Reproductive correlates of eggshell thickness in European woodpeckers

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Woodpeckers excavate their own nesting holes, have small eggs relative to their body size and many species have small clutches. Based on data from the eight European woodpecker species it was found that the mean thickness of eggshells increases with egg volume, whereas large woodpeckers lay smaller eggs with thinner eggshell relative to their body mass. It is speculated that woodpeckers minimize their reproductive costs by laying energy-poor eggs that are relatively cheap to produce, and with their low adult mortality rates, increase their lifetime reproductive success.

Key words: Picidae, woodpeckers, eggshell thickness, egg volume

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INTRODUCTION

Woodpeckers, Picidae, are perching or climbing birds with a characteristic pattern of reproduction. Almost all the species excavate their own holes for nesting and roosting. Woodpeckers have one of the shortest incubation periods among birds (del Hoyo *et al*. 2002), and hatch chicks at a relatively immature stage of development while they are naked, have fused eyelids and poor thermoregulatory capacity and being about 5% of adult weight (e.g. Yom-Tov & Ar 1993, Winkler *et al*. 1995). Woodpeckers also have among the smallest eggs relative to their body size of any bird (Rahn *et al*. 1975, Yom-Tov & Ar 1993). However, information on egg composition and eggshell thickness in woodpeckers is scanty or lacking (Wiebe 2006). In some handbooks it is mentioned that woodpeckers have small eggs with thin shells, but without giving thickness values. I have earlier shown that woodpecker eggs have thinner shells than that of secondary hole-nesting passerines (Hogstad 2006a). In this paper, it is examined how eggshell thickness varies with different factors of reproduction in European woodpeckers.

METHODS

Only the «true» woodpeckers, subfamily Picinae, are examined. The subfamily Jynginae, the Wryneck *Jynx torquilla*, is excluded because the Wryneck has a passerine-like mode of locomotion and breeds in natural cavities and old woodpecker holes, and does not excavate its own nest.

Data on the size of the birds (female body mass in g), incubation and nestling periods (days),

mean clutch size, egg weight (g) and egg volume index (length x breadth^2/1000) were extracted from Cramp (1985) and Winkler *et al*. (1995), and supplemented with own data (Appendix). Eggshell thickness was measured with a modified micrometer (Starrett Model 101M) to the nearest 0.01 mm on eggs in collections at zoological museums in Oslo and Trondheim, Norway. In the analyses, I have used the eggshell thickness index (thickness x 100).

The species examined are the Black *Dryocopus martius*, the Green *Picus viridis*, the Grey-headed *Picus canus*, the Great Spotted *Dendrocopos major*, the Middle Spotted *D. medius*, the White-backed *D. leucotos*, the Lesser Spotted *D. minor* and the Three-toed *Picoides tridactylus* Woodpeckers (Table 1).

All tests are two-tailed, and were performed using SPSS 15. Data were analysed using nonparametric tests. Means are presented ± 1 SD.

RESULTS

The mean eggshell thickness index of the eight species varies between 10.00 (0.1 mm) in the Lesser Woodpecker and 16.70 (0.17 mm) in the Black Woodpecker (Table 1, Fig. 1). Differences in shell thickness among the species are significant (one-way ANOVA; $F_{7, 185}=63.74$, $p<0.001$).

The regressions to determine allometric relationships between eggshell thickness and reproductive parameters showed that the thickness of eggshells increased with egg weight ($r_s=0.71$, $p=0.047$, $n=8$), egg volume ($r_s=0.81$, $p=0.015$; Fig. 2) and clutch weight ($r_s=0.86$, $p=0.007$), but decreased with relative egg weight (egg weight/female body mass; $r_s=-0.86$, $p=0.007$). Thus, although eggshell thickness increases with the size of the eggs, larger woodpecker species lay smaller eggs with thinner eggshell relative to their body mass. No significant correlations are found between eggshell thickness and incubation or nestling periods or clutch size.

