Reproductive differences between woodpeckers and secondary hole-nesters

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Woodpeckers differ from most birds in several ways. They have powerful bills and excavate nesting cavities, and compared with most other birds of equivalent size they have relatively small clutches, relatively small eggs, and short incubation periods whereas the chicks remain in the nest for a relatively long time. Based upon the literature, I have compared the reproductive patterns of seven «true» Nordic woodpeckers (Picinae) with that of eight secondary hole-nesting species (particularly five passerines).

The mean incubation period of the woodpeckers (12.4 ± 2.2 days) does not differ significantly from that of the secondary hole-nesters (17.6 ± 6.3 days; t-test, p=0.057). However, the incubation period of *Picus canus* and *P. viridis* (15.5 days) differs from the mean of the remaining woodpeckers (11.1 days; p<0.001). If the two *Picus* species are omitted from the analysis, the mean incubation period of the woodpeckers is shorter than that of the secondary hole-nesters (2.3 days; p=0.045). The secondary hole-nesting woodpecker species *Jynx torquilla* also has a shorter incubation period (12 days) than any of the other secondary hole-nesters. The mean nestling period of the woodpeckers (24.3 ± 2.9 days) does not differ from that of the secondary hole-nesters (22.7 ± 6.9 days; p=0.57). However, the woodpeckers have a longer nestling period (p=0.013) than the five passerines (mean 18.5 days). The ratio nestling period:incubation period differs, being 2.01 in woodpeckers and 1.31 in secondary hole-nesters (p<0.001).

Woodpecker eggs are small and thin-shelled with a mean weight, related to the body mass of females, of 6.2 ± 2.0, and they are significantly lighter than those of the eight secondary hole-nesters (9.5 ± 2.0; p=0.007). The mean eggshell thickness in relation to egg volume is less in woodpeckers (1.3 ± 0.5) than in the secondary hole-nesting passerines (2.4 ± 0.7; p=0.01). The mean clutch size of the woodpeckers (5.5 ± 1.5 eggs) does not differ from that of the eight secondary hole-nesters (5.9 ± 2.2 eggs; p=0.15). However, if the two *Picus* species are omitted because of their tendency to reuse nest holes and their clutch size (mean 7.3 ± 1.1) that is larger than that of the other woodpeckers (mean 4.9 ± 0.9; p=0.03), the woodpeckers have a smaller clutch size than the secondary hole-nesters (p=0.04). The mean clutch weight related to the female body mass is lower in woodpeckers (0.33 ± 0.11) than in the secondary hole-nesters (0.57 ± 0.24, p=0.03).

Hypotheses proposed to explain why reproduction in woodpeckers differs from that of other hole-nesters are differences in nest predation, limitation in nest sites of the secondary hole-nesters, energy costs expended in excavation, differences in food supply, adult survival and life duration.

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INTRODUCTION

Woodpeckers are one of the oldest known avian forms and differ from most birds in several ways (e.g. Short 1982, Sibley & Ahlquist 1990, Bock 1999). They exhibit unique morphological adaptations and their anatomy enables them to exploit niches that are unavailable to most other birds. For one thing, they have a strong, chisel-shaped bill used to bore into wood and excavate nesting cavities. Most species construct a new hole each breeding season. In general, hole-nesting birds have relatively large clutches compared with open nesters, which has been explained by a lower rate of nest predation in tree holes (Lack 1968, Alerstam & Högstedt 1981, Skutch 1985, Martin 1991). However, even compared with those of hole-nesting birds that do not excavate their own holes, the secondary hole-nesters, many woodpeckers have small clutches (cf. Winkler *et al*. 1995, del Hoyo *et al*. 2002).

Compared with open nesters, woodpeckers have relatively small clutches and short incubation periods (cf. del Hoyo *et al*. 2002). As woodpecker chicks remain in the nest for a relatively long time, the combined incubation and nestling periods in woodpeckers is similar to that of most altricial birds of equivalent size. The ratio of nestling period:incubation period is therefore higher in woodpeckers than in altricial birds (del Hoyo *et al*. 2002). Woodpeckers also have smaller eggs than most other birds of equivalent size (Winkler *et al*. 1995). Ecological differences among nest types are important for understanding the life-history traits of nesting birds. However, woodpecker reproduction has mostly been compared with that of open-nesting species. Its characteristic patterns are probably best revealed by comparing them with the secondary hole-nesters. So far, few reproductive data have been gathered to illustrate the differences between these groups.

Here, I compare some reproductive parameters in woodpeckers and secondary hole-nesting birds and discuss previous proposals put forward to explain the characteristic reproduction in woodpeckers.

METHODS

The data are extracted mainly from Haftorn (1971), Winkler *et al*. (1995) and Cramp (1985), and are supplemented with my own data. For each species, the following mean values were noted: female body mass (g), egg volume index (length x breadth^2/1000), egg weight (g), relative egg weight (egg weight in % of female body mass), incubation period (d), nestling period (d), total nesting period (incubation + nestling periods). For all the above variables, I have used the midpoint of the range of values of the nominate subspecies. Eggshell thickness was measured with a modified micrometer (Starrett Model 101M) to the nearest 0.01 mm on egg collections at zoological museums in Oslo and Trondheim, Norway.

