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Evolution of Clutch Size in Cavity-Excavating Birds: The Nest Site Limitation Hypothesis Revisited

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ABSTRACT: There are two major competing hypotheses for variation in clutch size among cavity-nesting species. The nest site limitation hypothesis postulates that nesting opportunities are more limited for weak excavators, which consequently invest more in each breeding attempt by laying larger clutches. Alternatively, clutch size may be determined by diet; the clutch sizes of strong excavators may be smaller because they are able to specialize on a more seasonally stable prey. We built a conceptual model that integrated hypotheses for interspecific variation in clutch size and tested it with comparative data on life-history traits of woodpeckers (Picidae) and nuthatches (Sittidae). In most analyses, diet explained more variation in clutch size among species than did propensity to excavate. Migratory status was positively associated with clutch size but was difficult to distinguish from diet since resident species consumed more bark beetles (a prey available in winter) and had smaller clutches than migratory species. The literature suggests that cavities are not limited in natural, old-growth forests. Although our data do not rule out nest site limitation, we conclude that annual stability of food resources has a larger impact on the evolution of clutch sizes in excavators than does limitation of nest sites.

Keywords: woodpecker, clutch size, nest site limitation, cavity nester, life history, Ashmole's hypothesis.

Explaining clutch size variation in birds has a long history in ornithology (Lack 1947; Klomp 1970; Ricklefs 1980; Slagsvold 1982). Among the general patterns that have been identified, relatively large clutches of cavity-nesting birds compared with open nesters have been traditionally attributed to a lower rate of nest predation in tree holes (Lack 1954; Alerstam and Högstedt 1981). Predation risk may limit clutch sizes if, for example, frequent feeding visits by parents to the nest attracts predators (Skutch 1949; Lima 1987) or if nutrient reserves are saved for renesting after nest failure (Slagsvold 1982). Martin (1993) argued that the supposed link between predation risk and clutch size was an artifact of the unusually large clutches of nonexcavating hole-nesting species (i.e., secondary cavity nesters) and proposed that nest site limitation may explain variation in clutch size across species of cavity-nesting birds. According to the nest site limitation hypothesis (NSLH; Beissinger and Waltman 1991; Martin 1993), nest sites for weak or nonexcavators are limited, and so individuals take advantage of unpredictable breeding opportunities by maximizing reproduction in the current attempt. In support of the NSLH, Martin (1993) reported significant positive correlations between clutch size and the propensity to reuse existing nest holes among woodpeckers (Picidae) and nuthatches (Sittidae). A similar correlation was found for chickadees (Paridae), although different conclusions may result when different populations are considered (Mönkkönen and Orell 1997; Mönkkönen and Martin 2000).

Here we reexamine the NSLH and investigate alternate explanations for clutch size variation in excavating birds. There are several reasons why such a reanalysis is appropriate. First, although there is good evidence that suitable nesting trees for excavation may be limited in managed forests where most studies of cavity nesters have been conducted (von Haartman 1957; Newton 1994; Holt and Martin 1997; Twedt and Henne-Kerr 2001), studies conducted in mature or primeval forests where clutch sizes presumably evolved have generally concluded that nest sites are not limited (Edington and Edington 1972; Wesolowski and Tomialojc 1986; Walankiewicz 1991; Welsh and Capen 1992; Bai et al. 2003; Aitken and Martin 2004; Brightsmith 2005). Also, the experimental addition of nestboxes has

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failed to reveal population increases of nonexcavators in old-growth plots with a natural density of snags (Higuchi 1978; Brawn and Balda 1988; Waters et al. 1990; Brightsmith 2005), contradicting a key assumption of the NSLH.

Second, there is anecdotal data contradicting the predictions of the NSLH. For example, a population of great spotted woodpeckers (for Latin names, see the appendix) with strong competition from European starlings *Sturnus vulgaris* excavated more new cavities each year compared with a population with few starling competitors (Mazgajski 2002*a*). In this case, excavation occurred when nest sites were limited, and nest reuse was high when there were surplus nesting cavities, exactly opposite of the pattern predicted by Martin (1993). Clearly, nest reuse may be influenced by factors other than a lack of breeding opportunities. Third, new data have emerged on a wider variety of cavity-nesting species and on more populations in natural forest conditions, allowing a more comprehensive evaluation of the relative importance of several factors involved in the evolution of clutch sizes.

