

## RESEARCH ARTICLE

**Nest cavity reuse by the cooperatively breeding Acorn Woodpecker**Walter D. Koenig,<sup>1,2,\*</sup> Eve M. Hallock,<sup>1</sup> David J. Weber,<sup>1</sup> and Eric L. Walters<sup>3,6</sup><sup>1</sup> Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA<sup>2</sup> Hastings Natural History Reservation, University of California Berkeley, Carmel Valley, California, USA<sup>3</sup> Department of Biological Sciences, Old Dominion University, Norfolk, Virginia, USA\* Corresponding author: [wdkoenig@berkeley.edu](mailto:wdkoenig@berkeley.edu)

Submission Date: July 27, 2020; Editorial Acceptance Date: November 11, 2020; Published March 22, 2021

**ABSTRACT**

Although primary cavity-nesting species are capable of excavating new cavities, they often reuse old ones. To determine potential factors driving such reuse, we studied nest-cavity reuse in the Acorn Woodpecker (*Melanerpes formicivorus*), a cooperatively breeding species that reuses old cavities for 57.2% of nests at Hastings Reservation in central coastal California, USA. We found no evidence for significant fitness costs or benefits of cavity reuse compared to using newly constructed cavities. In contrast, several lines of evidence supported a role for constraints on both cavity reuse and on new cavity construction. The main constraint on reuse was cavities failing to survive from one year to the next, usually because the limb fell apart, filled with water, or was usurped by another species. Evidence that constraints on new cavity construction may be important included more frequent cavity reuse when groups re-nested and use of artificial cavities when they were experimentally provided. Nest-cavity reuse in this population appears to be driven primarily by constraints, including the energetic costs and time required to excavate a new cavity, rather than fitness consequences, even though Acorn Woodpeckers regularly excavate small holes in trees for acorn storage and the energetic costs of new cavity construction are apparently insufficient to significantly depress reproductive success. Constraints play a significant role in cavity reuse and may affect both the intraspecific and interspecific frequency of cavity reuse among facultative excavating species.

**Keywords:** Acorn Woodpecker, cavity reuse, cavity survivorship, *Melanerpes formicivorus*, nest-site limitation

**LAY SUMMARY**

- We investigated the costs and benefits of cavity reuse in the cooperatively breeding Acorn Woodpecker (*Melanerpes formicivorus*), in which groups reuse old cavities for over half of nesting attempts.
- We found no differences in the fledgling success of family groups that reused an old cavity compared to excavating a new one. Why, then, do birds reuse old cavities?
- The answer appears to be constraints, both on cavity reuse and new cavity construction.
- The main constraint on cavity reuse was that many cavities become unusable from one year to the next, usually because the tree limb disintegrates, fills with water, or is taken over by another species.
- Birds frequently use artificial cavities when they are provided, suggesting that old cavities are reused because excavating a new one takes time and energy.
- Constraints appear to play a significant role in cavity reuse and may affect both the frequency of cavity reuse among species and across populations of excavating species.

**Reutilización de nidos en cavidades por *Melanerpes formicivorus*, especie que cría cooperativamente****RESUMEN**

Aunque las especies que anidan primariamente en cavidades son capaces de excavar nuevas cavidades, usualmente reutilizan las viejas. Para entender los factores potenciales que determinan esta reutilización, estudiamos la reutilización de nidos en cavidades en *Melanerpes formicivorus*, una especie que cría de modo cooperativo y que reutiliza las viejas cavidades en el 57.2% de los casos en la Reserva Hastings en la costa centro de California, EEUU. No encontramos evidencia de costos o beneficios significativos en la adecuación biológica debido a la reutilización de las cavidades en comparación con el uso de nuevas cavidades construidas. En contraste, varias líneas de evidencia apoyan el rol de las limitaciones que existen tanto en la reutilización de las cavidades como en la construcción de nuevas cavidades. La principal limitación de la reutilización fue las cavidades que no sobrevivieron de un año al otro, usualmente debido a que la rama se cayó, se llenó con agua o fue usurpada por otra especie. La evidencia de que las limitaciones para la construcción de nuevas cavidades pueden ser importantes incluyen más frecuencia de reutilización de la cavidad cuando los grupos vuelven a anidar y el uso de cavidades artificiales cuando fueron provistas experimentalmente. La reutilización de nidos en cavidades en esta población parece

estar determinada principalmente por las limitaciones, incluyendo los costos energéticos y el tiempo requerido para excavar una nueva cavidad, más que por las consecuencias para la adecuación biológica, aunque *Melanerpes formicivorus* excava regularmente pequeños huecos en los árboles para el almacenamiento de bellotas y los costos energéticos de la construcción de nuevas cavidades son aparentemente insuficientes como para disminuir significativamente el éxito reproductivo. Las limitaciones juegan un rol significativo en la reutilización de las cavidades y pueden afectar tanto la frecuencia intraespecífica como interespecífica de la reutilización de cavidades entre especies que excavan de modo facultativo.

*Palabras clave:* limitación del sitio de anidación, reutilización de cavidades, supervivencia de la cavidad, *Melanerpes formicivorus*

## INTRODUCTION

Nest construction, an activity often repeated multiple times within a breeding season, can be costly (Moreno et al. 2010, Mainwaring and Hartley 2013). This is particularly true for primary cavity-nesting species, for which locating a suitable substrate and excavating a nest hole can have limiting effects on clutch size and life-history characters such as incubation patterns and hatching intervals (Beissinger and Waltman 1991, Martin 1993).

Alternatively, birds can potentially save time and energy by using a naturally occurring cavity (Cockle et al. 2011) or reusing a cavity that either they or some other species has constructed (Newton 1994, Wiebe et al. 2006). There are, however, costs and benefits of cavity reuse (Wiebe et al. 2007, Kosiński and Walczak 2019). Increased parasite loads are a particularly important potential cost (Clark and Mason 1985). For example, female Blue Tits (*Cyanistes caeruleus*), a secondary cavity-nesting species, have reduced body mass and lower reproductive success attributable to greater ectoparasite loads when nesting in previously used nestboxes (Tomás et al. 2007). Hematophagous mites are common in old nests of Barn Swallows (*Hirundo rustica*), but the birds differentially select unparasitized old nests, thus avoiding this potential toll of nest reuse (Barclay 1988).