Seven of the eight woodpeckers (Picidae) that occur in the Nordic countries belong to the subfamily Picinae («true» woodpeckers), whereas the Wryneck *Jynx torquilla* is the only member in the subfamily Jynginae. The Wryneck does not excavate nesting holes, but breeds in old woodpecker holes or in nest-boxes. The reproductive parameters of the woodpeckers have been compared with five passerine species and three non-passerine species, eight species that all are dependent on nest holes excavated by others or on naturally holes (Table 1). Eggshell thickness was measured only on eggs from the true woodpeckers and the passerine species. Unless particularly mentioned, I use the term woodpeckers for the seven true woodpeckers (Picinae). In some analyses, the two ground-foraging *Picus* species, Grey-headed and Green Woodpeckers, are omitted because of their tendency to reuse nest holes. Likewise, in some analyses, the non-passerine hole-nesters are omitted because of their reproductive traits: small egg size and clutch size of the Stock Dove *Columba oenas* (pigeons generally have small eggs, 2.6-8.3% of the female body mass, and a clutch of 1-2 eggs; del Hoyo *et al*. 1997) and because the clutch size of the two owls (see Table 1) varies with the density of small rodents.

All tests are two-tailed. Means are presented ± 1 SD. The tests were performed using SPSS 11.0 for Windows.

RESULTS

Incubation period

The mean incubation period differs markedly among the four groups listed in Table 1: woodpeckers, Wryneck, secondary hole-nesting passerines and non-passerines (ANOVA $F_{3,15}$=10.70, p=0.001). If the Wryneck is omitted from the analysis and the two secondary hole-nesting groups are combined, no such variation is found (ANOVA $F_{1, 14}$=4.34, p=0.057). Thus, the mean incubation period of the seven woodpecker species (12.4 days; Table 1) does not differ significantly from that of the eight secondary hole-nesters (17.3 days: t-test, t_{13}=2.08, p=0.057). However, the incubation period of the *Picus* species, the Grey-headed and Green Woodpeckers (15.5 days), differs significantly from the mean of the remaining woodpecker species (11.1 days; t_5=10.74, p<0.001). If these two *Picus* species are omitted from the analysis, the mean incubation period of woodpeckers (11.1 ± 0.55 days) is significantly shorter than that of the secondary hole-nesters (t_{11}=2.26, p=0.045). Moreover, when the mean incubation period of the woodpeckers (except *Picus*) is compared with the hole-nesting passerine species, the woodpeckers have the shortest period (mean of five species: 13.8 days; t_8=3.29, p=0.011). Even the secondary hole-nesting woodpecker species, the Wryneck, has a shorter incubation period than all the other secondary hole-breeders (Table 1).

Nestling period

The mean nestling period of woodpeckers (24.3 days; Table 1) does not differ from that of the secondary hole-nesters (22.7 days; t_{13}=0.57, ns). However, when woodpeckers are compared with the five passerine species (mean 18.5 days), they are seen to have a significantly longer nestling period (t_{10}=3.03, p=0.013).

There is a tendency for larger woodpeckers to have longer nestling periods (r=0.73, p=0.06), whereas such a relationship is weaker for the secondary hole-nesters (r=0.51, ns).

Table 1. Reproductive patterns in Nordic woodpeckers and secondary hole-nesters. Data from Cramp 1985, Winkler et al. *1995, own data.*

Species	Incubation period (d)	Nestling period (d)	Incubating + nestling	Nestl./incub.
Picinae				
Grey-headed *Picus canus*	15.5	25	40.5	1.61
Green *Picus viridis*	15.5	25	40.5	1.61
Black *Dryocopus martius*	12	28	40	2.33
Great Spotted *Dendrocopos major*	11	21	32	1.91
White-backed *D. leucotos*	10.5	27	37.5	2.45
Lesser Spotted *D. minor*	11	20	31	1.82
Three-toed *Picoides tridactylus*	11	24	35	2.00
Jynginae				
Wryneck *Jynx torquilla*	12	22	34	1.83
Secondary hole-nesters				
Passerines				
Starling *Sturnus vulgaris*	12.5	21	33.5	1.68
Pied Flycatcher *Ficedula hypoleuca*	14	15	29	1.07
Redstart *Phoenicurus phoenicurus*	12	14.5	26.5	1.21
Nuthatch *Sitta europaea*	16.5	23	39.5	1.39
Great Tit *Parus major*	14	19	33	1.36
Non-passerines				
Stock Dove *Columba oenas*	17	24	41	1.41
Tengmalm's Owl *Aegolius funereus*	27	33	60	1.22
Pygmy Owl *Glaucidium passerinum*	28	32	60	1.14
Picinae, average:	12.36±2.19	24.29±2.93	36.64	2.01±0.37
Sec. hole-nesters, average:	17.63±6.34	22.69±6.94	40.31	1.31±0.19

Ratio nestling period:incubation period

Because the combined incubation and nestling periods are almost identical in length in the two groups (woodpeckers have a mean of 36.6 days, secondary hole-nesters 40.3 days; Table 1, Fig. 1), the mean nestling:incubation ratio differs: 2.01 in woodpeckers and 1.31 in secondary hole-nesters; t_{13}=4.68, p<0.001).