Hypotheses of Clutch Size Evolution in Excavators

According to the NSLH, excavating ability is linked to clutch size through its effect on the availability of breeding opportunities. However, the ability to excavate may also affect clutch size by other pathways (fig. 1). Prominent among these is Ashmole's (1963) hypothesis, which postulates that annually stable food supply allows populations to remain near carrying capacity such that food availability per breeding pair is relatively low and clutches are small. Excavator species are characterized by different adaptive modifications of the bill, skeleton, and musculature that make them optimal foragers in different feeding niches (Kirby 1980; Koenig 1987). Strong excavators with reinforced skulls, ribs, and chisel-like bills can penetrate into hard sapwood and extract a concentrated food source, beetle larvae, from beneath the bark during winter (Connor 1981; Korol 1985). Weaker excavators, unable to penetrate thick bark and hard wood, efficiently exploit seasonally abundant prey on the ground, in bark crevices, or on leaf and bark surfaces but must broaden feeding niches in winter (Connor 1981) or migrate. Following the logic of Ashmole's hypothesis, this may lead to a negative correlation between excavating strength and clutch size, the same predicted by the NSLH.

A second alternative to the NSLH suggests that if energy invested in excavation is great, stronger excavators may have smaller clutches because of a trade-off with energy available to invest in egg production. Unfortunately, this cost of excavation hypothesis is difficult to link to morphological adaptations for excavation (e.g., bill strength), because both strong and weak excavators may expend similar fractions of their energy budgets depending on the hardness of the substrate they excavate.

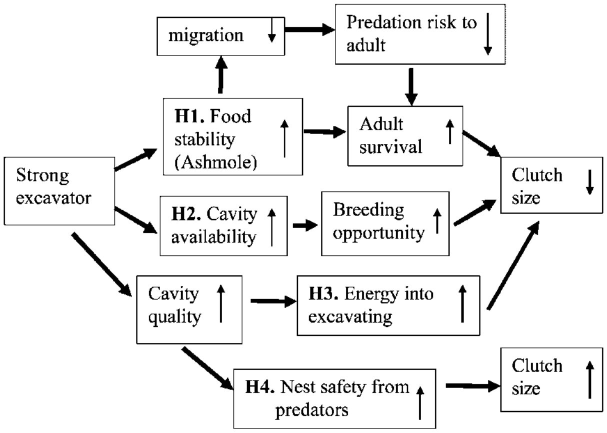

Figure 1: Potential pathways explaining the evolution of clutch size in excavating birds, showing causal links from left to right. The arrows within the boxes indicate whether that factor increases or decreases in response to the causal agent preceding it in the pathway; for example, increasing food stability causes increasing adult survival. The figure encapsulates the following hypotheses: (*H1*) stability of food resources, (*H2*) nest site limitation, (*H3*) energy costs of excavation, (*H4*) predation risk on the nest. Other factors that affect adult survival independent of excavation ability may also influence clutch size.

A third hypothesis is that strong excavators excavate tree cavities in strong, live wood that is safer from predation (Kilham 1979; Wesolowski 2002). Increased safety of nest sites leads to larger clutches according to conventional ideas of predation risk (see above). This pathway suggests that better excavators should have larger clutches, opposite of that predicted by the previous three hypotheses (fig. 1). Finally, other factors linked to life-history parameters such as adult survival may also affect clutch sizes independent of excavating morphology. For example, any extrinsic source of mortality on adults, such as high predation risk, may select for "fast" (or *r*-selected) life histories with large clutches (Martin 2004; Sandercock et al. 2005).

In this article, we first reexamine correlations reported by Martin (1993) between nest reuse and clutch size using a larger, updated data set. We then test the dietary hypothesis by testing whether the proportion of beetles in the diet, most of which are obtained by excavating into wood, is correlated with clutch size. Finally, we combine the variables in a multiple regression to see which best predicts clutch size in cavity excavators. We also discuss the potential importance of the costs of excavation hypothesis and other life-history traits such as migration that have a potential to influence clutch size variation in this guild.

Material and Methods

Sources of Data

Data on clutch size and the percentage of nests in existing holes within closely related taxonomic subsets were collected from various sources. Following Martin (1993), we classified species into nuthatches (Sittidae), North American Picidae, and European Picidae. Data on rates of cavity reuse were obtained from our long-term studies of cavity-nesting birds at Riske Creek, British Columbia (Aitken et al. 2002; Martin et al. 2004), and of acorn woodpeckers at Hastings Reservation, California (Hooge et al. 1999). We also used data from Martin (1993) and incorporated updated, unpublished values provided by T. Martin for his study area in central Arizona. Additional information was gathered from the literature and through personal communication with other researchers (appendix).

To control for possible latitudinal effects on clutch size, a corresponding clutch size from the same population was matched to the cavity reuse data whenever possible. When the study reporting reuse rates did not also report a clutch size, an average clutch size reported in Cramp et al. (1993) was used for the European species. For the North American species, an average clutch size corrected for latitude was estimated from an extensive database on museum egg sets collected by Koenig (1986). For the two species that often breed cooperatively (acorn and red-cockaded woodpeckers), we included clutch size estimated from breeding pairs only.

