

# Costs and benefits of nest reuse versus excavation in cavity-nesting birds

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Cavity nesters may either reuse an old cavity or excavate a new one. Nest reuse among cavity nesting birds has been considered traditionally to be a characteristic of weak excavators that lack nest sites and to be a strong force in the evolution of life history traits such as clutch size. We develop a simple model to examine factors that may favour one or the other nesting strategy, assuming a trade off between investment in excavation of a new hole and investment in offspring. Consistent with time and energy costs of excavation, male northern flickers *Colaptes auratus* that excavated were in better body condition than those that reused cavities, and a greater proportion of second nests were in reused holes. Data for other facultative excavators including woodpeckers, nuthatches and chickadees revealed a general pattern of earlier laying dates and larger clutches in reused compared to freshly excavated holes. We suggest that nest reuse is motivated by multiple causes, but may often be adaptive by offering time and energy savings.

## Introduction

Most birds construct new nests for each breeding attempt (Cavitt *et al.* 1999, Hansell 2000), but many cavity-nesting species may reuse old tree holes multiple times (Kilham 1983, Sedgwick 1997, Aitken *et al.* 2002). Secondary cavity nesters, which do not excavate their own nests by definition, always use an old, existing cavity. However, excavating species such as woodpeckers (Picidae), nuthatches (Sittidae), and some chickadees and tits (Paridae) may create a new cavity or reuse an old one at a

frequency that varies among species and populations (Mönkkönen & Martin 2000, Wiebe *et al.* 2006). The cause of nest cavity reuse among these latter species is controversial. Martin (1993) proposed that those species that reused nests were weak excavators and limited by suitable (presumably soft) substrates to excavate. Alternatively, Mönkkönen and Orell (1997) proposed that socially dominant species were able to defend existing holes, forcing subordinate species to evolve as excavators.

We propose that the evolutionary significance of nest reuse in cavity nesting birds can

be understood under a broader theoretical framework of costs and benefits of excavation, which may vary according to ecological context (Table 1). Reuse may occasionally be forced upon birds with weak excavating morphology and limited nest substrates, i.e., “best of a bad situation”, but nest reuse may also have benefits as an alternate nesting strategy to excavation. Here, our aims are to summarize potential costs and benefits of excavation, to develop a simple model of costs of excavation, and to highlight the balance between the costs and benefits of a major influence on nest choice in excavators.

### The cost of excavation model

The idea that time and energy costs of nest construction may explain nest reuse has been applied to non-excavating birds (Hauber 2002) but has not been previously emphasized for cavity nesters. However, excavating a new hole always requires time and energy so there must be survival benefits for the eggs, nestlings, or parents in a fresh cavity for excavation to be favoured over the option of nest reuse. Such survival benefits may derive from the fact that predators have not learned the location of new cavities (Sonerud 1985), or because new cavities are structurally stronger and more resistant to predators (Walankiewicz 1991, Wesołowski 2002). New cavities may also offer survival advantages for nestlings because of fewer parasites (Short 1979), a more stable microclimate in a living tree

(Wiebe 2001), or simply allow breeding in an area with no existing cavities to reuse.

Let  $S_o$  be the survival probability of a clutch or brood in an old cavity,  $S_n$  survival in a new cavity, and  $R$  the energy resources available for breeding. Then excavation should be favoured over nest reuse when

$$S_n(R - f(t) - C) > S_o(R). \quad (1)$$

Equation 1 assumes two costs associated with excavating a new hole. First is the energy cost of excavation,  $C$ , which for simplicity is assumed to be independent of breeding time although it may be lower for late than early clutches because smaller cavities may be needed for smaller broods. Although male woodpeckers often do the majority of nest excavation (Lawrence 1967), females still participate and so may have an energetic trade-off with egg laying if their energy budgets are limited. The second cost is reduced reproductive output caused by delayed onset of breeding,  $f(t)$ , where  $t$  is the time it takes to find a suitable substrate and excavate the new cavity. A decline of clutch size with laying date is prevalent among bird species and may be associated with declining reproductive value of offspring during the season (Daan *et al.* 1988). Rearranging Eq. 1 gives

$$S_n > S_o[R/(R - f(t) - C)]. \quad (2)$$

If we let  $R_c$  equal the energy resources available for breeding after a new cavity has been