A second potential cost of nest reuse is an increased chance of nest failure if predators remember nest locations (Walters and Miller 2001, Wiebe et al. 2007). Otterbeck et al. (2019), for example, found that in Eurasian Sparrowhawks (*Accipiter nisus*), an open-nesting species, pairs that reused nest sites laid eggs earlier and had greater reproductive success, but also experienced increased nest depredation. A third cost is that constructing a new nest is likely to require more time than reusing an old nest (Conrad and Robertson 1993). For example, Northern Flickers (*Colaptes auratus*) in British Columbia, Canada, reusing an old cavity nest two days earlier, on average, and lay significantly larger clutches than individuals excavating new holes (Wiebe 2014). More generally, Wiebe et al. (2007) found an overall trend for earlier laying and larger clutch size in reused compared to newly constructed cavities in a meta-analysis of excavating species. Given the widespread pattern of the seasonal decline in clutch size observed in birds (Lack 1947, Rowe et al. 1994), such a delay will potentially result in lower reproductive success.

There is wide variability across cavity-excavating birds in the incidence of cavity reuse. Interspecifically, the percent of nests in existing cavities runs the gamut from 0% to 100% among woodpeckers and nuthatches (Wiebe et al. 2006). Intraspecific differences among populations can vary considerably as well; for example, nest reuse among five populations of Northern Flickers varied between 5% and 65% (Wiebe et al. 2006). Such variability within and between species suggests that a variety of ecological factors affect nest cavity reuse.

Acorn Woodpeckers (*Melanerpes formicivorus*) are cavity-excavating, cooperative breeders that live in groups of up to 15 individuals (Koenig et al. 2020). Groups consist of between 1 and 7 cobreeder males sharing one or, in ~20% of cases, 2 or more joint-nesting females, along with up to 10 nonbreeding helpers of either sex who are offspring from prior breeding efforts (Koenig et al. 1984). When groups contain more than one breeder female, females lay their eggs in the same nest cavity and groups can attempt up to several renests, and, when successful, a second nest, within a season (Koenig et al. 2016).

Acorn Woodpeckers are unique not only in their social behavior but in storing acorns, often by the thousands, individually in small holes in “granaries” located centrally within their territory that are passed down through generations of birds. Acorn storage provides a critical food resource at times when aerial insects, their preferred food, are unavailable during inclement weather, allowing birds to remain resident and prosper in a dynamic oak woodland ecosystem (Koenig and Mumme 1987, Koenig et al. 2020).

Reproduction in Acorn Woodpeckers is an energetically expensive activity requiring 11 days of incubation and 30–32 days between hatching and fledging (Weathers et al. 1990). Besides being used for nesting, cavities are also used for nocturnal roosting, a communal activity in which birds engage nightly throughout the year. Cavity choice has significant thermoregulatory and fitness consequences: communal roosting in artificial cavities created from oak limbs significantly reduces heat loss compared to solitary roosting (Du Plessis et al. 1994), and reproductive success is higher in cavities built in large, east-facing live limbs, characteristics that provide more favorable microclimatic conditions (Hooge et al. 1999).

Although groups fledge more offspring when they nest in live limbs, most nesting cavities are in suboptimal dead limbs (Hooge et al. 1999). This contradiction suggests demographic and ecological constraints on nest-site selection in this species, a conclusion supported by the relatively high incidence of nest cavity reuse in Acorn Woodpeckers (Wiebe et al. 2006). Here we address this issue by examining the dynamics of cavity reuse in a long-term study of this species.

### Cavity Reuse: Fitness Effects and Constraints

**Fitness effects.** The two main costs potentially associated with cavity reuse by Acorn Woodpeckers are increased parasite loads affecting the number of young fledged and higher predation rates affecting nesting success. Increased predation would likely be caused by predators returning to cavities where they had found active nests in the past. Both factors would result in lower reproductive success in reused compared to newly excavated cavities. A third potential cost is the potential for species dependent on ephemeral food resources such as insect outbreaks to more efficiently exploit them by moving to and excavating new cavities near outbreaks (Wiebe et al. 2007). Acorn Woodpeckers are permanent residents but are dependent on, and will sometimes temporarily move to access, acorns when the crop is poor (Hannon et al. 1987, Koenig and Mumme 1987, Koenig et al. 2015). Such complete crop failures are

rare, however. Moreover, the acorn crop matures in the autumn and the majority of breeding takes place in the spring (Koenig and Stahl 2007). Thus, such movements are unlikely to play a significant role in cavity reuse in this population.

Potential benefits of cavity reuse include lower predation if groups reuse cavities that are relatively safe from predators, and being less costly in time and energy than constructing a new cavity. To the extent that the latter is important, the savings in time and energy might result in egg-laying in reused cavities being initiated earlier and nests in reused cavities being more successful than nests in newly excavated cavities. Earlier nesting confers an advantage both because nesting success in this population declines seasonally, at least in part due to conditions that decline with date (Koenig and Walters 2018), and, more generally, because earlier nesting provides a greater chance for a second nesting attempt within a season (Hauber 2002).

**Constraints.** Ultimately, a key constraint on cavity reuse is cavity survivorship: the probability that a cavity will remain usable by the birds from one year to the next and not be usurped by some other species. Beyond this, the second category of constraints consists of factors limiting new cavity construction.

We considered 6 predictions of the hypothesis that new cavity construction is costly in time or energy and thus limiting (Table 1):

**TABLE 1.** Potential fitness consequences and constraints on cavity reuse by Acorn Woodpeckers, along with their predictions/evidence and results.

Type of effect (direction)	Prediction/evidence	Result
<b>Fitness Effects</b>		
Increased parasite load (–)	Young fledged declines with cavity age and reuse	No (Figure 1)
Increased predation (–)	Nesting success lower in reused cavities	No (see text)
Decreased predation (+)	Reuse more likely if the cavity was successful the prior year <i>and</i> increased success if reusing the cavity	Reuse more likely, but no difference in subsequent success (see text)
Conserves time and energy (+)	First nest initiated earlier in the season	No (Table 2)
	Larger clutch size Enhanced fledging success for the season	No (Table 2) No (Table 2)
<b>Constraints</b>		
On cavity reuse	Cavity survivorship and usurpation	Figure 3A
On new cavity construction	Reuse more frequent in renests and second nests	Yes (see text)
	Reuse more frequent following a poor acorn crop	Yes (see text)
	Reuse more frequent when group size is smaller	No (see text)
	Reuse less frequent if the group did not experience a turnover in breeder composition from the prior year	No (Figure 4)
	Reuse more frequent when a cavity is in a living limb	Yes (Figure 3B)
	Use of artificial cavities	Yes (see text)

**Cavity reuse in first vs. later nests.** Renesting after a failed attempt often occurs quickly and second nests can even overlap a successful first nest by several days (Koenig et al. 2020). Thus, there is likely to be little time for the construction of a new cavity for such attempts. Consequently, if new cavity construction is costly, cavity reuse should be more frequent among renesting attempts, both after nest failure or following a successful first nest.