Information on year-round diets came from the three sources providing the largest comparative data within each of the three groups of species: Beal (1911) for North American woodpeckers, Pechacek and Kristin (1993) for European woodpeckers, and Anderson (1976) for North American nuthatches. In addition, we used the wryneck on the basis of information in Freitag (2000). In all cases, we used estimates for the proportion of the diet (usually based on weight or volume) made up of beetles (order Coleoptera) as an index of the degree to which different species of woodpeckers excavate into wood in order to obtain food (appendix). Although the diet estimate may be coarse, the presence of wood-boring beetles should be a proxy of the ability of the species to penetrate wood where these prey are found. Wood-boring beetles in particular are often available all year and are thus likely to be more stable prey than insects on surfaces.

Average body mass for North American species and information on migration were obtained from the Birds of North America Species accounts and from Cramp et al. (1993) for the European species. Using these two sources, we classified species as "migratory" (appendix) if they annually withdrew from the northern part of their continental range for the winter period. Sporadic fall and winter movements or altitudinal shifts were not classified as migration.

Statistical Analyses

Percent nest cavity reuse and percent beetles in the diet were arcsine transformed, and body mass and clutch size were log transformed, after which the variables were normally distributed (Kolmogorov-Smirnov tests for normality, all $P > .65$). Thus, parametric tests were used when possible. To avoid pseudoreplication, we followed Martin's (1993) procedure of averaging nest reuse data across studies if there was more than one per species and used partial correlations between clutch size and other variables. To reduce the number of variables, we also ran simple bivariate correlations that did not control for body mass, but these tests, except in one case that we report, had r and P values similar to the partial correlations. Subsequently, we investigated the potential influence of intraspecific variation in nest reuse and clutch size estimates with a bootstrapping procedure as in Mönkkönen and Martin (2000). Where there was more than one estimate per species, bootstrapping randomly selected a set of data representing one of the populations and entered it into the regression. Bootstrap trials were run 1,000 times, and we calculated the proportion of those in which the slope of the regression was significantly >0 ($P > .05$). Finally, a multiple regression was used to examine the simultaneous effect of different independent variables as predictors of clutch size. Collinearity among the independent variables was not a serious problem because reuse and percent beetles in the diet were not correlated among nuthatches ($r = -0.43$, $P = .47$) and only weakly so among European ($r = -.80$, $P = .05$) and North American woodpeckers ($r = -0.51$, $P = .05$). Body mass was not correlated with the other variables considered in the analysis.

The regressions were tested for robustness by removing potential outlier species. In addition to the woodpecker species analyzed by Martin (1993), we included two species that often breed cooperatively. Inspection of the data suggested that one of these, the red-cockaded woodpecker, had the potential to strongly influence the regressions, so we performed analyses with and without this species. Martin (1993) included another potential outlier, the European wryneck, a nonexcavator sometimes put in a different family from typical woodpeckers (Short 1982) and currently classified in a different subfamily. Therefore, we also performed analyses with and without this species. The four data sets available for the three-toed woodpecker, whose distribution is holarctic, were separated into those from European and North American populations. We did not do phylogenetic independent contrasts because the phylogenies of these species are not fully resolved. Furthermore, such contrasts, by decreasing the degrees of freedom, tend to reduce the significance of relationships and would argue against the NSLH. We therefore view nonsignificant results of partial correlations as a stronger indicator of no relationship.

Results

Clutch Size and Nest Reuse

Within each of the three taxonomic groups, body mass was not significantly correlated with clutch size (all $P >$ .32), but we retained it in partial correlations with nest reuse for direct comparison with Martin (1993). Among the eight species of European woodpeckers, there was a significant positive relationship between clutch size and the tendency to reuse holes (partial correlation $r = 0.81$, $P = .025$; fig. 2, *top*). However, the relationship was highly influenced by the wryneck, a nonexcavating species with particularly large clutch size, and the effect size decreased when this species was removed (partial $r = 0.66$, $P =$ .16).

In general, only a single study was available for each European species, with the exception of the great spotted woodpecker that exhibited strikingly large variation in the propensity to excavate new cavities ranging from 4% to 91% across five different studies (fig. 2; appendix). Excavation and fecundity were unlinked for this species because there was a weak and negative correlation between clutch size and nest reuse among the five populations, opposite of that predicted by the NSLH ($r = -0.35$, $P = .56$).

Clutch size was positively but not significantly correlated with nest reuse for 18 species of North American woodpeckers (partial correlation controlling for body mass $r = 0.32$, $P = .20$; fig. 2, *middle*). However, removal of the red-cockaded woodpecker made the relationship significant, almost doubling the effect size (partial $r =$ 0.59, $P = .015$). Some of the North American species for which multiple studies were available, such as the pileated woodpecker, showed consistently low reuse in different populations. Others exhibited considerable variability, including the northern flicker (ranging from 5% to 65% across five populations; appendix) and Lewis's woodpecker (ranging from 54% to 100% across four populations). Again, there was no significant relationship between clutch size and nest reuse within these latter two species (flicker: $r = 0.28$, $P = .64$; Lewis's: $r = 0.44$, $P = .56$).

