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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

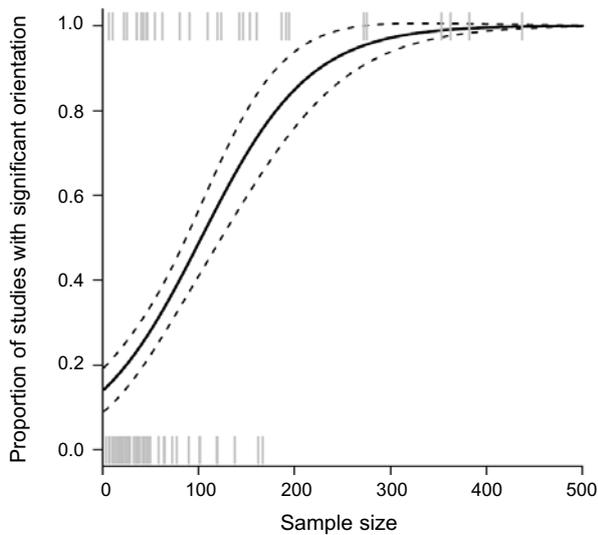


Fig. 1. The proportion of studies in which a significantly non-random cavity entrance orientation was found in relation to increasing sample size. Solid black line shows GLM model fit, \pm standard error (dotted lines). Data are represented by grey “|” symbols.

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

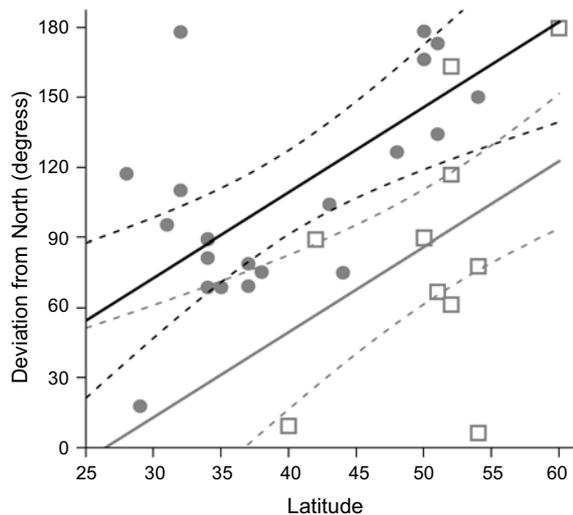


Fig. 2. Relationship between latitude of study site and angular deviation of study population mean vector from North for all studies from which a mean orientation vector could be extracted ($n = 31$). North American studies — black lines \pm 95% CI and closed symbols; Eurasian studies — gray lines \pm 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	Aulèn 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. Natural Park	Random	Fauvel et al. 2001	77	0.124	0.31	
	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
	Yellow-bellied Sapsucker <i>Sphyrapicus varius</i>	Canada, Ontario	S	Lawrence 1967	42	0.44	< 0.01
USA, Colorado		Random	Inouye 1976	36	0.22	0.18	
White-headed Woodpecker <i>Picoides albolarvatus</i>	USA, Washington State	Random	Kozma et al. 2009	41	0.2	0.2	
Red-naped Sapsucker <i>Sphyrapicus nuchalis</i>	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	