The eggshell thickness was also found to be positively related to the tendency to reuse (%) nesting holes ($r_s=0.89$, $p=0.007$, $n=7$). However, as larger woodpeckers tend to reuse holes more frequently than smaller ones (correlation between percentage reuse and female body size, $r_s=0.70$, $p=0.077$, $n=7$) and also have larger eggs (correlation between body mass and egg volume, $r_s=1.0$), the relationship between reuse and eggshell thick-

Table 1. Eggshell thickness index (thickness in mm x 100; mean ± SD) of eight European woodpeckers. The eggshell thickness/egg weight (t/w), eggshell thickness/egg volume (t/v), eggshell thickness/female body mass (t/m), eggshell thickness/clutch size (t/c) and eggshell thickness/clutch weight (t/cw) are also given.

Species	n	Thickness	t/w	t/v	t/m	t/c	t/cw
Grey-headed	29	15.21 ± 1.01	2.03	1.12	0.12	1.90	0.25
Green	49	16.56 ± 1.32	1.95	0.98	0.08	2.55	0.30
Black	66	16.70 ± 0.84	1.35	0.73	0.06	3.34	0.27
Great Spotted	13	15.23 ± 0.93	3.11	1.41	0.18	2.54	0.52
Middle Spotted	1	15.00	3.75	1.50	0.23	2.73	0.68
White-backed	14	12.86 ± 1.03	2.14	1.04	0.13	3.22	0.54
Lesser Spotted	7	10.00 ± 0.58	5.00	2.34	0.44	1.67	0.83
Three-toed	7	13.71 ± 1.11	2.54	1.52	0.23	3.61	0.67

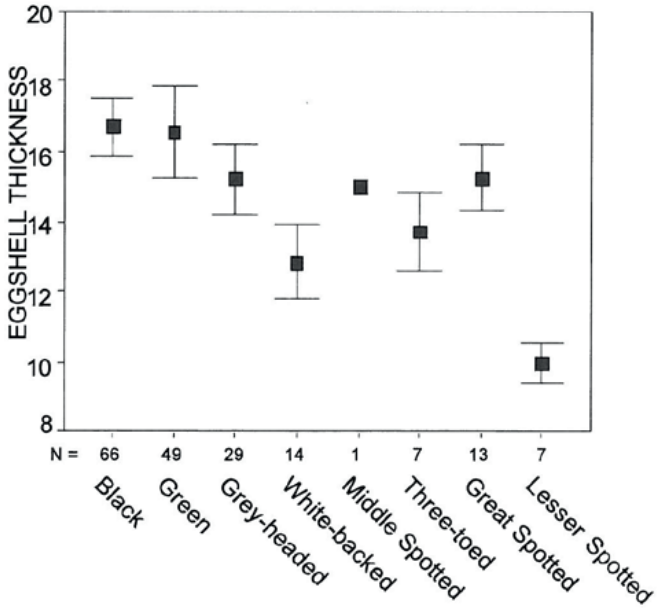

Figure 1. Mean eggshell thickness (± 1 SD) of eight woodpeckers arranged according to decreasing body mass of the species.

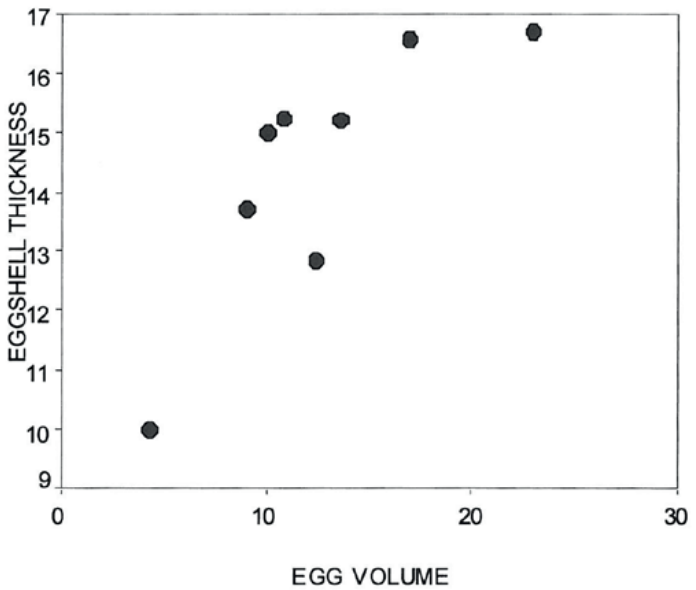

Figure 2. Relationship between egg volume and eggshell thickness (r_s=0.81, p=0.015).

ness may partly be a result of the female body mass. When a control is performed for female body mass in a partial correlation, the correlation between reuse and eggshell thickness is no longer significant (r=0.65, p=0.165, df=4).