Among the five nuthatch species, clutch size was also not significantly correlated with reuse rates, although the effect size was large and positive (partial $r = 0.60$, $P =$ .41; fig. 2, *bottom*). The correlation could be influenced to a large extent by the clutch size estimate of the nonexcavating European nuthatch. However, when the correlation was repeated with the largest reported mean clutch size that would maximize the probability of a correlation (8.3 eggs; Cramp et al. 1993), the relationship was still not significant ($P = .18$).

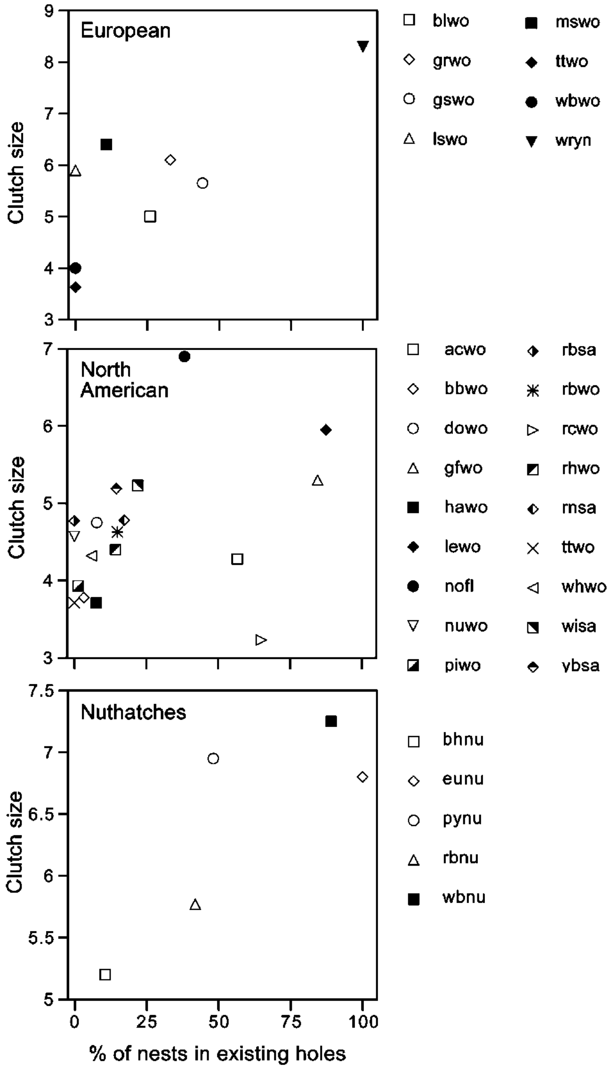

Figure 2: Mean clutch size according to the proportion of individuals in a population that reused an existing nest hole for European woodpeckers (*top*), North American woodpeckers (*middle*), and nuthatches (*bottom*). Associated data and species codes are in the appendix. Where there were data from multiple populations, a mean value was calculated across the populations and used in partial correlations. With all species included, the correlation was significantly positive for European woodpeckers but not for the other two groups.

With all North American and European woodpeckers combined, there was a significant positive correlation between reuse propensity and clutch size (partial r controlling for body mass = 0.52, $P = .008$), but significance