**Table 1.** Potential costs and benefits to the reuse of cavity nests, and ecological factors that may select for nest reuse.

| Cost of reuse   | Benefit of reuse   | Factor favouring reuse                              |
|---|--|---|
| More competition <sup>a</sup>   | Less costly (time and energy)                            | Time constraints (migration, late spring phenology) |
| More parasites  | May be predictably good site (structurally good or safe) | Cold winters killing parasites                      |
| Higher predation  | Adults safer from predators <sup>b</sup>                 | Predators not long-lived                            |
| Male can not display his quality to females                             |  | Structurally hard substrate for excavation          |
| Difficult to breed close to a food source that varies annually in space |  | Predictable food source in space                    |

<sup>a</sup> Not always the case as secondary cavity nesters may also usurp newly-excavated cavities.

<sup>b</sup> If a bird is at greater risk from predators while excavating (can't see or hear predators approach).

excavated ( $R_c = R - f(t) - C$ ), then

$$S_n > S_o(R/R_c). \quad (3)$$

That is, a new cavity should be excavated whenever the survival of the nest in the new cavity is greater than the survival of the nest in an old cavity times the ratio of the total amount of energy available for reproduction divided by the amount of energy remaining for reproduction after excavating a new cavity.

This model gives three straightforward predictions. First, when there is no improvement in survival in a new cavity, excavation is never the better option even if excavating costs are low. Thus, if individuals are forced into excavating a new cavity because of competition, it will be less economical than reuse, and we predict clutch size or productivity will be lower relative to those species or individuals with access to existing holes. This follows from the assumption of the model that there is a trade-off between the amount of energy available for reproduction and that devoted to nest excavation. Second, excavation becomes more beneficial as excavation costs decrease or as the relative survival advantage of using new cavities increases. Finally, as the amount of resources for reproduction ( $R$ ) increases, the ratio  $R/R_c$  approaches unity and the relative cost of excavation diminishes. This leads to a prediction that higher quality individuals or those with access to abundant food sources may be more prone to excavate as long as there are survival benefits.

Energy costs of excavation presumably vary depending on the strength of the bird's bill and skeletal musculature relative to the hardness of the substrate. Similarly, survival benefits to the clutch may vary according to tree hardness, the type of predators, and predator behaviour. If a bird has trees of different decay classes from which to choose, or snags at different locations on the landscape such as near or far from favoured edges (Aitken & Martin 2004, Fisher & Wiebe 2006), it may weigh localized costs and benefits on a tree-by-tree basis. Excavation propensity may therefore vary not only between species according to morphology, but also between and within populations according to the spatial distribution of substrates, food resources, and predators.

The  $f(t)$  term in the model incorporates the idea that excavation may cause a delay in breeding relative to the optimal laying time during a season. Time is spent in excavation itself, and perhaps also in searching for a suitable site. Time costs are likely more relevant for migrants than residents as the latter may be able to partially or completely excavate well before the optimal time of laying. Such costs may also be higher for re-nesting attempts late in the season as compared with those for early nests. The cost of excavation model predicts smaller clutches in new cavities because of a trade-off in resource allocation between excavation and egg formation, the same pattern predicted by the nest site limitation hypothesis (Martin 1993).

In this paper, we test a prediction of the model that excavating a new hole causes a delay in breeding, and/or is linked to smaller clutches in new cavities. With intraspecific comparisons, we also quantify differences in predation rates, nestling survival, and fledging success in old *versus* new cavities to address the question of whether these nesting strategies are equally good alternatives, or if one may be superior to the other. Using northern flickers *Colaptes auratus* as a model, we also test whether individuals in better body condition were more likely to excavate, whether second nesting attempts were more likely to be in reused cavities and whether freshly excavated cavities were smaller than reused ones.

