38	0.39
Weight	1	69.5 ± 1.7	0.36 ± 0.03	12.4 ± 1.2
	2	55.8 ± 0.6	0.42 ± 0.10	11.1 ± 2.6
	3	64.2 ± 1.0	0.32 ± 0.05	14.1 ± 2.4
	4	62.6 ± 2.6	0.31 ± 0.01	14.4 ± 0.6
	5	51.4 ± 1.0	0.50 ± 0.02	8.7 ± 0.3
	CV	0.11	0.21	0.19
Wing	1	98.2 ± 3.4	0.31 ± 0.03	11.5 ± 0.4
	2	90.3 ± 1.3	0.36 ± 0.00	12.1 ± 0.0
	3	97.3 ± 2.3	0.37 ± 0.00	12.0 ± 1.0
	4	98.2 ± 3.4	0.31 ± 0.03	14.4 ± 1.7
	5	89.8 ± 0.8	0.36 ± 0.01	12.0 ± 0.7
	CV	0.05	0.09	0.09

Table 3. Model selection from linear mixed effects models of the growth rate constant of the truncated logistic growth curve in 13 Black-backed Woodpecker nestlings (5 nests) where we evaluated the effect of the hatching order (Hatch Order) and the amount of old coniferous habitat (Old conif) in each breeding home range on 4 growth traits. All models contained nest as a random effect to control for repeated observations. The null model contained only this random effect without either fixed effect.

Model	log(L)	AIC _c	Δ AIC _c	w _i	K
Culmen					
Null	23.66	-40.13	0	0.71	2
Hatch Order	23.86	-37.06	3.07	0.15	3
Old Conif	23.67	-36.66	3.46	0.13	3
Old Conif + Hatch Order	23.87	-32.73	7.40	0.02	4
Tarsus					
Null	0.42	4.36	0	0.59	2
Old Conif	1.40	5.87	1.51	0.28	3
Hatch Order	0.44	7.78	3.42	0.11	4
Old Conif + Hatch Order	1.48	10.05	5.69	0.03	3
Weight					
Old Conif	15.53	-22.40	0	0.63	3
Null	12.78	-20.36	2.04	0.23	2
Old Conif + Hatch Order	15.60	-18.20	4.20	0.08	4
Hatch Order	13.17	-17.67	4.73	0.06	3
Wing					
Hatch order	28.20	-47.72	0	0.56	3
Null	25.71	-46.22	1.50	0.26	2
Old Conif	26.41	-44.15	3.58	0.09	3
Old Conif + Hatch Order	28.47	-43.94	3.79	0.08	4

than other habitats in the study area, providing more suitable habitats to forage (Tremblay et al. 2009). Parents with greater amount of old coniferous habitat within their home range can forage closer from their nest which likely increases provisioning of food to nestlings. In this sense, Tremblay et al. (2009) showed that the spatial distribution of preferred foraging habitat patches influenced space use of breeders, with home range area increasing with the median distance between old coniferous habitat patches available within the landscape.

Heavier nestlings have better thermoregulation, which enhances their survival and has direct fitness consequences (Dawson et al. 2005). Furthermore, faster weight gain benefits nestlings in reducing the period of exposure to nest predators (Lack 1968), and our data indicate that daily nest survival rate of Black-backed Woodpeckers increased throughout the nestling period (Tremblay et al. unpublished). The three other body traits were not influenced by the amount of old coniferous habitats but caution is needed given our small sample size. The growth of culmen and tarsus, both skeletal structures, may be limited by the availability of minerals such as

calcium rather than by energy limitations (Dawson & Bidwell 2005). Body reserves (i.e. lipids) may be an important parameter in juvenile survival (Alatalo et al. 1990), but distinction between body weight and body reserve is not often made (Kunz & Ekman 2000). It would be interesting to evaluate whether increase in weight reflect greater body reserves; an increase in body weight (muscles) may enhance thermoregulation (and nestling survival; Dawson et al. 2005) while an increase in body reserve (fat) may enhance fledgling survival (Alatalo et al. 1990). Nestling growth may be influenced by others factors not examined in this study, such as environmental conditions (i.e. precipitations and temperature), parental age and physical condition (Ricklefs 1983). Although most growth variation in nestlings may be related to food supply (Gebhardt-Heinrich & Richner 1998), further studies should include abiotic and biotic factors that may influence nestling growth rate constants. Our study assumed that order of hatching may have an important influence on nestling growth rates and our results justify our decision to use this factor in our model, although significant effects were only observed for wing length growth. Indeed, number of nestlings may affect amount of food obtained by each nestling and our results showed that older nestlings have generally higher growth rates than their younger siblings. In many avian species, parents preferentially feed the largest, most competitive nestlings in a brood (review in Mock & Parker 1997).