**Cavity reuse and the acorn crop.** When food resources are limited, birds are likely to be in poorer condition and have less time to excavate a new cavity, and thus cavity reuse should be more frequent. For Acorn Woodpeckers, food availability is strongly dependent on the acorn crop, which is a significant food resource during winter and into the spring breeding season (Koenig and Mumme 1987, Koenig and Walters 2014). Thus, cavity reuse should be more common following poor acorn crops.

**Cavity reuse and group size.** Assuming that larger family groups can excavate new cavities more readily and with less cost to each individual, we expected that cavity reuse should be more frequent when family groups are small.

**Cavity reuse and breeder turnovers.** A breeder turnover occurs when all breeders of one sex die or disappear, after which there is typically a “power struggle” among neighboring helpers to fill the vacancy (Koenig 1981a). Such changes in group composition entail considerable social disruption (Hannon et al. 1985, Barve et al. 2020) and result in significantly lower reproductive output than for groups where no breeder turnover has occurred (Koenig 1981b). Thus, turnovers are likely to leave less time for new cavity excavation. To the extent this is true, cavity reuse should be more common following a breeder turnover within a group.

**Vital status of nest cavities.** Acorn Woodpecker nests in cavities in living limbs are structurally more stable and associated with greater reproductive success. Nonetheless, nest cavities in live limbs appear to be *less* common than expected (Hooge et al. 1999). If this discrepancy is the cause of constraints on new cavity excavation, then we predict that cavities in live limbs should both survive longer and be reused more frequently than cavities in dead limbs.

**Use of artificial nest cavities.** Although most studies are to some extent equivocal (Wiebe 2011), suitable cavities are generally thought to limit populations and reproduction of secondary cavity-nesting species (Newton 1994, 1998). A good example is the endangered Red-cockaded Woodpecker (*Dryobates borealis*), for which artificial cavities have been used to successfully increase the number of breeding groups in recovering populations (Copeyon et al. 1991). Thus, the use of artificial cavities, although not definitive, provides evidence supporting the hypothesis that natural cavities limit breeding densities of birds and that the use of new cavities is constrained by the time and energy required to construct them.

## METHODS

### Study System

Acorn Woodpeckers breed in groups of 2–15 birds in western oak woodland habitat extending from southern Washington State (USA) through Central America and as far south as northern Colombia (Koenig et al. 2020). At our Hastings Reservation study site in upper Carmel Valley, central coastal California (36.387°N, 121.551°W), Acorn Woodpeckers have been studied since 1968 (MacRoberts and MacRoberts 1976, Koenig and Mumme 1987). Over 6,000 birds have been color-banded and nearly 2,000 nesting attempts have been followed as of 2019.

### Data

Data on cavity reuse were available for a limited sample of cavities beginning in 1973. From 2001 to 2018 we tagged nesting cavities with unique metal tree tags for permanent identification. Nest cavities were tracked each year until visual inspection indicated they were no longer useable by the birds. This was usually due to the limb falling or the cavity breaking apart.

The number of eggs in the nest (clutch size), number of young fledged, and whether cavities were in a living or dead limb were recorded. Because of egg destruction among joint-nesting females (Mumme et al. 1983, Koenig et al. 1995), nest initiation was uncertain, especially for groups with 2 or more joint-nesting females. Thus, for the timing of nests, we used the estimated date the last egg of the clutch was laid rather than the more typical first egg date. Other demographic factors included in analyses were social group size and whether there was a breeder turnover from the prior year, an event following the death of all cobreeders of one or both sexes in the group. Four categories of turnovers were defined: male turnover, female turnover, turnover of both sexes, and no turnover from the prior year.

Acorn Woodpeckers are dependent on stored acorns as a supplemental food resource in times of inclement weather during the winter and during breeding, when acorns are eaten by both adults and fed to nestlings (Koenig and Mumme 1987, Koenig et al. 2008). Thus, reproductive success and demography are dependent on an acorn crop that is highly variable from year to year (Koenig et al. 2011, 2015). To estimate annual acorn abundance, we used data from the California Acorn Survey (Koenig et al. 1994a, 1994b). Each autumn, ~250 oaks (genus *Quercus*) distributed among the 5 species common at the field site (Griffin 1974) were surveyed for acorn abundance using standardized visual surveys during which two observers with binoculars counted as many acorns as they could in 15 s. Counts were summed, *ln*-transformed, and averaged across all trees to yield an estimate of the overall acorn abundance at the study site.



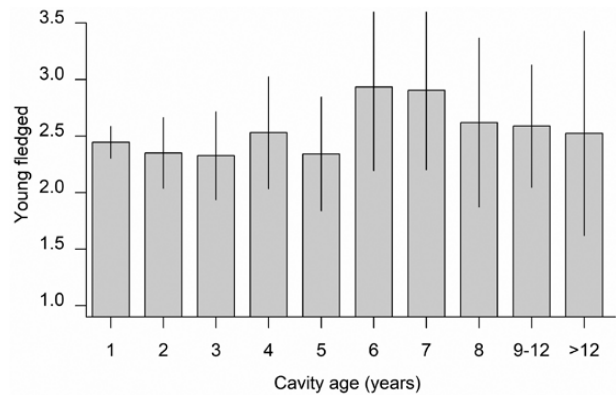
Over the course of the study, we occasionally provided groups with artificial nest cavities constructed out of hollowed-out trunk sections. In autumn 2006, however, we conducted an experiment where we randomly supplemented two artificial cavities to one territory in each of 7 paired groups, resulting in paired experimental and control territories. The goal of the experiment was to test the effects of cavity addition on the reproductive success of groups, the hypothesis being that if cavities are sometimes limiting, groups provided with artificial cavities will, on average, have more options, be less limited, and should outperform control groups. Here we report on the use of these artificial cavities and compare the reproductive success of control vs. experimental groups during the two years of the experiment.