## Material and methods

We surveyed the literature for studies reporting nest reuse rate for facultative cavity excavators, focusing on reviews in Martin (1993), Mönkkönen and Orell (1997), the Birds of North America Species Accounts and Cramp *et al.* (1993). Several researchers also kindly provided their unpublished data. We also obtained data on cavity use and reproductive performance from our long-term studies of cavity nesting birds at Riske Creek (1995–2005), British Columbia, Canada (Aitken *et al.* 2002, Wiebe 2003), and of acorn woodpeckers *Melanerpes formicivorus* at Hastings Reservation (1972–1992), California (Hooge *et al.* 1999). At Riske Creek, nests

from the entire cavity-nesting community of 26 species have been monitored in a variety of forest types (Martin *et al.* 2004); however, northern flickers *Colaptes auratus* were the primary target species and so reproductive variables for this species were particularly well-known and include the years 1998–2006. We report data for other species for which visual nest checks were done to determine total clutch size. If a complete clutch was found, the initiation date was calculated by subtracting the average incubation period from the day the nestlings hatched, and assuming one egg was laid per day. Nests were considered to be freshly excavated if birds were seen excavating and/or there was a pile of fresh wood chips on the ground beneath the cavity.

Northern flickers were trapped while incubating or feeding nestlings as described elsewhere (Wiebe 2001, 2005) and aged according to moult criteria (Pyle 1997). Flickers can be aged up to 4 years based on moult, but we used three age classes in statistical tests (1, 2, and 3+ years) because there were few old individuals. We controlled for age class when analyzing reproductive parameters of flickers, because performance varies with age. Structural body size was calculated as the weighting on the first axis of a principal components analysis (PCA1) based on six measures of body size (Elchuk & Wiebe 2003a). To evaluate the role of body reserves in the decision to excavate, we then calculated an index of body condition as the residual of a reduced major axis regression between body mass and PCA1 (Green 2001). This residual was entered as a covariate in ANCOVA models.

Characteristics of cavity nests at Riske Creek, and their interior dimensions were measured after nestlings fledged as described in Wiebe and Swift (2001). A given nest cavity was included only once in the analyses. We used ANCOVA models to test for associations between excavation status of the nest (new *versus* old) and initiation date and clutch size (dependent variables). Interaction terms were deleted from the final model if they were not significant. Values presented are means ± SD, and statistical tests were two-tailed. Such detailed analyses were not possible for several species in Table 2 because of small samples or lack of access to original data, so results for those species should be interpreted with caution.

**Table 2.** Reproductive parameters (mean ± SD, n) in newly excavated vs. reused holes (old cavities or natural holes). Differences between values set in boldface were tested statistically (Mann-Whitney U-tests or t-test) and significance (P < 0.05) is indicated with an asterisks (\*).