DISCUSSION

Several hypotheses have been set forward to explain the special reproductive traits in woodpeckers (see Hogstad 2006a). One of the most remarkable patterns is their small eggs relative to their body size. In North American woodpeckers, their small eggs have been associated with alternative reproductive strategies of females, such as conspecific egg parasitism (Bower & Ingold 2004) and polyandry (Andersson 2004, Wiebe 2005).

The small eggs of woodpeckers are probably relatively cheap to produce. Generally, eggs of altricial species contain relatively smaller yolks and less energy than eggs of precocial birds (Carey *et al*. 1980, Sotherland & Rahn 1987, Williams 1994, Hill 1995). Although less is known about egg contents of birds within altricial species, the relative yolk size of woodpeckers eggs seems small. Thus, Carey *et al*. (1980), using bomb calorimetry on three homogenized eggs of the Northern Flicker *Colaptes auratus*, found that the eggs contained only 3.3 kJ g^{-1}, compared to 5.0 kJ g^{-1} for altricial birds in general. The eggs of the Northern Flicker, living in North America, are among the most energy-poor of any bird species due to their relative small yolks, averaging 16% of wet egg mass (Wiebe 2006). Reviews of more than 200 bird species gave fractions between 15 and 69% yolk (Carey *et al*. 1980, Sotherland & Rahn 1987). Thus, the Northern Flicker eggs fell at the low extreme of this range. The other species reported by Carey *et al*. (1980) and Sotherland & Rahn (1987) that have a similarly low yolk fraction were a corvid, a thrush, a starling, and a cormorant. It is therefore difficult to make generalizations about the ecology or phylogeny of birds with energy-poor eggs. Compared to other species, however, flicker eggs contain relatively little energy and are probably cheap for flicker females to produce. Thus, after a period of incubation and total clutch failure, the time to reinitiate a new clutch was only eight days (Wiebe 2003), suggesting that the ovary and oviduct can produce new eggs rapidly, although earlier findings has shown that oviduct regrowth is energetically costly (Vezina & Williams 2003, Williams & Ames 2004).

It is unknown whether the energy-poor eggs of the Northern Flicker are representative for woodpeckers in general. In any case, micronutrients, calcium or other biochemical components may limit the clutch size or egg size in woodpeckers and other birds (Williams 2005). As egg size has been found to increase with food abundance in some altricial species (e.g. Otto 1979, Högstedt 1981, Murphy 1986), egg size and shell thickness may be indirect measures of energy limits in woodpeckers living in temperate regions. The energy budget of the insect-eating woodpeckers is probably under considerable constraint during the winter, and their breeding abundances have been found positively correlated with winter temperature (e.g. Marchant *et al*. 1990, Nilsson *et al*. 1992, Rolstad & Rolstad 1995, Wiktander 1998). Within the North American species of the genus *Picoides*, there is a significant inverse correlation between clutch size and Coeloptera in the diet, and species that eat more beetles also have relatively smaller eggs (Koenig 1987). Since approximately 95% of the dry weight of the eggshell is calcium carbonate, calcium is required in large quantities during egg laying (Graveland 1996, Perrins 1996). It is known that woodpeckers and other woodland birds may suffer from calcium shortage (Perrins 1996). An increase in the breeding success of early breeders of Lesser Spotted and White-backed Woodpeckers (Hogstad & Stenberg 1997, Wiktander 1998) indicates a payoff between early breeding and the physical condition of the females (Hogstad & Stenberg 2005). Thus, Lesser Spotted Woodpecker females suffered high mortality in spring before egg laying (Wiktander 1998), and the physical

condition (ratio of body mass to wing length) of White-backed Woodpecker females decreased from January-February to May, whereas that of males was significantly better and relatively stable in the same period (Hogstad & Stenberg 2005).