However, because of the relative long nestling period and short incubation period of the Starling, the nestling:incubation ratio score of the Starling is higher than that of the other secondary hole-nesters (Fig. 1). Due to the relatively long incubation period of the Grey-headed and Green Woodpeckers (15.5 d), the score of the nestling: incubation ratio of the Starling (1.68) is slightly higher, but not significant, than each of the two *Picus* species (1.61; Table 1).

No significant correlations were found between the female body mass and the ratio nestling period:incubation period in woodpeckers (r=0.08) and secondary hole-nesters (r=0.21). That is because the ratio nestling:incubation period is relatively constant across the species (coefficient of variation CV=18.4% in woodpeckers, 14.5% in secondary hole-nesters), independent of the body mass of the birds.

Eggs

Woodpecker eggs are small, with a mean weight as a percentage of the female body mass of 6.2 ± 2.0 (6.5% in the Wryneck), significantly lower than that of the eight secondary hole-nesters (mean = 9.5 ± 2.0, t_{13}=3.23, p=0.007; Table 2, Fig. 2).

Except for the small eggs of the Stock Dove, and in part also of the Tengmalm's Owl (Fig. 2), the eggs of the secondary hole-nesters are relatively larger than those of the woodpeckers. Thus, the mean relative weight of woodpecker eggs is also less than that of the passerines (10.2 ± 1.4; t_{10}=3.89, p=0.003).

The egg weight correlates with the female body mass in woodpeckers (r=0.97, p=0.000, n=7)

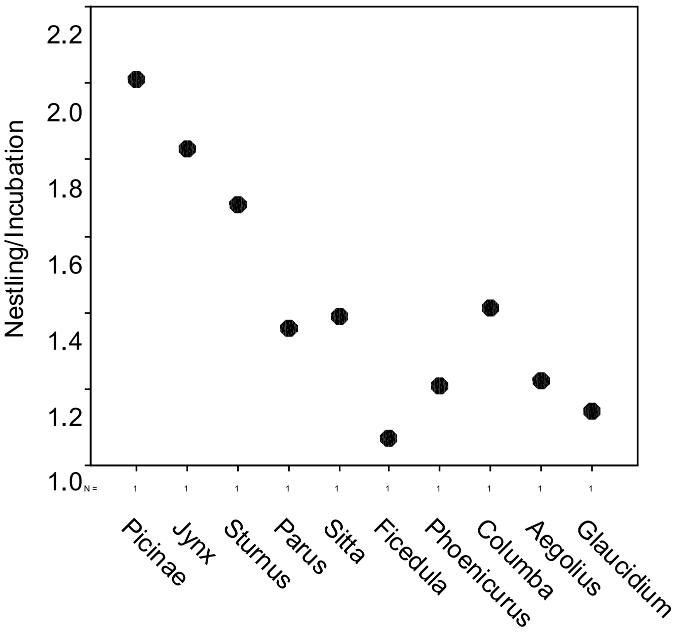

Figure 1. The ratio nestling period:incubation period in true woodpeckers Picinae, Wryneck Jynx *and secondary hole-nesters of five passerine species and three nonpasserine species (for species names, see Table 1).*

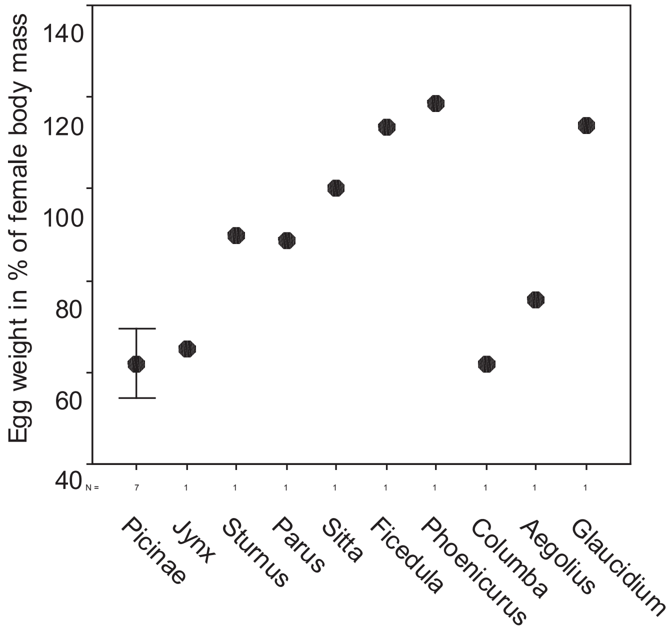

Figure 2. The egg weight in % of female body mass of woodpeckers and secondary hole-nesters of five passerine species and three nonpasserine species.