| Species  | Source                           | Clutch size              |                          | Laying date             |                         |
|--|----------------------------------|--------------------------|--------------------------|-------------------------|-------------------------|
|  |                                  | New                      | Old                      | New                     | Old                     |
| Acorn woodpecker <i>Melanerpes formicivorus</i>    | W. Koenig                        | <b>4.35 ± 0.85 (120)</b> | <b>4.43 ± 0.95 (211)</b> | <b>120 ± 15.6 (185)</b> | <b>121 ± 16.2 (201)</b> |
| Red-cockaded woodpecker <i>Picoides borealis</i>   | J. Walters, pers. com.           | <b>3.29 ± 1.03 (153)</b> | <b>3.40 ± 0.80 (332)</b> |                         |                         |
| Northern flicker <i>Colaptes auratus</i>           | K. Wiebe                         | <b>8.23 ± 1.45 (142)</b> | <b>8.10 ± 1.43 (437)</b> | <b>134 ± 7.3 (148)</b>  | <b>133 ± 7.1 (459)</b>  |
| Red-naped sapsucker <i>Sphyrapicus nuchalis</i>    | K. Martin                        | <b>4.56 ± 0.77 (48)</b>  | <b>5.00 ± 0.0 (6)*</b>   |                         |                         |
| —  | Walters <i>et al.</i> 2002       | <b>4.61 ± 0.69 (28)</b>  | <b>5.15 ± 0.99 (13)*</b> |                         |                         |
| —  | Ivanchev 1997                    | 6.05 (92)                | 6.09 (33)                |                         |                         |
| Great spotted woodpecker <i>Dendrocopos major</i>  | Mazgajski, pers. com.            | <b>5.38 ± 1.06 (8)</b>   | <b>5.67 ± 0.87 (9)</b>   | <b>124 ± 3.5 (12)</b>   | <b>121 ± 3.1 (7)*</b>   |
| —  | (Kabaty pop., Ciechanow pop.)    | <b>6.67 ± 0.71 (9)</b>   | <b>6.43 ± 0.68 (7)</b>   | <b>122 ± 1.8 (6)</b>    | <b>118 ± 1.4 (4)*</b>   |
| Black woodpecker <i>Dryocopus martius</i>          | Nilsson <i>et al.</i> 1991       | 4.8 (48)                 | 4.6 (13)                 |                         |                         |
| —  | Lange 1996                       | —                        | —                        |                         |                         |
| Black-backed woodpecker <i>Picoides arcticus</i>   | A. Nappi & P. Drapeau pers. com. | <b>3.8 ± 0.9 (22)</b>    | <b>3.6 ± 0.7 (15)</b>    | <b>144 ± 6.3 (22)</b>   | <b>144 ± 6.2 (15)</b>   |
| Red-breasted nuthatch <i>Sitta canadensis</i>      | K. Martin                        | <b>5.63 ± 1.3 (32)</b>   | <b>5.94 ± 1.5 (51)</b>   | <b>150 ± 10.6 (16)</b>  | <b>141 ± 8.4 (14)*</b>  |
| Black-capped chickadee <i>Poecile atricapillus</i> | K. Martin                        | <b>5.29 ± 0.91 (14)</b>  | <b>6.00 ± 1.09 (6)</b>   | <b>140 ± 10.8 (4)</b>   | <b>133 ± 3.87 (4)</b>   |

\*later in new cavities"

## Results

### Northern flickers

Newly excavated flicker cavities had smaller mean basal areas ( $149 \text{ cm}^2 \pm 29$ ) than reused cavities ( $t$ -test:  $172 \text{ cm}^2 \pm 55$ ,  $n = 205$ ,  $t = 2.69$ ,  $P = 0.008$ ). A lower proportion of renesting attempts were in fresh cavities as compared with first nesting attempts (freshly excavated nests = 22% [first nests] vs. 8% [renests];  $\chi^2 = 6.56$ ,  $n = 706$ ,  $P = 0.01$ ), supporting the hypothesis that it is costly to excavate new cavities, at least late in the breeding season. Excavation propensity did not vary between the three age classes for either males or females (both  $\chi^2 < 6.6$ ,  $df = 2$ ,  $P > 0.30$ ). Considering only first nests, an ANCOVA which controlled for parental age class and year showed that excavation status (reused vs. old cavity) was not related to initiation date in flickers ( $F_{1,671} = 0.14$ ,  $P = 0.71$ ; Table 2). A second ANCOVA that also controlled for initiation date indicated no significant difference in clutch size between cavity types ( $F_{1,578} = 1.16$ ,  $P = 0.28$ ) but males that used old cavities were in poorer body condition (condition index =  $-1.22 \pm 9.4$ ,  $n = 333$ ) than males that excavated (condition index =  $0.57 \pm 9.8$ ,  $n = 181$ ;  $t = 2.04$ ,  $P = 0.04$ ). The body condition of females was not associated with whether or not they nested in old or new cavities ( $t = 0.39$ ,  $n = 520$ ,  $P = 0.70$ ).