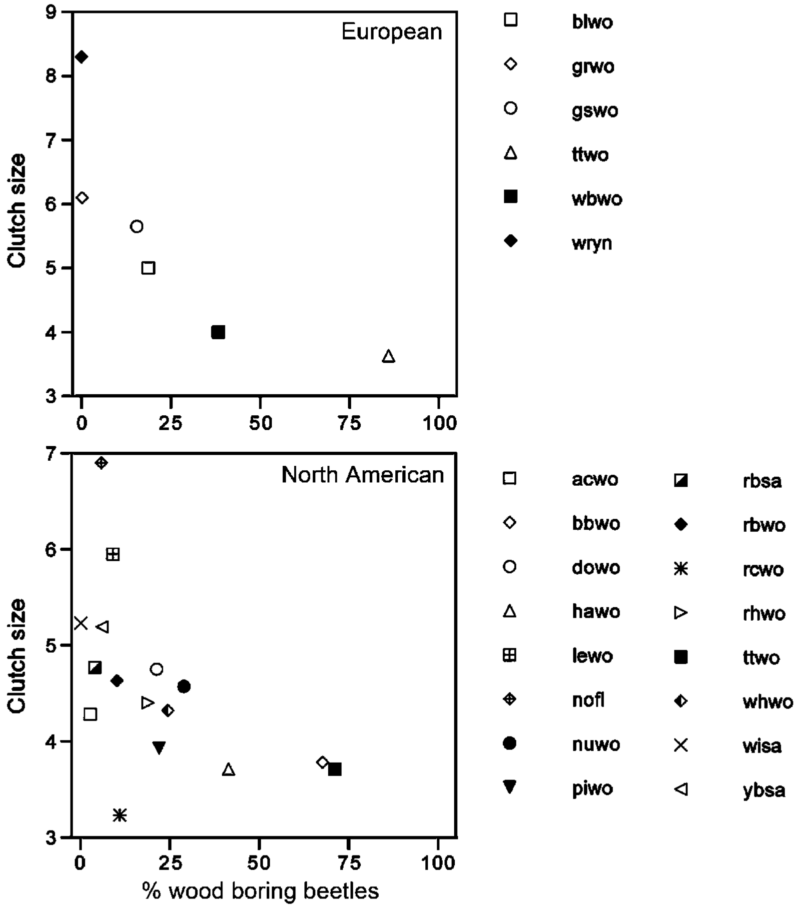

Figure 3: Mean clutch size of European woodpeckers (*top*) and North American woodpeckers (*bottom*) according to percent of wood-boring beetles in the diet.

was dependent on the presence or absence of a single species. The correlation was stronger without the red-cockaded woodpecker (partial $r = 0.68$, $P < .001$) but became nonsignificant when the wryneck was excluded (partial $r = 0.33$, $P = .12$).

Finally, we investigated the influence of population variability by calculating the fraction of 1,000 bootstrap trials that resulted in a regression with a slope significantly >0. No nuthatch trial was significant. For North American and European woodpeckers respectively, 1.6% and 39% of trials were significant, and with all woodpeckers combined, the value was 91.9%. Removing the wryneck reduced the proportion of significant trials to 88%, whereas removing the red-cockaded woodpecker increased the significant trials to 100%. Finally, removing both species showed that 80.0% of the bootstrapped estimates were significant.

Diet and Migration

Partial correlations controlling for body mass between clutch size and percent beetles in the diet (both appropriately transformed) were significantly negative for European woodpeckers (all species: partial $r = -0.96$, $P = .008$; fig. 3, *top*) and nearly so with wryneck removed (partial $r = -0.94$, $P = .06$; bivariate $r = -0.93$, $P = .02$). A significant negative correlation was also found for the North American woodpeckers (partial $r = -0.56$, $P = .03$; red-cockaded woodpecker removed: partial $r = -0.69$, $P = .007$; fig. 3, *bottom*). There was no correlation among nuthatches (partial $r = 0.81$, $P = .19$), but sample size was small, with data for only four species.

Migratory woodpeckers had larger clutches than resident species (all species pooled: *t*-test: $t = 2.4$, df = 24, $P = .024$; without the red-cockaded woodpecker: *t*-test:

$t = 2.3$, df = 23, $P = .034$; without the wryneck: $t = -2.0$, df = 23, $P = .06$). However, interpretation of migratory status may be confounded by phylogeny because the trait was not present in all genera (appendix). The effect of migration was also difficult to separate from diet because the two were strongly associated. Migratory woodpeckers ate fewer beetles than nonmigratory species, both considering only the North American species (t-test: $t = 2.9$, df = 11.1, $P = .014$) and when all woodpeckers were pooled ($t = 3.4$, df = 19.7, $P = .003$; without wryneck: $t = 3.1$, df = 18.6, $P = .006$). Migratory woodpeckers did not reuse cavities more frequently than resident species (North American: $t = 0.54$, df = 16, $P = .60$; all species: $t = 1.53$, df = 24, $P = .14$).

Excluding nuthatches, for which there were few species, we tested the relative importance of nest reuse, body mass, and diet as predictors of clutch size in a multiple regression model (table 1). Diet was the only significant predictor of clutch size when all woodpecker species were included in the data and when the wryneck was removed. Diet and nest reuse were both significant predictors when the red-cockaded woodpecker was removed.

Table 1: Predictors of clutch size (logged) in woodpeckers using multiple regression models with Type III sums of squares

Independent variable	B	t	P
Beetles (%)	−.346	2.28	.035 (.018, .004)
Nest reuse (%)	.177	1.56	.14 (.76, .014)
Body mass	.019	.33	.75 (.36, .73)

Note: Percent wood-boring beetles in diet and nest site reuse were arcsine transformed, and body mass was log transformed for a normal distribution. Values outside parentheses are for the data set including all species. Within parentheses, the P values refer to analyses without the wryneck and without the red-cockaded woodpecker, respectively.