### Statistical Analyses

All statistical analyses were performed in R3.5.3 (R Core Team 2019). Survivorship of cavities was estimated with the *survreg* procedure in the *survival* package using a Weibull error distribution (Therneau and Grambsch 2000), which performed better than an exponential error distribution (comparison by ANOVA,  $P < 0.001$ ). Survivorship of live vs. dead cavities was tested using a Wilcoxon signed-rank test. Statistical significance was set at  $P < 0.05$ , and unless otherwise stated, values presented are means  $\pm$  standard errors (SE).

Cavities “died” when the limb or tree fell, the cavity disintegrated, filled with water, or was taken over by another species whose occupancy effectively “destroyed” the cavity for subsequent use by Acorn Woodpeckers (Wiebe et al. 2020). The main species usurping cavities in our study was the European Starling (*Sturnus vulgaris*), which used Acorn Woodpecker nesting cavities in 120 of 1,283 (9.4%) cavity-years (Koenig and Walters 2014). Other species, including feral European honeybees (*Apis mellifera*), rodents (dusky-footed woodrats [*Neotoma fuscipes*] or mice [*Peromyscus* spp.]), and small owls (Northern Pygmy-Owl [*Glaucidium gnoma*], Western Screech-Owl [*Megascops kennicottii*], and Northern Saw-whet Owl [*Aegolius acadicus*]), accounted for a total of 43 cases (3.4%) of cavity-year reuse. Cavities whose fate was unknown, still being used through the end of the period covered here, or that were inadvertently affected by our research activities were marked as having exited the study and were right-censored in the survival analysis.

Linear mixed models and generalized linear mixed models were produced with the *lme4* package (Bates et al. 2015). Depending on the analysis, year, cavity, group size (number of breeder females in the case of clutch size), and breeder turnover were included as random factors: year controlled for annual variation, including the acorn crop; cavity controlled for differences among cavities, including whether they were in a live or dead limb (Hooge et al. 1999); and group size and breeder turnover controlled



**FIGURE 1.** Mean ( $\pm 95\%$  confidence interval) young fledged by cavity age. Differences were not statistically significant (linear mixed model including all four random factors, effect size =  $-0.0003 \pm 0.0205$ ,  $t = 0.2$ ,  $df = 463$ ,  $P = 0.99$ ). Although combined in the figure, older age categories of nests were not combined for the statistical test.

for two of the main factors affecting group reproductive success (Koenig et al. 2011). When the dependent factor was binomial, such as for whether a nest was successful or not, a generalized mixed model with a binomial error structure was used. Most analyses compared cavities used for the first time vs. cavities used previously (reused cavities), but analyses of the effects of cavity age on reproductive success used age since the cavity was first used for nesting (in years) as a fixed effect, and the analysis of nest reuse vis-à-vis prior success partitioned reused cavities into those that had been used the previous year and those that were used previously, but not the prior year.

We used Fisher exact tests to compare the incidence of cavity reuse among first nests of the season vs. subsequent nesting attempts, and between cavities in live vs. dead limbs. The artificial cavity addition experiment was analyzed with a paired Wilcoxon signed-rank test comparing the control with their a priori paired experimental group.

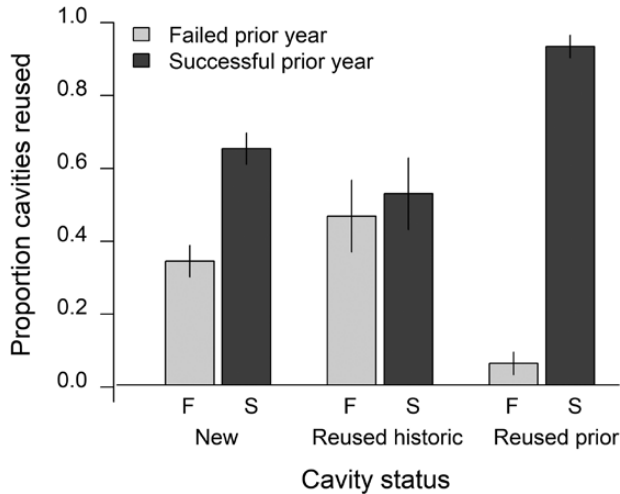
## RESULTS

We obtained data on the cavities used in 1,500 nesting attempts between 1973 and 2018. Of these, 858 (57.2%) were in natural cavities that had been used previously for nesting by Acorn Woodpeckers. Of nesting attempts, 864 were made in 359 unique, tagged cavities.

### Fitness Effects

Using all nesting attempts, there was no significant effect of cavity age on the number of young fledged (Figure 1). Results were unchanged using only the first nesting attempt of each year.

Considering only the first nests of the year, there was no difference between new and reused cavities in whether a nest successfully fledged young or not (linear mixed model



**FIGURE 2.** Proportion of nests from the prior year that failed and successfully fledged young ( $\pm 95\%$  confidence interval) in the subsequent year, partitioned into three categories: those that constructed a new cavity, those that reused an historic cavity not from the prior year, and those that reused the same cavity from the prior year. Proportions add to 1 within each of the three categories (new, reused historic, and reused prior); differences in proportions among the three categories is highly significant ( $\chi^2 = 84.1$ ,  $df = 2$ ,  $P < 0.001$ ).

including all four random factors [year, cavity, group size, and breeder turnover] and binomial errors, effect size of reusing a cavity vs. a new cavity =  $0.090 \pm 0.216$ ,  $t = -0.4$ ,  $P = 0.68$ ).

There may still be a benefit to reusing a cavity if it produced a successful nest the prior year, indicating that the cavity was a “safe” choice. There were three possibilities: (1) groups used a new cavity; 65.5% of such groups successfully fledged young the prior year. (2) Groups reused an older historic cavity (not the one they used the prior year); 53.1% of such groups successfully fledged young the prior year. Finally, (3) groups reused the same cavity as the previous year; 93.5% of such groups successfully fledged young the prior year. These differences were highly significant (Figure 2). Thus, groups were highly likely to reuse a cavity if the nest in that same cavity was successful the prior year.