Table 2. Mean body masses of females (g), egg weight (g), egg weight in % of female body mass, clutch size and clutch weight in % of female body mass in woodpeckers and secondary hole-nesters.

Species	**Body mass (g)**	**egg weight**	**egg weight%**	**clutch size**	**clutch weight %**
Grey-headed	130	7.5	5.8	8	46
Green	215	8.5	4.0	7	26
Black	300	12.4	4.1	4	21
Great Spotted	85	4.9	5.8	6	35
White-backed	100	6.0	6.0	4	24
Lesser Spotted	23	2.0	8.7	6	49
Three-toed	60	5.4	9.0	4	34
Wryneck	40	2.6	6.5	9	59
Starling	78	7.0	9.0	6	54
Pied Flycatcher	15	1.7	11.3	6	68
Redstart	16	1.9	11.9	6	71
Nuthatch	23	2.3	10.0	7	70
Great Tit	18	1.6	8.9	10	89
Stock Dove	275	17.0	6.2	2	12
Tengmalm's Owl	165	12.5	7.6	5	38
Pygmy Owl	73	8.3	11.4	5	57

and the secondary hole-nesters (r=0.98, p=0.000, n=8). The mean egg weight as a percentage of the female body mass in woodpeckers, Wryneck and Stock Dove is almost identical, but when compared with the ratio nestling:incubation period, the woodpeckers and the Wryneck differ from the other species. Only the Picidae, i.e. woodpeckers and Wryneck, have small eggs and a high score for the ratio nestling:incubation period.

The eggshell thickness varies among the woodpecker species ($F_{6, 184}$=74.30, p<0.001) and increases with the egg volume (r=0.83, p=0.02) as it also does in the passerines (r=0.98, p=0.004). However, the thickness tends to increase more with the egg volume in woodpeckers (b_1=0.63) than in the secondary hole-nesters (b_1=0.35). The mean ratio eggshell thickness:egg volume is significantly higher in the secondary hole-nesting passerines (2.42 ± 0.72) than in the woodpeckers (1.30 ± 0.53; t_{10}=3.12, p=0.011; Fig. 3). Thus, the woodpeckers have relatively thinner eggshells than the secondary hole-nesters.

Clutch size

The mean clutch size of the seven woodpecker species is 5.5 ± 1.5 eggs and does not differ from that of the eight secondary hole-nesters (5.9 ± 2.2). Even if the three non-passerine species are omitted from the analysis, there is no significant difference between the clutch size of woodpeckers and secondary hole-nesters (7.0 ± 1.7; t_{10}=1.58, p=0.15). However, when the mean clutch size of the woodpeckers (excluding the two *Picus* species, Green and Grey-headed Woodpeckers, because of their tendency to reuse nest holes and their larger clutches (mean 7.3 ± 1.1) than the other woodpeckers (4.9 ± 0.9; t_5=2.94, p=0.032; see the Discussion) is compared with that of the passerines, the woodpeckers are seen to have a significantly smaller clutch size than the secondary hole-nesting passerines (t_8=2.42, p=0.042).

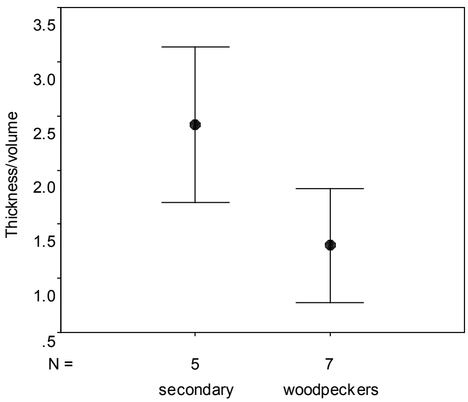

Figure 3. Relative eggshell thickness (thickness/egg volume) of five secondary hole-nesting passerine species and seven woodpecker species Picinae. Mean ± 1 SD.

Woodpeckers with small clutches have a high nestling:incubation ratio (r=-0.85, n=7, p=0.017), whereas no such relationship is found in the secondary hole-nesters (r=0.04, ns; Fig. 4).

The mean relative clutch weight (clutch weight: female body mass) of the seven woodpeckers (0.33 ± 0.11) is significantly lower than that of the eight secondary hole-nesters (0.57 ± 0.24; t_{13}=2.45, p=0.029). When the woodpeckers are compared with the five passerines (0.70 ± 0.12), the difference is even more marked (t_{10}=5.45, p<0.001).