Discussion

The Nest Site Limitation Hypothesis

Our analyses confirm a positive correlation between clutch size and nest reuse for woodpecker species but not nuthatches. However, the correlations were dependent on the exclusion of the red-cockaded woodpecker and the inclusion of the wryneck. Furthermore, the positive relationship may be even weaker than we reported because a lack of quantitative data precluded the gila woodpecker *Melanerpes uropygilais* and gilded flicker *Colaptes chrysoides* from the analysis because both species had small clutches and "high" rates of reuse (Kerpez and Smith 1990). The bootstrapping approach, which took into account variability among populations within species, generally supported the findings of the partial correlations: significance was assured only with the exclusion of the red-cockaded woodpecker and was weaker with the exclusion of the wryneck. With all Picids included, about 8% of trials were not significant, suggesting that population variability was sufficient to alter interpretations of the data in a small fraction of cases. Overall, our results suggest that there is a modest but not particularly compelling positive correlation between clutch size and nest reuse among Picids that is strongly influenced by the presence of a small number of outlying species and weakly influenced by variation among populations. Strong conclusions for nuthatches are especially difficult given the small sample sizes and low power of analyses.

Martin (1993) used cavity reuse as a surrogate measure for excavating ability and hypothesized that species with weaker morphology should be cavity limited (fig. 1). However, available data argue against a strong link between excavating ability, reuse rate, and clutch size. Within species, variation in clutch size and excavation propensity were unrelated. The great variation in reuse rates among populations within some species (greater in some cases than variation between species) suggests that local features such as habitat type or competition may explain excavation propensity better than morphology. Another example is the case of the northern and gilded flickers, until recently considered a single species and which have similar morphology and "high" average rates of cavity reuse. Yet, the northern flicker has large clutches averaging 7.8 eggs, and the gilded flicker has a small clutch of about 4.2 (Koenig 1984).

Ultimately, such statistical correlations do not prove or disprove the NSLH. The assumption must be tested directly that soft substrates and suitable snags are limiting in natural, unmanaged landscapes where clutch sizes evolved (Beissinger 1996). A corollary of this assumption is that cavity occupancy should be high in such habitats. A calculation of snag density relative to woodpecker density in old second-growth forest in the eastern United States concluded that existing and potential nest sites were not limiting cavity nesters (Welsh and Capen 1992). Only 1.2% of 94 usable cavities were occupied in a mature tropical forest (Brightsmith 2005), and two other studies in old forests found occupancy rates of only 5.2% (Bai et al. 2003) and between 5.3% and 9.1% (Carlson et al. 1998). In the latter study, at least 50% of the cavities were considered suitable for nesting on the basis of actual inspections and measurements. With similar types of nest checks, Aitken and Martin (2004) found about 10% cavity occupancy in interior forest and 50% occupancy near edges, the more preferred location. Raphael and White (1984) concluded that harsh weather kept population densities of cavity nesters in old forests below the level where cavities were limiting. Similarly, Wesolowski (1989) and Walankiewicz (1991) suggested that population sizes of hole-nesting birds in European primeval forests were limited by factors other than cavity availability. In summary, there appears to be little support for the assumption that natural cavities are limited in old forests and hence that limited breeding opportunities provide a general explanation for variation in clutch sizes of cavity-nesting species.

Ashmole's Hypothesis and Diet

The partial correlations revealed a significant correlation between diet and clutch size of excavators. The migratory status of excavators was strongly correlated with diet; migratory species eat fewer beetles than do residents. The diet of migratory species, containing more surface-dwelling arthropods, ants, and tree sap (Beal 1911; Moore 1995; Walters et al. 2002), presumably varies more on a seasonal basis and may necessitate migration. Clutch size of the woodpeckers considered here was associated both with diet and with migratory status such that it was difficult to tease apart the causal mechanism. Migration may simply reflect diet, or else migration may be associated with higher extrinsic sources of mortality on adults, such as predation. Regardless, these patterns are consistent with Ashmole's (1963) hypothesis, which proposes that species kept below the carrying capacity because of seasonal fluctuations in resources or low overwinter survival have greater reproductive rates. Although costs of migration are difficult to quantify in birds, at least one study of passerines suggested that the greatest annual loss occurred during migration (Sillet and Holmes 2002). Clearly, the role of migration as a driving factor in the evolution of avian life history merits further study (Martin 2004).

Energy Costs and Predation Risk

The cost of excavation hypothesis suggests energy invested in excavation comes at a trade-off with clutch size. If stronger excavators invest more in cavity construction, this idea predicts that they should have smaller clutches, as do the NSLH and Ashmole's hypothesis (fig. 1). Martin (1993) suggested that costs of excavation were not relevant to clutch size in woodpeckers because males do the greater share of nest construction. However, although females may spend less on excavation than males in an absolute sense, any energy expended could still come at a trade-off with egg formation if their energy budgets are limited; indeed, such a trade-off could provide an explanation for the greater investment of males to begin with. Furthermore, the prevalent seasonal decline of clutch size with laying date, perhaps because of the declining reproductive value of offspring (Daan et al. 1988), may mean that energy limitation is not the principal reason that clutch size may decline when cavities take a long time to excavate.