However, such reuse only enhances fitness if the group is more likely to be successful when they reuse the previously

successful cavity. There was no corresponding increase in the probability of success among groups that nested successfully the prior year and subsequently reused the same nest cavity (89.4% successfully fledged young) and those that subsequently used a new cavity or reused an older cavity (86.6% successfully fledged young; Fisher exact test,  $P = 0.31$ ). Thus, groups were more likely to reuse a cavity if they successfully fledged young from it the prior year, but were no more likely to be successful using the cavity the second time around than if they used a new cavity or reused an older, historic cavity.

Reusing a cavity may not increase the success of any one nest, but may allow groups to nest earlier and reneest more often within a season. However, in linear mixed models that included all four random factors, there were no significant differences in the timing of first nests of the spring, clutch size of first nests, or the total number of young fledged per season in groups whose first nest was in a new vs. reused cavity (Table 2).

### Constraints

The mean annual survivorship of cavities was 86.7% (95% CI: 82.0–89.2%) (Figure 3A). Thus, on average, there was about a 1 in 7 chance that a cavity used one year would not survive or be available for reuse the next.

We examined 6 lines of evidence testing for constraints on new cavity construction:

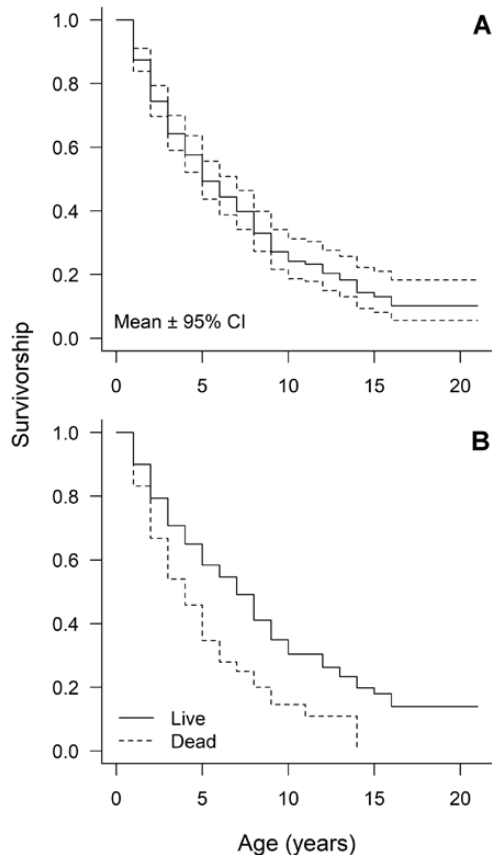
**Cavity reuse in first vs. later nests.** Of a total of 1,059 first nests of the season, 54.3% were in old cavities that had been previously used by Acorn Woodpeckers compared to 70.5% of 285 second and renests (Fisher exact test,  $P < 0.001$ ). Thus, later nests were more likely to occur in reused rather than new cavities.

**Cavity reuse and the acorn crop.** In a generalized linear mixed model with binomial errors and breeder turnover and cavity as random factors, cavity reuse increased when the acorn crop the prior autumn was smaller (estimate =  $-0.609 \pm 0.137$ ,  $t = 4.5$ ,  $P < 0.001$ ).

**Cavity reuse and group size.** In a generalized linear mixed model with binomial errors and breeder turnover and cavity as random factors, group size was positively related to the incidence of cavity reuse (estimate =  $0.111 \pm 0.046$ ,  $t = 2.4$ ,  $P = 0.02$ ). Larger groups reused cavities more often than smaller groups.

**TABLE 2.** Mean  $\pm$  SE ( $n$  nests) last egg date of first nests of the season, mean clutch size of first nests of the season, and mean young fledged per season for groups whose first nests were in a new cavity vs. reused cavity. All tests by linear mixed models with year, cavity, group size (number of breeder females in the case of mean clutch size), and breeder turnover as random factors.

Variable	New cavity ( $n = 609$ )	Reused cavity ( $n = 518$ )	Estimate $\pm$ SE	$t$ (df)	$P$ -value
Mean last egg date of first nests (day of year)	$119.8 \pm 0.7$	$121.5 \pm 0.6$	$0.81 \pm 1.15$	0.7 (661)	0.48
Mean clutch size of first nests	$4.99 \pm 0.08$	$5.05 \pm 0.07$	$0.17 \pm 0.13$	1.3 (505)	0.20
Total young fledged	$3.16 \pm 0.09$	$3.18 \pm 0.08$	$-0.13 \pm 0.15$	-0.9 (642)	0.37

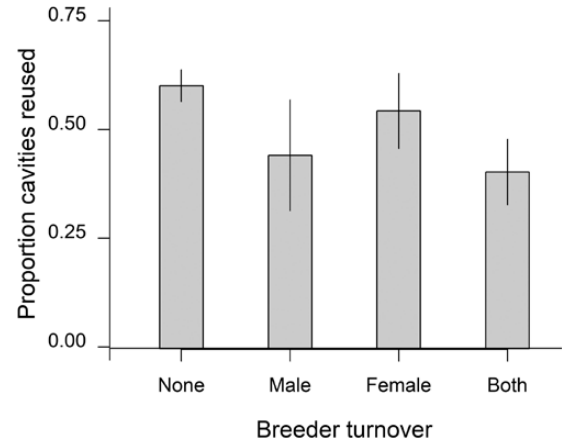


**FIGURE 3.** (A) Overall mean ( $\pm 95\%$  confidence interval) of cavity survivorship. (B) Mean cavity survivorship of cavities in live and dead limbs.

**Cavity reuse and breeder turnovers.** Groups experiencing no turnover in breeders from the prior year were significantly *more* likely to reuse old cavities than groups undergoing turnovers of breeder males, breeder females, or both (Figure 4).

**Vital status of nest cavities.** Cavities in live limbs survived significantly longer than those in dead limbs (mean annual survivorship of cavities in live limbs = 88.8%, in dead limbs = 80.7% [Figure 3B]; Wilcoxon signed-rank test,  $P < 0.001$ ). This difference (8.1%) was comparable to the difference in the proportion of cavities reused that were built in live (58.4%) vs. dead (46.8%) limbs (difference = 11.6%;  $n = 1126$ ).