Of 1006 northern flicker nesting attempts where fate could be determined reliably, 69% survived to hatching with about 21% lost to nest predators, primarily red squirrels *Tamiasciurus hudsonicus*, and European starlings *Sturnus vulgaris*. Defining a successful nest as one that fledged at least one nestling, new nests ( $n = 141$ ) were slightly more successful than reused ones ( $n = 560$ , 80% vs. 73% success respectively;  $\chi^2 = 3.4$ ,  $df = 1$ ,  $P = 0.06$ ). This was partly a result of new nests having a lower depredation rate by squirrels (18% vs. 15%) but mainly because old nests were more likely to be usurped by starlings (8.3%) than freshly excavated ones (2%: Fisher exact test:  $n = 531$ ,  $P = 0.03$ ). Excluding the depredated nests, the number of fledglings did not differ between new nests ( $6.14 \pm 2.2$  SD) and old ones ( $6.12 \pm 2.3$  SD; ANCOVA controlling for female age category, year and laying date: excavation status  $F_{1,557} = 0.3$ ,  $P = 0.95$ ). Neither was there a difference in the proportion of the brood that fledged according to cavity type (Mann-Whitney  $U$ -test:  $P = 0.41$ ).

### Other cavity nesting species

Despite an intense literature search and personal communication with other researchers, surprisingly few studies reported reproductive parameters in new vs. reused holes. Intraspecific comparisons were available for 14 populations of 10 species of excavators (Table 2). In 9 of 13 populations, average clutch size was larger in old than in new cavities but it was statistically significant within only one species, the red-naped sapsucker *Sphyrapicus nuchalis*. Average laying dates were earlier in reused cavities in 6 of 8 populations but were statistically different in only two species (Table 2). With each species as a datapoint, a paired  $t$ -test indicated no overall significant difference in either clutch size ( $t = 1.4$ ,  $P = 0.18$ ) or laying date ( $t = 1.4$ ,  $P = 0.56$ ) according to cavity type.

Among the other species, there was also no significant difference in success between new (84%,  $n = 25$ ) and reused (86%,  $n = 22$ ) red-breasted nuthatch *Sitta canadensis* cavities (Fisher exact test:  $P = 1.0$ ). There was a trend for newly excavated cavities of red-naped sapsuckers to be more successful (93%,  $n = 45$ ) than reused cavities (67%,  $n = 6$ ), but the sample size of reused cavities was small and the statistical significance was weak (Fisher exact test:  $P = 0.09$ ).

## Discussion

### Benefits of nest reuse

Reusing nests may offer the advantage of earlier laying dates, larger clutches, and in some cases, more renesting attempts (review in Hauber 2002). This was the pattern for most populations of facultative excavators although statistically significant differences could only be confirmed in a few cases (Table 2). In support of the cost of excavation hypothesis, a greater proportion of second nests of northern flickers were in old

cavities, suggesting such nests offered a time savings near the end of the breeding season. Among first nests of northern flickers, initiation date and clutch size did not differ between new and reused nests, but males in better body condition tended to excavate. It appears that higher quality males with more energy reserves may have initiated excavation quite early in spring and so were not delayed relative to others that reused existing holes.

The time needed to excavate varies within and among species and according to the substrate chosen. It may take 12–15 days for northern flickers (Moore 1995) but more than 11 years for red-cockaded woodpeckers *Picoides borealis* which use structurally hard, living pine trees with flowing sap (Jackson 1977, Walters *et al.* 2002). The substantial time and energy costs of excavation in the latter species may explain why cavity reuse is high as compared with that in many other woodpeckers. Generally, early breeding is linked to higher fitness through more recruiting offspring as has been shown in lesser spotted woodpeckers *Dendrocopos minor*; Wiktander *et al.* 2001) and many non-excavating bird species (Perrins 1970, Nilsson & Smith 1988). Such benefits linked to time savings may especially promote cavity reuse among migrants if there is little time during a short breeding season for prospecting and building a new nest. Not all species that reuse cavities are migratory, but those which are, such as the northern flicker, Lewis's woodpecker *Melanerpes lewis*, and sapsuckers often do show relatively high rates of reuse (Wiebe *et al.* 2006).