Because species may vary in their morphology, in the hardness of the substrates they excavate, and in the time they take to excavate, an assessment of energy expenditure across species is complicated. Still, the fact that clutch size is not strongly linked to nest reuse among species suggests that excavation costs cannot explain much of the observed variation in clutch size among species. While heavy investment in a strong cavity may entail higher energy costs, such a nest may be safer from predators, perhaps favoring greater investment in the clutch (fig. 1; see also Kilham 1979). More data on predation rates and clutch sizes in cavities of different qualities are needed to test these opposing predictions. The patterns may be easier to examine within populations where reproductive parameters can be compared between individuals that excavate new cavities versus those that reuse existing holes.

Other Life-History Correlates

Assuming stable population sizes, it must be true that species with larger clutches have a reduced proportion of offspring recruiting into the breeding population compared with species with smaller clutches. Excavating ability may be one of the main underlying factors driving life-history traits in cavity-nesting birds (fig. 1), but it is likely that factors unrelated to excavation also influence adult survival and the number of recruiting offspring. For example, excavators with large clutches may be trading off offspring number with offspring quality (survival), but there are few data on fledgling growth and survival within cavity-nesting species to test this. Furthermore, accurate estimates of adult mortality and its causes are lacking for most excavators, making it difficult to examine the role of this critical life-history trait. However, there is some evidence for a negative relationship between clutch size and life span for several woodpecker species. For example, the mortality rate of adult northern flickers (about 58%) is higher than the average for other woodpeckers, and northern flickers also have one of the largest clutches of any woodpecker (Fisher and Wiebe 2006). In contrast, red-cockaded woodpeckers with relatively low adult mortality (7%–15%) have much smaller clutches (fig. 2, *middle*). Both species reuse nest sites extensively, suggesting that clutch size may be more directly linked to adult mortality than to excavating propensity.

In summary, clutch size in cavity nesters may be influenced along multiple pathways that need not be mutually exclusive (fig. 1). In multiple regressions, excavation propensity did not explain variation in clutch size when diet was included in the model, except when the red-cockaded woodpecker was excluded from the analysis (table 1). Although our statistical analysis does not rule out some influence of cavity limitation, a review of the literature suggests it is implausible in the forest types in which clutch sizes most likely evolved. Ashmole's hypothesis therefore provides the most likely alternative for a correlation between excavation ability and clutch sizes in cavity-nesting birds: strong excavators tend to have smaller clutches because they are less dependent on seasonally variable food resources. Further advances in this area are likely to be made with a modeling framework where multiple factors are considered simultaneously and which includes critical life-history variables such as adult mortality rates and predation risk.

Acknowledgments

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APPENDIX

Nest Reuse, Clutch Size, and Diet of Cavity Nesters

Table A1: Data used in the partial correlation analyses between clutch size and nest reuse rate and their sources