**Use of artificial cavities.** Quantitative data on the use of artificial cavities were available from the experiment where 2 artificial cavities were randomly supplemented to each of seven paired groups. Of the 14 artificial cavities provided in 2006, four (28.6%) were subsequently used a total of five times by three (42.9%) of the groups (one group used the same cavity twice and one used both artificial cavities) over the next two years. There was, however, no significant difference in



**FIGURE 4.** Mean probability ( $\pm 95\%$  confidence interval) of reusing an old cavity for the first nest of the season depending on whether groups experienced no breeder turnover from the prior year (“None”), a turnover in male breeders (“Male”), a turnover in female breeders (“Female”), or a turnover of both sexes (“Both”). Comparisons by a generalized mixed model with binomial errors including year and cavity as random factors; effect sizes compared to no turnover: male turnovers:  $-1.24 \pm 0.43$ ,  $z = -2.86$ ,  $P = 0.004$ ; female turnovers:  $-0.64 \pm 0.29$ ,  $z = -2.22$ ,  $P = 0.03$ ; turnovers of both males and females:  $-1.11 \pm 0.25$ ,  $z = -4.47$ ,  $P < 0.001$ ).

the reproductive success of the experimental groups compared to the a priori chosen control groups (paired Wilcoxon signed-rank test,  $P = 0.40$ ).

## DISCUSSION

We detected no significant fitness consequences of cavity reuse: reproductive success was unaffected by cavity age or reuse, and groups reusing cavities failed to nest earlier, have larger clutches, or experience enhanced fledging success either per nest or per season (Table 1). Reuse of a cavity was more likely if a group successfully fledged young from that cavity the prior year, but reuse of such cavities did not result in a higher probability of success the subsequent year compared to using a new cavity or reusing a different cavity.

If cavity reuse entails no significant fitness costs or benefits, what determines the degree of cavity reuse? The answer appears to be constraints—both constraints on reusing old cavities and on new cavity construction.

The first constraint is straightforward: the fact that cavities fall apart or otherwise become unusable forces groups to construct new cavities as a hedge against the possibility—about 1 in 7—that a cavity they are currently using will no longer be available the following season. This puts an upper limit on the potential for reuse of the same cavity from one year to the next at 86.7%, lower (80.7%) if the cavity is in a dead limb. A slightly higher, but still comparable, value for nest cavity survivorship (89%) was

found for Northern Flickers in British Columbia nesting primarily in trembling aspen (*Populus tremuloides*; Wiebe 2001, 2017).

The difference between these maximum reuse values and the observed frequency of cavity reuse of 57.2% is apparently due to bet-hedging: most groups do not have more than a small number of useable cavities at any one time, and thus the cost to a group of losing a cavity is almost certainly higher than the cost of making a new cavity and having an extra available if needed. Furthermore, Acorn Woodpeckers roost in cavities throughout the year, sometimes together as a group, but often divided among two or more cavities (W. Koenig and E. Walters, personal observations). The use of cavities throughout the year puts an even greater premium on excavating new cavities to replace old ones that become unusable for whatever reason.

Multiple lines of evidence supported a role for constraints on new cavity construction (Table 1). These included the finding that reuse was more frequent among re-nest and second nest attempts than first nests, reuse was more likely following poor acorn crops, reuse was more frequent in cavities built-in living limbs, and groups frequently used artificial cavities when they were provided. The results of two predictions did not support constraints: cavity reuse was less, rather than more, frequent among smaller groups and among groups experiencing turnovers in breeder composition (Figure 4). Also, providing artificial cavities to groups did not significantly enhance reproductive success, although the sample size was small.

Overall, however, the hypothesis that the incidence of cavity reuse in this population is influenced by constraints on cavity reuse and new cavity construction was supported. Groups frequently reuse cavities—even artificial cavities—when they are available. Conversely, they appear to construct and use new cavities as a hedge against the possibility that previously used cavities will not be available the next year. When conditions are poor, such as following a small acorn crop, birds are probably in poorer condition and more likely to reuse an old cavity rather than devote the time necessary to construct a new one.

A meta-analysis by Wiebe et al. (2007) comparing 14 populations of 10 cavity-excavating species found a tendency for nests in reused cavities to have earlier laying dates and larger clutches. These differences were not statistically significant, but a more extensive analysis of Northern Flickers confirmed that birds reusing cavities initiated their nests earlier and laid larger clutches than those excavating new cavities (Wiebe 2014). Despite these fitness advantages, time constraints were still an important influence on cavity reuse, as Northern Flickers, a migratory species, frequently reused cavities when they were available and tended to excavate new cavities only when necessary (Wiebe 2017).

In terms of predation, nest predation among excavating species appears to be more strongly related to the structural qualities of cavities—the substrate in which they are built—than age or reuse of the cavity (Wiebe et al. 2007). A notable exception, however, is the Black Woodpecker (*Dryocopus martius*), in which clutch size does not seem to vary between new and reused cavities but fledging success does. In one study, fledgling success was significantly greater in reused cavities (Kosiński and Walczak 2019), but in a second study, success was significantly greater in new cavities as a result of differential depredation of old nests by pine martens (*Martes martes*; Nilsson et al. 1991), a species that is known to revisit, and presumably remember the location, of nests from year to year (Sonerud 1985). Such depredation of Acorn Woodpecker nests by mammalian predators is rare at our study site.

Woodpecker species do not use nest material. This, combined with the observation that Acorn Woodpeckers generally excavate the bottom of cavities prior to nest reuse (W. Koenig and E. Walters, personal observation), suggests that parasite loads are likely to be at most small, even in cavities reused multiple times. Northern Flickers in British Columbia are regularly parasitized by the blood-sucking fly *Carnus hemapterus*; nonetheless, an experimental study of the effect of parasites on nesting success found no significant fitness effects (Wiebe 2009). In contrast, we have rarely noted any significant parasitism on nestling Acorn Woodpeckers in our population, making the probability of effects of nest parasite loads in this population even smaller.