Actual energy costs of excavating a new cavity remain to be quantified, and indeed doing so would entail numerous logistical challenges. Although resident excavators might mortgage energy and time costs by working on nest cavities slowly, throughout the winter, resident black woodpeckers *Dryocopus martius* waited with excavation until April (Nilsson *et al.* 1991), perhaps because foraging took up all available time in winter, or because birds did not want to give cues of the nest site location to resident predators. Thus, energy costs of excavation may be a bottleneck even for resident species. Time or energy costs of excavation may also explain

why new cavities are generally smaller in interior dimension than reused cavities. Contrary to the pattern in most species (Table 2), flicker pairs that excavated cavities did not have smaller clutches than those that reused nests so good quality males may have excavated near rich food patches which can be patchy on spatial and temporal scales (Elchuk & Wiebe 2003b). Alternatively, nest construction by males may have been a costly display to attract more fecund females as part of mate choice (Soler *et al.* 1998). If females have a large role in accepting an appropriate site, they may attempt to optimize their own fitness irrespective of the male's.

### Benefits of excavation

According to our model, individuals may be willing to invest in excavation if there is a benefit. For flickers, there was a weak pattern that newly excavated cavities were more successful. New northern flicker cavities were safer from usurpation by European starlings, perhaps because new cavities were unavailable early in spring at the peak of starling nesting (Wiebe 2003). A prevalent idea, that new cavities are safer than reused ones because predators have not learned their locations (Sonerud 1985; Table 1), was supported in black woodpeckers with pine marten *Martes martes* predators (Nilsson *et al.* 1991). However, there was no association between cavity reuse and predation risk in two populations of great spotted woodpeckers (Ivanchev 1997, Mazgajski 2002a), and in a third population, failure was greater in new holes (Smith 1997). The relationship between cavity reuse and predation risk probably depends on lifespans, search images, and diet of the local suite of predators. The possibility that fresh excavation chips on the ground, or the sound and activity of excavation, in fact, attracts predators needs to be investigated.

Comparisons across species showed that excavators tended to have lower nest predation than secondary cavity nesters (Martin 1995). In our data for facultative excavators, the link between nest success and cavity reuse rate was not straightforward. For example, both red-cock-

aded woodpeckers and northern flickers reused cavities extensively but the former has a relatively low rate of nest loss (10%–14%) compared to flickers that lose 20%–30% of nests annually (Wiebe 2003). Red-cockaded woodpecker cavities were in structurally hard, live pine trees with drilled resin wells that deter snakes (Walters *et al.* 2002) whereas flickers used more decayed substrates than many other woodpeckers (Martin *et al.* 2004). These comparative data suggest that the loss of clutches is not strongly associated with the reuse of cavities *per se*, but may depend on the structural quality or characteristics of the cavity used. Among Paridae, structurally strong cavities were safer than those in decayed wood (Christman & Dhondt 1997, Wesolowski 2002).

A second proposed benefit of new cavities, increased health or survival of nestlings because of reduced parasite loads, may be relatively unimportant for woodpeckers, which do not use nest material. Rendell and Verbeek (1996) found that parasite species not dependent on nest material infected old and new swallow nests equally. We found that an equal proportion of the brood fledged in old and new flicker cavities, similar to the great spotted woodpecker (Ivanchev 1997). Brood size and nestling mass was also equivalent between old and new nests of the black woodpecker (Nilsson *et al.* 1991), suggesting that parasitism is not greater in old cavities. No study on fitness consequences of parasitism in natural tree cavities has yet been conducted and it needs to be determined whether parasite loads are costly for facultative excavators, especially for nuthatches or chickadees which use nest material in natural cavities.