To summarize, compared with secondary hole-nesters, woodpeckers have a shorter incubation period, a higher nestling:incubation period ratio, relatively smaller eggs that have thinner shells, and a smaller clutch weight in relation to female body mass. Because of the large clutches of the two *Picus* species, the mean clutch size of the woodpeckers does not differ significantly from that of the secondary hole-nesters.

DISCUSSION

The breeding and the social system of the woodpeckers differ from that of most other birds. In contrast to most altricial birds, woodpecker males take a great share in parental duties. They

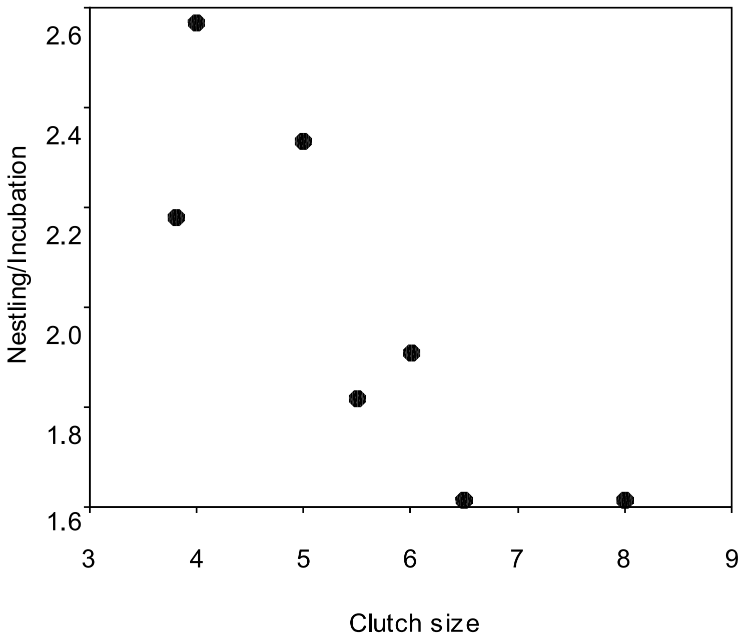

Figure 4. The relationship between clutch size and the ratio nestling:incubation period in woodpeckers (r=-0.85, p=0.017).

Table 3. Eggshell thickness and egg volume index (length x breadth²/1000) in woodpeckers and secondary hole-nesters.

Species	**n**	**Eggshell thickness**	**Volume index**	**Thickness/ volume**
Grey-headed	29	15.21 ± 1.01	13.55	1.12
Green	49	16.56 ± 1.32	16.93	0.98
Black	66	16.70 ± 0.84	22.98	0.73
Great Spotted	13	15.23 ± 0.93	10.80	1.41
White-backed	14	12.86 ± 1.03	12.35	1.04
Lesser Spotted	7	10.00 ± 0.58	4.28	2.34
Three-toed	7	13.71 ±1.11	9.03	1.52
Starling	8	15.50 ± 1.07	13.35	1.16
Pied Flycatcher	14	9.07 ± 0.83	3.12	2.91
Redstart	17	9.53 ± 1.07	3.56	2.68
Nuthatch	8	11.25 ± 1.16	4.44	2.53
Great Tit	15	9.60 ± 0.51	3.42	2.81

generally undertake most of the excavating work, remain in the hole with the eggs or young during the night, and spend a comparatively long time guarding the nest (del Hoyo *et al*. 2002). This is an unusual arrangement in the avian world. In other bird species that share incubation, it is the female that most frequently stays on the nest overnight. In daytime, both parents are required to incubate and raise the young. Thus, a single woodpecker would face great difficulties raising a brood from hatching to fledgling on its own. In the Lesser Spotted Woodpecker, Wiktander (1988) found that more than 40% of females stopped feeding the nestlings in the last stage, whereas males responded to this by increasing their feeding rate, which fully compensated for the absence of the females. Accordingly, monogamy is the predominant breeding system among woodpeckers. Although little is known about whether they breed with the same mate for consecutive years, breeding partners of some species may remain together over several breeding seasons, and the divorce rate may be rather low (e.g. Wiktander 1998, del Hoyo *et al*. 2002). Mate fidelity is high among White-backed Woodpeckers (68% for females and 75% for males) and the divorce rate low; and territory tenacity was 83% for females and 81% for males (Stenberg 1988).

Among the secondary hole-nesters mentioned in this study, however, bigamy is demonstrated in several populations of Starlings, Pied Flycatchers and Redstarts, and these species also usually have a new breeding partner each year. Nuthatches, Great Tits and Tengmalm's Owls are monogamous, with rare cases of bigamy (Cramp 1993).

The main differences between woodpeckers and secondary hole-nesters, however, are the small and thin-shelled eggs, the relatively small clutch weight and the larger ratio in the nestling:incubation period of the woodpeckers.

In the following, I will mention current hypotheses that try to explain the special reproductive traits in woodpeckers.