Wiebe et al. (2007) proposed two hypotheses for why facultative excavating species reuse nest cavities: a limited supply of suitable substrates or because reuse is more profitable than excavation because of savings in time or energy. There is no evidence to support the hypothesis that substrates for cavity construction are limited for Acorn Woodpeckers: nest cavities at our study site have been built in limbs ranging from 13 to 116 cm in diameter, which are abundant. Instead, what appears to be the more important factor driving cavity reuse is the cost of new cavity excavation (Hooge et al. 1999). In addition, our results emphasize the constraint on cavity reuse inevitably resulting from the probability of cavities being destroyed or usurped prior to the next time they are needed. No doubt this latter constraint varies considerably among tree species and habitats and is likely to play a significant role in affecting the wide range among and within species in the incidence of cavity reuse (Wiebe et al. 2006).

In summary, Acorn Woodpeckers reuse cavities regularly; yet, there appear to be no significant fitness costs or benefits of cavity reuse compared to nesting in newly constructed cavities. Instead, constraints on both old cavity reuse due to cavity loss or usurpation and on new cavity construction appear to be the main driving forces determining



the incidence of cavity reuse. Acorn Woodpeckers live in cooperatively breeding groups and have excellent excavating abilities as evidenced by the thousands of holes they drill for acorn storage. Nonetheless, they are limited by the costs of new cavity excavation, although those costs do not have a detectable effect on the clutch size or reproductive success. Such constraints may play a significant role in cavity reuse, affecting both the intraspecific and interspecific incidence of cavity reuse among facultatively excavating species.

## ACKNOWLEDGMENTS

We thank the reviewers and Karen Wiebe for comments, Joey Haydock and Mark Stanback for contributing nest site data, and the 162 field assistants that have assisted with the project since 1979.

**Funding statement:** Financial support for E.M.H. and D.J.W. came from the National Science Foundation (NSF) REU grants; general support for the project came from NSF grants IOS-1455881/IOS-1455900 and DEB-1256394.

**Ethics statement:** All applicable institutional guidelines for the care and use of animals were followed. The authors declare there are no competing interests.

**Author contributions:** W.D.K. and E.L.W. designed the study. All authors participated in data collection. W.D.K., E.M.H., and D.J.W. performed the analyses. Initial drafts were written by E.M.H. and D.J.W.; subsequent drafts were written by W.D.K. All authors helped revise the final manuscript.

**Data deposits:** Analyses reported in this article can be reproduced using the data provided by [Koenig et al. \(2021\)](#).

## LITERATURE CITED

- Barclay, R. M. R. (1988). Variation in the costs, benefits, and frequency of nest reuse by Barn Swallows (*Hirundo rustica*). *The Auk* 105:53–60.
- Barve, S., A. S. Lahey, R. M. Brunner, W. D. Koenig, and E. L. Walters. (2020). Tracking the warriors and spectators of Acorn Woodpecker wars. *Current Biology* 30:R982–R983.
- Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software* 67:1–48.
- Beissinger, S. R., and J. R. Waltman (1991). Extraordinary clutch size and hatching asynchrony of a Neotropical parrot. *The Auk* 108:863–871.
- Clark, L., and J. R. Mason. (1985). Use of nest material as insecticidal and anti-pathogenic agents by the European Starling. *Oecologia* 67:169–176.
- Cockle, K. L., K. Martin, and T. Wesołowski (2011). Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Frontiers in Ecology and the Environment* 9:377–382.
- Conrad, K. F., and R. J. Robertson (1993). Patterns of parental provisioning in Eastern Phoebe. *The Condor* 95:57–62.
- Copeyon, C. K., J. R. Walters, and J. H. Carter III (1991). Induction of Red-cockaded Woodpecker group formation by artificial cavity construction. *The Journal of Wildlife Management* 55:549–556.
- Du Plessis, M. A., W. W. Weathers, and W. D. Koenig (1994). Energetic benefits of communal roosting by Acorn Woodpeckers during the non-breeding season. *The Condor* 96:631–637.
- Griffin, J. R. (1974). Botanical resources of the hastings reservation, Monterey County, California. *Madrone* 22:329–332.
- Hannon, S. J., R. L. Mumme, W. D. Koenig, and F. A. Pitelka. (1985). Replacement of breeders and within-group conflict in the cooperatively breeding Acorn Woodpecker. *Behavioral Ecology & Sociobiology* 17:303–312.
- Hannon, S. J., R. L. Mumme, W. D. Koenig, S. Spon, and F. A. Pitelka (1987). Poor acorn crop, dominance, and decline in numbers of Acorn Woodpeckers. *Journal of Animal Ecology* 56:197–207.
- Hauber, M. E. (2002). Is reduced clutch size a cost of parental care in Eastern Phoebe (*Sayornis phoebe*)? *Behavioral Ecology and Sociobiology* 51:503–509.
- Hooge, P. N., M. T. Stanback, and W. D. Koenig (1999). Nest-site selection in the Acorn Woodpecker. *The Auk* 116:45–54.
- Koenig, W. D. (1981a). Space competition in the Acorn Woodpecker: power struggles in a cooperative breeder. *Animal Behaviour* 29:396–409.
- Koenig, W. D. (1981b). Reproductive success, group size, and the evolution of cooperative breeding in the Acorn Woodpecker. *The American Naturalist* 117:421–443.
- Koenig, W. D., and R. L. Mumme (1987). *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton University Press, Princeton, NJ, USA.
- Koenig, W. D., and J. T. Stahl (2007). Late summer and fall nesting in the Acorn Woodpecker and other North American terrestrial birds. *The Condor* 109:334–350.
- Koenig, W. D., and E. L. Walters (2014). What we don't know, and what needs to be known, about the cooperatively breeding Acorn Woodpecker *Melanerpes formicivorus*. *Acta Ornithologica* 49:221–232.
- Koenig, W. D., and E. L. Walters (2018). Causes of seasonal decline in reproduction of the cooperatively-breeding Acorn Woodpecker. *Journal of Avian Biology* 49:e01784.
- Koenig, W. D., E. M. Hallock, D. J. Weber, and E. L. Walters (2021). Data from: nest cavity reuse by the cooperatively breeding Acorn Woodpecker. *Ornithology* 138:1–10. doi:[10.5061/dryad.gtht76hk8](#)
- Koenig, W. D., J. M. H. Knops, W. J. Carmen, M. T. Stanback, and R. L. Mumme (1994b). Estimating acorn crops using visual surveys. *Canadian Journal of Forest Research* 24:2105–2112.
- Koenig, W. D., R. L. Mumme, W. J. Carmen, and M. T. Stanback. (1994a). Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75:99–109.
- Koenig, W. D., R. L. Mumme, and F. A. Pitelka (1984). The breeding system of the Acorn Woodpecker in central coastal California. *Zeitschrift für Tierpsychologie* 65:289–308.
- Koenig, W. D., R. L. Mumme, M. T. Stanback, and F. A. Pitelka (1995). Patterns and consequences of egg destruction among joint-nesting Acorn Woodpeckers. *Animal Behaviour* 50:607–621.
- Koenig, W. D., D. J. Schaefer, S. Mambelli, and T. E. Dawson (2008). Acorns, insects, and the diet of adult versus nestling Acorn Woodpeckers. *Journal of Field Ornithology* 79:280–285.