Within the genus *Picoides* (33 species, including the four European *Dendrocopos* species, cf. Winkler *et al*. 1995), the species living in temperate regions are in average larger and have a shorter incubation period than those in southern regions (Hogstad 2006b). Although data of egg size and shell thickness is lacking of woodpeckers living in southern regions, the short incubation period of the northern species may indicate thinner eggshell of the latter species (incubation period - shell thickness: r_s=0.64, p=0.086, n=8; this article).

It may therefore be speculated that woodpeckers living in temperate regions, being relatively long-lived birds (Cramp 1985), in addition to phylogenetic effects lay small and energy-poor eggs and have small broods to minimize the costs of yearly reproduction (e.g. Hogstad 2006b). With low annual reproductive and mortality rates, they may increase their lifetime reproductive success.

SAMMENDRAG

Korrelasjoner mellom eggskalltykkelse og reproduksjon hos europeiske hakkespetter

Hakkespettene har en spesiell reproduksjon som er forskjellig fra andre arters. De hakker selv ut hull for hekking og overnatting, legger relativt små egg, har små kull og en av de korteste rugeperiodene blant alle fugler. Ungene klekkes nakne og blinde og veier bare omlag 5% av hunnens vekt. Hakkespettene har tynnere eggskall enn det vi finner hos sekundære hullrugende arter. For å undersøke om skalltykkelsen kan settes i forbindelse med hakkespettenes eiendommelige reproduksjonsbiologi, er det prøvd å finne eventuelle sammenhenger mellom den gjennomsnittlige skalltykkelsen og hekkebiologiske parametre hos de forskjellige artene. Opplysninger om fuglenes vekt, rugetid, ungenes reirperiode, kullstørrelse, eggvekt og eggvolum er hentet fra Cramp (1985) og Winkler m.fl. (1995) (Appendix). De åtte artene som er undersøkt er grønn- og gråspett, svartspett, flaggspett, mellomspett, hvitryggspett, dvergspett og tretåspett (Tabell 1).

Den gjennomsnittlige skalltykkelsen av eggene viste seg å øke med fuglenes vekt (Figur 1) og eggenes størrelse (Figur 2), og at de større artene i forhold til kroppsvekten legger små egg med tynnere skall; indeksen eggskalltykkelse/eggvolum avtar med hunnens vekt. Det er tidligere vist at hakkespetter legger egg med svært liten plomme og inneholder lite energi og er relativt billig å produsere. Siden de europeiske hakkespettene lever relativt lenge, kan det tenkes å være en lønnsom strategi for hakkespettene å minimalisere de årlige kostnadene ved reproduksjonen (små og energifattige egg, små kull) og derved øke deres livstids reproduktive suksess.

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APPENDIX

Data used in correlation analyses. Mean values of female body mass (g), incubation and nestling periods (days), clutch size, egg volume index (length x breadth^2/1000) and clutch weight (g) are extracted from Cramp (1985), Winkler et al. *(1995) and own data. Data about the tendency to reuse nesting holes are gathered from Blume (1961), Wesolowski & Tomialojc (1986), Aulén (1988) and Ivanchev (1997).*

Species	Body mass (g)	Incub. period (days)	Nestl. period (days)	Clutch size	Egg weight (g)	Egg vol.	Clutch weight (g)	Reuse %
Grey-headed	130	15.5	25	8	7.5	13.55	60.0	-
Green	215	15.5	25	6.5	8.5	16.93	55.3	33
Black	300	12.0	28	5	12.4	22.98	62.0	26
Great Spotted	85	11	21	6	4.9	10.80	29.4	13
Middle Spotted	65	12	23	5.5	4.0	10.00	22.0	21
White-backed	100	10.5	27	4	6.0	12.35	24.0	0
Lesser Spotted	23	11	20	6.0	2	4.28	12.0	0
Three-toed	60	11	24	3.8	5.4	9.03	20.5	0