Considering our low sample size, our analysis should be treated only as exploratory and more extensive sampling is needed to confirm our findings. Nevertheless, our results provide new insights on habitat/fitness relationships of boreal birds in a managed landscape. Nestling growth could be a sensitive tool to detect reductions in species fitness and to investigate habitat/fitness relationships. Future studies should examine differences in growth rates under different environmental conditions found in boreal forests, for example across a complete chronosequence of forest succession from disturbances (natural and anthropogenic) to old-growth forests. Our results suggest that Black-backed Woodpecker fitness may be affected by the reduction of old coniferous habitat in managed forest landscapes. For instance, the quantity, quality and spatial repartition of high-quality habitat (i.e. old coniferous forest stands) are important attributes in the home range establishment of breeding Black-backed

Woodpeckers (Tremblay et al. 2009). The use of nestling growth as an avenue to address habitat/fitness relationships on boreal birds needs to be investigated further.

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STRESZCZENIE

[Związek pomiędzy powierzchnią starych drzewostanów iglastych w obrębie terytorium i wzrostem piskląt dzięcioła północnego]

Analizując wpływ różnych czynników środowiskowych na lęgi ptaków najczęściej określa się go w odniesieniu do sukcesu lęgowego. Tymczasem inne zmienne, takie jak tempo wzrostu piskląt, także mogą być wykorzystywane do tego celu, pokazując jednocześnie bardziej subtelne zmiany, które potencjalnie mogą wpływać na dostosowanie osobnika. Niższe tempo wzrostu może być przykładowo związane z niższą przeżywalnością młodych po opuszczeniu gniazda, ale także mieć długoterminowe konsekwencje w postaci obniżonej zdolności do pozyskania terytorium, czy też obniżonej płodności. Rozwój piskląt znajduje się pod silnym wpływem dostępności pokarmu (zarówno jego ilości, jak i jakości), dlatego też przebieg wzrostu piskląt może odzwierciedlać różnice w jakości siedliska, w którym wychowują się.

Badaniami objęto dzięcioła północnego — gatunek, który występuje w strefie borealnej Ameryki Północnej, żywiący się głównie larwami owadów żerującymi w drewnie. Dzięcioł północny bardzo często gniazduje na terenach pogorzeliisk po pożarach lasu, ale może także występować na obszarach nie dotkniętych pożarami, choć uważa się takie tereny za suboptymalne dla tego gatunku. Autorzy założyli, że najwięcej martwego drewna, istotnego dla żerowania tego gatunku, może znajdować się na terenach starych drzewostanów (starszych niż 90 lat). Celem pracy było określenie tempa wzrostu zarówno masy ciała, jak i długości dzioba, skoku i skrzydła piskląt

dzięcioła północnego w powiązaniu z powierzchnią starodrzewia na terytorium danej pary.

Gniazda dzięcioła północnego monitorowano na obszarach niezaburzonych przez pożary, na których prowadzona była wycinka drzew. W drzewach z dziuplami wycięto otwory, które umożliwiały dostęp do piskląt. W większości przypadków piskląta były mierzone i ważone co 2 dni. Dla terytorium danej pary (ok. 150 ha) określano powierzchnie starych drzewostanów (powyżej 90 lat). Analizowano tempo wzrostu każdego pisklącia osobno, biorąc pod uwagę także kolejność ich wykluwania się. W przypadku jednego gniazda jedno z piskląt zdechło w związku ze zniknięciem samicy w okresie karmienia młodych (pisklą to nie było uwzględnione w dalszych analizach). W wynikach uwzględniono dane uzyskane dla 5 gniazd (13 piskląt, Tab. 1).

Zaprezentowano współczynniki tempa wzrostu w poszczególnych gniazdach (Tab. 2). Stwierdzono, że powierzchnia starych drzewostanów wpływała na tempo wzrostu masy ciała, które było wyższe na terytoriach z większym udziałem starych lasów (Tab. 3). Wzrost długości dzioba, skoku czy skrzydła nie był istotnie związany z badanym siedliskiem. Dla wszystkich analizowanych parametrów stwierdzono związek z kolejnością klucia, tj. później klujące się piskląta rosły gorzej, choć tylko dla długości skrzydła zależność ta była istotna statystycznie (Tab. 3).

Autorzy sugerują, że na terytoriach z większą powierzchnią starych drzewostanów ptaki dorosłe mogą znajdować więcej pokarmu, jak i żerować bliżej gniazd, co może wpływać na tempo wzrostu masy piskląt. Natomiast wzrost długości dzioba czy skoku może być związany z dostępnością składników mineralnych (wapnia) i stąd może nie być obserwowany prosty związek z powierzchnią najlepszych środowisk do żerowania.

Autorzy wskazują na fakt, że w związku z małą próbą wyniki należy traktować jako wstępne, ale sugerują, że warto analizować tempo wzrostu piskląt w powiązaniu z jakością siedliska, gdyż może to pokazać jak utrata siedlisk może wpływać na badany gatunek.