- Koenig, W. D., E. L. Walters, and J. Haydock. (2011). Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. *The American Naturalist* 178:145–158.
- Koenig, W. D., E. L. Walters, and J. Haydock (2016). Acorn Woodpeckers: helping at the nest, polygynandry, and dependence on a variable acorn crop. In *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior* (W. D. Koenig and J. L. Dickinson, Editors). Cambridge University Press, Cambridge, UK. pp. 217–236.
- Koenig, W. D., E. L. Walters, J. M. H. Knops, and W. J. Carmen (2015). Acorns and Acorn Woodpeckers: ups and downs in a long-term relationship. In *Proceedings of the 7th California Oak Symposium: Managing Oak Woodlands in a Dynamic World* (R. B. Standiford and K. L. Purcell, Technical Coordinators). Pacific SW Forest & Range Experiment Station General Technical Report PSW-GTR-251, Berkeley, CA, USA. pp. 23–33.
- Koenig, W. D., E. L. Walters, P. B. Stacey, M. T. Stanback, and R. L. Mumme (2020). Acorn Woodpecker (*Melanerpes formicivorus*), version 1.0. In *Birds of the World* (P. G. Rodewald and B. K. Keeney, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Kosiński, Z., and Ł. Walczak (2019). Does cavity reuse affect timing of reproduction and fledging success in the Black Woodpecker? *Journal of Ornithology* 160:79–89.
- Lack, D. (1947). The significance of clutch size. *Ibis* 89:302–352.
- MacRoberts, M. H., and B. R. MacRoberts (1976). Social organization and behavior of the Acorn Woodpecker in central coastal California. *Ornithological Monographs*, no. 21. American Ornithologists' Union, Washington, D.C., USA.
- Mainwaring, M. C., and I. R. Hartley (2013). The energetic costs of nest building in birds. *Avian Biology Research* 6:12–17.
- Martin, T. E. (1993). Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities? *The American Naturalist* 142:937–946.
- Moreno, J., E. Lobato, S. González-Braojos, and R. Ruiz-de Casteñeda (2010). Nest construction costs affect nestling growth: a field experiment in a cavity-nesting passerine. *Acta Ornithologica* 45:139–145.
- Mumme, R. L., W. D. Koenig, and F. A. Pitelka. (1983). Reproductive competition in the communal Acorn Woodpecker: sisters destroy each other's eggs. *Nature* 306:583–584.
- Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* 70:265–276.
- Newton, I. (1998). *Population Limitation in Birds*. Academic Press, San Diego, CA, USA.
- Nilsson, S. G., K. Johnsson, and M. Tjernberg. (1991). Is avoidance by Black Woodpeckers of old nest holes due to predators? *Animal Behaviour* 41:439–441.
- Otterbeck, A., V. Selås, J. Tøttrup Nielsen, É. Roualet, and A. Lindén. (2019). The paradox of nest reuse: early breeding benefits reproduction, but nest reuse increases nest predation risk. *Oecologia* 190:559–568.
- R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical computing, Vienna, Austria.
- Rowe, L., D. Ludwig, and D. Schluter. (1994). Time, condition, and the seasonal decline of avian clutch size. *The American Naturalist* 143:698–722.
- Sonerud, G. A. (1985). Nest hole shift in Tengmalm's Owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. *Journal of Animal Ecology* 54:179–192
- Therneau, T. M., and P. M. Grambsch (2000). *Modeling Survival Data: Extending the Cox Model*. Springer, New York, NY, USA.
- Tomás, G., S. Merino, J. Moreno, and J. Morales (2007). Consequences of nest reuse for parasite burden and female health and condition in Blue Tits, *Cyanistes caeruleus*. *Animal Behaviour* 73:805–814.
- Walters, E. L., and E. H. Miller (2001). Predation on nesting woodpeckers in British Columbia. *Canadian Field-Naturalist* 115:413–419.
- Weathers, W. W., W. D. Koenig, and M. T. Stanback (1990). Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. *The Condor* 92:341–359.
- Wiebe, K. L. (2001). Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? *The Auk* 118:412–421.
- Wiebe, K. L. (2009). Nest excavation does not reduce harmful effects of ectoparasitism: an experiment with a woodpecker, the Northern Flicker *Colaptes auratus*. *Journal of Avian Biology* 40:166–172.
- Wiebe, K. L. (2011). Nest sites as limiting resources for cavity-nesting birds in mature forest ecosystems: a review of the evidence. *Journal of Field Ornithology* 82:239–248.
- Wiebe, K. L. (2014). Responses of cavity-nesting birds to fire: testing a general model with data from the Northern Flicker. *Ecology* 95:2537–2547.
- Wiebe, K. L. (2017). Northern Flickers only work when they have to: how individual traits, population size and landscape disturbances affect excavation rates of an ecosystem engineer. *Journal of Avian Biology* 48:431–438.
- Wiebe, K. L., K. L. Cockle, M. K. Trzcinski, A. B. Edworthy, and K. Martin (2020). Gaps and runs in nest cavity occupancy: cavity “destroyers” and “cleaners” affect reuse by secondary cavity nesting vertebrates. *Frontiers in Ecology and Evolution* 8:205.
- Wiebe, K. L., W. D. Koenig, and K. Martin (2006). Evolution of clutch size in cavity-excavating birds: the nest site limitation hypothesis revisited. *The American Naturalist* 167:343–353.
- Wiebe, K. L., W. D. Koenig, and K. Martin (2007). Costs and benefits of nest reuse versus excavation in cavity-nesting birds. *Annales Zoologici Fennici* 44:209–217.