Species	Latin name	Code	Reuse (%)	Clutch	*N*	Beetle (%)	Source (nest reuse)
Family Picidae:							
Acorn woodpecker (N)	*Melanerpes formicivorus*	ACWO	56.7	4.28	615	2.7	W. Koenig, unpublished data
Black woodpecker (N)	*Dryocopos martius*	BLWO	26	4.8	15	18.7	Blume 1961
			26	4.8	264		Nilsson et al. 1991
Black-backed woodpecker (N)	*Picoides arcticus*	BBWO	2.8	3.4	35	67.7	Dixon and Saab 2000
			0	4.0			Saab et al. 2004
			7.1	3.94	14		M. McFaden, personal communication
Downy woodpecker (N)	*Picoides pubescens*	DOWO	0	4.63	22	21.3	J. Kellam, personal communication
			2.9	4.67	34		K. Martin, unpublished data
			20.6	5.0	63		T. Martin, personal communication
Great spotted woodpecker (N)	*Picoides major*	GSWO	74.6	5.4	79	15.5	G. Pasinelli, personal communication
			91	5.49	47		Blume 1961
			3.8	5.5	132		Wesolowski and Tomialojc 1986
			7.5	5.56	53		Mazgajski 2002*a*, 2002*b*
			26	6.24	125		Ivanchev 1997
Green woodpecker (N)	*Picus viridis*	GROW	33	6.1	18	.2	Blume 1961
Golden-fronted woodpecker (N)	*Melanerpes aurifrons*	GFWO	84.6	5.3	13	NA	Husak and Husak 2002
Hairy woodpecker (N)	*Picoides villosus*	HAWO	1.9	3.5	108	41.4	Saab et al. 2004
			5.2	3.43	38		K. Martin, unpublished data
			15.6	4.0	96		T. Martin, personal communication
Lesser spotted woodpecker (N)	*Picoides minor*	LSWO	0	5.9	19	NA	Wesolowski and Tomialojc 1986, Wiktander et al. 2001
Lewis's woodpecker (M)	*Melanerpes lewis*	LEWO	100	5.88	39	9.1	V. Saab and J. Dudley, cited in Tobalske 1997
			96	5.88	25		Bock 1970
			54	5.88	195		J. Dudley, personal communication
			100	6.18	51		K. Newlon, personal communication
Middle spotted woodpecker (N)	*Picoides medius*	MSWO	21.4	6.4	28	NA	Pasinelli 2001
			0	6.4	73		Wesolowski and Tomialojc 1986
Northern flicker (M)	*Colaptes auratus*	NOFL	13	6.5	16	5.8	Burkett 1989
			45	6.25	44		Ingold 1994
			63.1	7.83	739		K. Wiebe, unpublished data
			5	7.0	73		J. Dudley, personal communication
			64.9	6.6	436		T. Martin, personal communication
Nuttall's woodpecker (N)	*Picoides nuttallii*	NUWO	.0	4.57	57	28.9	Miller and Bock 1972
Pileated woodpecker (N)	*Dryocopus pileatus*	PIWO	.8	3.83	123	22.0	Bull 1987
			1.8	4.04	158		Bonar 2000
Red-breasted sapsucker (M)	*Sphyrapicus ruber*	RBSA	0	4.77	32	4.0	Joy 2000
Red-bellied woodpecker (N)	*Melanerpes carolinus*	RBWO	15	4.63	39	10.2	Ingold 1994
Red-cockaded woodpecker (N)	*Picoides borealis*	RCWO	66	3.27		11.0	Harlow 1983
			64.1	3.2			J. Walters, personal communication
Red-headed woodpecker (M)	*Melanerpes erythrocephalus*	RHWO	14.3	4.4	14	18.9	Ingold 1991
Red-naped sapsucker (M)	*Sphyrapicus nuchalis*	RNSA	9.1	4.57	33	NA	Daily 1993

Table A1 (*Continued*)

Species	Latin name	Code	Reuse (%)	Clutch	*N*	Beetle (%)	Source (nest reuse)
			35	4.8	86		Fleury 2000
			27	4.76	22		McClelland and McClelland 2000
			14.2	4.84	169		K. Martin, unpublished data
			9.2	4.9	250		T. Martin, personal communication
			27	4.8	56		Walters 1996
Three-toed woodpecker (N)	*Picoides tridactylus*	TTWO	0	3.87		85.9	Leonard 2001
			0	3.4	36		Ruge 1974
			0	3.4	19		Wesolowski and Tomialojc 1986
			0	3.86	32		K. Martin, unpublished data
White-backed woodpecker (N)	*Picoides leucotos*	WBWO	0	4.0	14	38.3	Wesolowski and Tomialojc 1986
White-headed woodpecker (N)	*Picoides albolarvatus*	WHWO	10	4.35	10	24.4	Grinnell and Storer 1924
			0	4.28			Dixon 1995
			7.7	4.35	13		Saab et al. 2004
Williamson's sapsucker (M)	*Sphyrapicus thyroideus*	WISA	21	4.91	28	.1	Conway and Martin 1993
			23.3	5.56	292		T. Martin, personal communication
Wryneck (M)	*Jynx torquilla*	WRYN	100	8.3		.0	Cramp et al. 1993
Yellow-bellied sapsucker (M)	*Sphyrapicus varius*	YBSA	24	5.44	29	6.0	Eberhardt 1994
			5.2	4.93	38		Gibbon 1970
Family Sittidae:							
Brown-headed nuthatch	*Sitta pusilla*	BHNU	9	5.1	290	17.0	McNair 1984
			12	5.3			Martin 1993
European nuthatch	*Sitta europaea*	EUNU	100	6.8			Nilsson 1986
Pygmy nuthatch	*Sitta pygmaea*	PYNU	48.1	7	268	60.0	T. Martin, personal communication
Red-breasted nuthatch	*Sitta canadensis*	RBNU	52	5.8	23	60.0	McClelland and McClelland 2000
			50.6	6.12	148		K. Martin, unpublished data
			22.9	5.4	401		T. Martin, personal communication
White-breasted nuthatch	*Sitta carolinensis*	WBNU	93.2	8	117	36.0	T. Martin, personal communication
			85	6.5	20		Raphael and White 1984

Note: Percent reuse refers to the proportion of breeding pairs that used an existing hole for a nesting attempt. Percent beetles is the proportion of the diet containing coleoptera. Sample size (*N*) is the number of nests where excavation status was determined. Each record is from a different population. M = migratory, N = nonmigratory, NA = not applicable.

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