Predation

Nest predation strongly reduces the reproductive success of birds (e.g. Nilsson 1984, Martin 1988), and about 60% of all losses of eggs and nestlings in temperate-zone passerines is due to predation (Ricklefs 1969). In contrast, the nesting success of woodpeckers, expressed as the relative number of clutches which produce at least one young, is high, often in excess of 70% (Winkler *et al*. 1995), and in the White-backed Woodpecker it reaches 91% (Hogstad & Stenberg 1997). A North American study showed that total (whole and partial) nest loss after egg laying was less (about 25%) in woodpeckers than in secondary hole-nesters (Martin & Li 1992). Nest predation is a major factor affecting reproductive success in cavity-nesting birds and is probably the most important factor in the evolution of nest-height preferences in hole-nesting birds (Nilsson 1984, Martin & Li 1992, Johnsson 1993). Secondary hole-nesters suffer a higher nest failure than woodpeckers because they use old cavities that are lower in height (Li & Martin 1991).

Predation risk may also limit clutch sizes if, for example, frequent feeding visits to the nest by parents attract predators (Skutch 1949, Lima 1987). Thus, the length of the nestling period has been found to be negatively related to the nest-failure rate (Martin & Li 1992, Martin 1995). The longer nestling period in woodpeckers may therefore be associated with a lower risk of predation.

Adult mortality, perhaps due to predation, may be the outcome of a trade-off between energy demand and predation risk, with higher energy demands in the breeding season leading to greater exposure to predation. Thus, the survival of adult Lesser Spotted Woodpeckers that raised young was lower than for birds without such a commitment (Wiktander 1988).

Nest-site limitation

It has been suggested that the relatively smaller clutch size in woodpeckers than secondary hole-nesters may be a result of a limited number of nest sites and unpredictable breeding opportunities for the latter. The secondary hole-nesters take advantage of unpredictable breeding opportunities by maximizing their reproduction in the current attempt (the nest-site limitation hypothesis; Beissinger & Waltman 1991, Martin 1993). The hypothesis seems strengthened by the findings of Martin (1993) who reported significant positive correlations between clutch size and the propensity to reuse nest holes among woodpeckers (see also this study). A corresponding correlation is found among *Parus* species (Hogstad, unpubl. data).

Energy costs of excavation and nest reuse

The energy costs of excavating nest holes and producing eggs may be high for woodpeckers. Hole construction takes one to several weeks, and in some species, even months (e.g. Jackson 1977). Black Woodpeckers may work on a hole one year and finish it the next (Nilsson *et al*. 1991). The physical condition of the females may therefore influence the clutch size. The relatively small clutches in woodpeckers may therefore be a trade-off with energy available to invest in egg production.

Most woodpeckers have small clutches, a pattern that has been related to the physical condition of the females in the pre-breeding season (Martin 1987, Martin & Li 1992, Hogstad & Stenberg 2005). The energy budget of the insect-eating woodpeckers is probably under considerable constraint during the winter, and the breeding abundance of woodpeckers has been found to be positively correlated with the winter temperature (Marchant *et al*. 1990, Nilsson *et al*. 1992, Rolstad & Rolstad 1995, Wiktander 1998, Hogstad & Stenberg 2005). Based on the caloric content of spruce beetle larvae, the most important food for the Three-toed Woodpecker in winter, it was estimated that an individual of the American Three-toed Woodpecker needed to eat about 3300 larvae daily to survive in a winter climate with a temperature of –18 °C (Backhouse 2005). It may be suggested that female woodpeckers are more vulnerable than males because they probably have to give up valuable feeding time for self-maintenance to find enough calcium to form eggs. Woodpecker eggs are relatively small and thin-shelled, probably as a result of energy stress due to laying early in the year when food is scarce. The females depend on a relatively high level of dietary calcium during the laying period, and they mostly obtain this by eating snail shells (e.g. Graveland 1996, Perrins 1996). The Great Spotted Woodpecker is among the woodland birds known to suffer from calcium shortage (Graveland *et al*. 1994). The suggestion that females have less time available for feeding is strengthened by the observations that Lesser Spotted Woodpecker females suffered high mortality in spring before egg laying (Wiktander 1998) and the physical condition 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). In addition to a relatively small clutch weight, reduced physiological condition may favour slower development, as is found in the woodpeckers (e.g. Price & Liou 1989).

On the other hand, woodpecker chicks, hatching at a relatively immature stage of development, obviously derive advantage from eggs with thin shells.

Generally, there is a positive correlation between clutch size and nest reuse in woodpeckers (e.g. Martin 1993, Winkler *et al*. 1995, this study). The more frequent reuse of holes for nesting by the Great Spotted than the White-backed Woodpecker (15% vs 1%; Aulén 1988) supports this suggestion. Martin (1993) suggested that reuse of holes is most frequent in physically weaker excavators, whose large clutch size is an adaptation to limited access to cavities and breeding opportunities. However, available data argue against correlations between excavating ability, reuse rate and clutch size (c.f. Wiebe *et al*. 2006).