Finally, fresh excavations may allow the tracking of food sources that vary in time and space. This may be especially important when the success of nestling-rearing depends on matched timing with an ephemeral resource. Three-toed woodpeckers *Picoides tridactylus* in Finland which relied on patchy outbreaks of wood-boring beetles often excavated subsequent nests hundreds of meters apart whereas great spotted woodpeckers with a more generalist diet remained within the same home range (P. Fayt pers. comm.) and are more likely to reuse cavities (Wiebe *et al.* 2006).

## Modelling nest selection

If there are benefits to new cavities, our model suggests that higher quality individuals will be more likely to excavate than lower quality birds within a population because they have more energy reserves. Such data were lacking for most species, but consistent with the prediction, Ivanchev (1997) found that older great spotted woodpeckers excavated more frequently than yearling birds and we found that male flickers in better body condition excavated more frequently than other males. In species such as pileated woodpecker *Dryocopus pileatus* or black-capped chickadee *Poecile atricapillus* where nearly all individuals in the population excavate, we predict that excavation costs are uniformly low or survival benefits in new cavities are relatively high.

A cost–benefit model may also explain nest use patterns at the level of populations or species (*see* Ecological factors in Table 1). Excavation propensity can certainly vary among populations, for example nest reuse of 4%–91% among populations of the great spotted woodpecker and between 4%–63% for the northern flicker (Wiebe *et al.* 2006). Different levels of competition for existing cavities or differences in availability of substrates that affect energy costs may explain such variation. For example, great spotted woodpeckers were forced to excavate new holes more frequently in forests with many European starling competitors (Mazgajski 2002b). Forestry practices that change the proportion of different tree species on the landscape, or the proportions of snags in different decay classes may have a significant impact on the energy balances and nesting behaviour of excavators.

Facultative excavators may reuse nests either because there is a limited supply of suitable substrates to excavate (“forced reuse”), or because reuse is more energetically profitable than excavation (“voluntary reuse”). Both the nest site limitation and cost of excavation hypotheses predict smaller clutches in freshly excavated cavities (Martin 1993) and are best distinguished by experimental addition, and removal of, nesting substrates or cavities (Table 3). Adding more substrates should result in more excavation, and a greater percentage of the nests being freshly

**Table 3.** Predictions of the Limited Nest Site vs. Cost of Excavation Hypotheses deriving from experimental addition and removal of nest sites.

| Manipulation                           | Limited nest site      | Cost of excavation |
|--|------------------------|--------------------|
| <b>Substrate addition</b>              |                        |                    |
| Higher % excavation                    | yes                    | no                 |
| Breeding density                       | increases <sup>a</sup> | stays the same     |
| Average individual reproductive output | higher                 | no change          |
| <b>Cavity removal</b>                  |                        |                    |
| Higher % excavation                    | no                     | yes                |
| Breeding density                       | decreases              | stays the same     |
| Average individual reproductive output | no change              | decreases          |

<sup>a</sup> assuming territoriality is not limiting density.

made if nest sites are limited, but not if reuse is voluntary. Conversely, removing substrates or blocking cavities should not affect excavating propensity in a situation of “forced reuse” because the birds simply lack the ability to excavate new holes. Voluntary cavity reusers may respond to blocked cavities by excavating fresh holes, although at an energetic cost and reduced reproductive output as compared with when they are able to reuse a cavity.

In sum, our review of reproductive performance suggests that reusing cavities sometimes offers advantages of earlier laying and larger clutches and that nest reuse may sometimes be favoured over excavation. Patterns of excavation in northern flickers were consistent with our energy trade-off model with higher quality males investing in excavation for higher nest success. While acknowledging that small sample sizes for some species preclude strong interpretations, we hope our framework generates fresh interest in the nesting strategies of birds and motivates experimental and quantitative assessments of the costs and benefits of nest cavity reuse.

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