An alternative explanation of why woodpeckers excavate a new hole each year is that parasite loads are lower in a new hole than in an old one (Short 1979, Bull *et al*. 1992). Previously used nest holes are frequently infested with mites or other parasites that have overwintered there and may attack nestlings the moment they hatch, weakening or even killing them. Most woodpeckers avoid this problem by excavating a fresh cavity each year. Nesting in an old cavity requires less effort, but may result in a lower reproductive success. Thus, a study of the North American Yellow-bellied Sapsucker *Sphyrapicus varius* showed that pairs that reused nest cavities fledged fewer young than pairs that nested in fresh cavities, even though the reusers laid larger clutches (Backhouse 2005). However, a study of Black Woodpeckers in Sweden gave no such effect (Nilsson *et al*. 1991). A higher total breeding failure in old nests of those Black Woodpeckers was mainly due to predation by pine martens *Martes martes*. Young fledged in only 38% of nests in old cavities compared to 71% in new ones, and Black Woodpeckers breeding in a new hole produced on average 2.6 fully feathered young compared with 1.4 in an old nest hole (Nilsson *et al*. 1991). Since pine martens probably remember the locations of nest holes and revisit them regularly (e.g. Sonerud 1985), the Black Woodpeckers may excavate a new hole mainly to avoid pine marten predation.

As early breeding is obviously important for the recruitment of fledglings to the breeding population in several birds (e.g. Perrins 1970, Nilsson & Smith 1988, Hogstad 1990, Hogstad & Stenberg 1997), breeding relatively early in an old hole may increase the fitness of an individual compared to breeding later in a new hole in the same territory, as suggested for the Black Woodpecker (Nilsson *et al*. 1991).

Stable food supply – small clutch size

Ashmole (1963) suggested that an annually stable food supply allows populations to remain near carrying capacity. Thus, breeding birds exploiting stable food resources have relatively little available food and their clutch size is small. Most woodpeckers, with their strong bills, can find insects in wood or beneath bark all the year round, whereas weaker excavators have to exploit more seasonal, less stable food resources. Several wood-boring beetles, as larvae or imagines, are available all year and are probably more stable as food for woodpeckers than surface insects are as prey for secondary hole-nesters. According to Ashmole (1963), there should therefore be a negative correlation between excavating strength and clutch size, which is also the result of the nest-site limitation hypothesis.

The ratio nestling:incubation period

Woodpeckers have small eggs relative to their body mass, and since most species have a shorter incubation period than secondary hole-nesters their hatchlings are small and need a relatively long period to reach their final size and fledge. The length of the nestling period has been found to be negatively related to daily nest failure (e.g. Williams 1966, Haukioja 1970, Martin & Li 1992). Thus, Lack (1968) suggested that the long nestling period relates to the relative safety of their nesting site. Yom-Tov & Ar (1993), however, suggested that the short incubation period and the low embryonic metabolism (Berger *et al*. 1994) can be explained by the poorly ventilated environment at the bottom of a nest cavity. While the chick is developing, there is an exchange of gases through the shell, oxygen passes in and carbon dioxide passes out. As the chick grows inside the egg, its respiration rate increases and so does possible stress associated with a shortage of oxygen. After hatching, the chicks are better able to manage a low oxygen level in the cavity because direct lung breathing is more efficient than exchange of gases through the eggshell. The parents' frequent feeding of their nestlings also increases the flow of fresh air from outside and encourages air circulation in the cavity.

Adult survival and lifetime

Adult survival may affect clutch sizes. Relatively high adult mortality due to predation may select for an *r*-selected life history with large clutches (Martin 2004).

Woodpeckers are relatively long-lived birds (Cramp 1985), and their adult survival is higher than that of secondary hole-nesting passerines. Interspecific comparisons indicate that clutch size and annual productivity (clutch size x number of broods) are inversely related to adult survival (Sæther 1987, Bennett & Harvey 1988). Thus, a negative relationship is found between clutch size and lifespan in several North American woodpecker species. For example, the mortality rate (about 58%) of adult Northern Flickers *Colaptes auratus* is higher than the average for other woodpeckers, and the species also has one of the largest clutches of any woodpeckers (Fisher & Wiebe 2006). In contrast, Red-cockaded Woodpeckers *Picoides borealis* with relatively low adult mortality (7%-15%) have much smaller clutches (Wiebe *et al*. 2006).

Phylogenetic effects

The non-excavating woodpecker, the Wryneck, has relatively small eggs. With a relative egg weight of 6.5%, similar to that of the true woodpeckers but less than that of the secondary hole-nesting passerines, this strongly indicates that phylogeny accounts for a large proportion of the difference in egg mass between woodpeckers and secondary hole-nesters. On the other hand, clutch size and clutch weight as a percentage of the female body mass in the Wryneck (59%) is higher than that of the woodpeckers (mean 34%) and corresponds better with that of the secondary hole-nesting passerines (mean 70%).

Although the Wryneck has the same clutch size as the other secondary hole-nesters, it has a shorter incubation period (12 days) than any of the other secondary hole-nesting birds. The high score of the ratio of the nestling:incubation period, 1.83, which is close to the mean of the other woodpeckers (2.0), is an effect of phylogeny.

Life-history traits

Being capable of excavating their nest holes is probably one of the main factors driving the life-history traits of woodpeckers. However, why the reproduction of these birds differs markedly from other hole-nesting birds is far from adequately explained. Our knowledge of the life-history traits of these birds is scanty (e.g Hogstad 2006) and emphasizes the need for comparative studies that control for phylogeny as well as for ecology.

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SAMMENDRAG

Forskjeller i reproduksjonen hos hakkespetter og sekundære hullrugere

Hakkespettene er en av de eldste fuglegruppene og det meste av deres anatomi er særegen for gruppen. En evolusjonær tilpasning som bare finnes hos hakkespetter er støtdempende bygningstrekk i hodet som gjør at de kan hakke selv i hardt trevirke uten å få hjernerystelse. Hakkespettenes hekkebiologi er spesiell og forskjellig fra andre arters. De fleste spettene hakker ut et reirhull hvert år og legger relativt små egg som ruges i kort tid. I motsetning til de fleste andre fugler, er det hannen som oftest utfører det meste av reirhakkingen. Han tar også alltid nattskiftet i reiret. Ungene klekkes nakne uten termoregulering og må varmes den første tiden. Ungenes reirtid er imidlertid lang.

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Den gjennomsnittlige rugetida hos hakkespettene (12.4 dager) er ikke statistisk forskjellig fra de sekundære hullrugende artenes (17.3 dager). Dette skyldes de to "jordspettene" grønn- og

The Lesser Spotted Woodpecker (above, photo: Harald Lygren) and the secondary hole-nesting Nuthatch (below, photo: Ingar J. Øien), both of same size (body mass 23 g), may illustrate the main difference between woodpeckers and secondary hole-nesters. The Lesser Spotted Woodpecker has smaller eggs (2 g vs 2.3 g) with thinner egg shell (1.0mm vs 1.13mm), lesser clutch weight (49% of female body mass vs 70%), shorter incubation period (11 d vs 16.5 d) and larger ratio of nestling period:incubation period (1.82 vs 1.39).

gråspett, som skiller seg noe ut fra de øvrige hakkespettene ved å ha lengre rugetid og større kull. Hvis de to artene utelates fra analysen, er hakkespettenes rugetid kortere (11.1 dager) enn de sekundære hullrugernes rugetid. Også den ”uekte” hakkespetten, vendehalsen, som ikke hakker ut reirhullet selv, har kortere rugetid enn hver av de sekundære hullrugende artene.

Den gjennomsnittlige reirtida hos ungene av hakkespetter (24.3 dager) er klart lengre enn hos de sekundære hullrugende spurvefuglene (18.5 dager). Ungene hos de store hakkespettartene har en noe lengre reirtid enn de mindre, noe som mindre tydelig hos de sekundære hullrugerne.

Det gjennomsnittlige forholdet mellom reirtid og rugetid (reirtid:rugetid) hos hakkespetter (2.01) er klart forskjellig fra de sekundære hullrugernes (1.31; Figur 1).

Eggene hos hakkespettene er små med en gjennomsnittlig vekt i prosent av hunnens vekt på 6.2%, klart mindre enn eggene hos de åtte sekundære artene av hullrugere (9.5%; Tabell 2, Figur 2). Vekten av eggene øker med vekten av hunnen både hos hakkespetter og hos sekundære hullrugere. Bare hakkespetter og vendehals har en kombinasjon små egg og høy faktor for reirtid: rugetid. Tykkelsen av eggskallet øker med eggets volum både hos hakkespetter og sekundære hullrugere, mest hos hakkespetter. Eggskallet er klart tynnere hos hakkespetter (Figur 3).

Gjennomsnittlig kullstørrelse hos hakkespetter (5.5 egg) er ikke forskjellig fra de sekundære hullrugernes (5.9 egg). Hvis grønn- og gråspett, som har større kull (7.0 egg) enn de øvrige hakkespettene (4.9 egg), utelates fra analysen, har hakkespettene klart mindre kullstørrelse enn de fem passerine sekundære hullrugerne (7.0 egg). Den gjennomsnittlige relative kullvekten (kullvekt:hunnens vekt) er lavere hos hakkespetter (0.33) enn hos sekundære hullrugerne (0.57). Hakkespetter med små kull har høy verdi for reirtid:rugetid (Figur 4), mens det er ikke tilfelle for sekundære hullrugere.

En rekke hypoteser prøver å gi svar på hvorfor hakkespettenes reproduksjon skiller seg ut fra andre hullrugeres: Forskjell i reirpredasjon hos de to gruppene, begrensete hekkemuligheter hos de sekundære hull-rugerne, kostnader ved hakkingen av reirhull, forskjell i næringstilgangen og i levetiden hos de adulte fuglene.

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