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The Evolution of Using Shed Snake Skin in Bird Nests

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ABSTRACT: Many species of birds use shed snake skin in nest construction, but this behavior remains poorly understood. Ecological context is likely key for understanding how this unusual, but widespread, behavior evolved. We use comparative and experimental approaches to suggest that the evolution of this behavior is mediated by nest morphology and predator communities. First, we reviewed the literature and found that 78 species from 22 families have been reported to use shed snake skin in nest construction. All but one of these species are passerines and, using comparative analyses, we show that this behavior is disproportionately observed in cavity-nesting species. Second, we examined a subsample of North American species, all of which are reported to use snake skin in nest construction, to see whether the proportion of nests with snake skin differs between cavity- and open cup–nesting species. This analysis suggested that the proportion of nests with snake skin is roughly 6.5 times higher in cavity- than in open cup–nesting species. Finally, we used a series of experiments and comparisons to test four hypotheses whereby snake skin could award fitness benefits (nest predation, nest microbiotas, nest ectoparasites, social signaling) and found support for the predation hypothesis. Snake skin reduced nest predation in cavity, but not open cup, nests. These unequal fitness benefits highlight different ecological conditions between nest morphologies and likely explains why, across species, cavity-nesting birds show this behavior more frequently than open cup–nesting birds.

Keywords: bird nest, shed snake skin, nest predation, cavity nests, nest morphology.

Introduction

Ecological context is central for understanding patterns in trait evolution. For example, contrasting rates of predation favor different life histories (Reznick and Endler 1982), climate variables shape physiological and morphological traits across a diversity of taxa (Thuiller et al. 2004; Youngflesh et al. 2022), and geographic variation in species interactions can influence trait evolution and coevolutionary dynamics between species (Thompson 2005; Mackin et al. 2021). These examples highlight the inextricable role of ecological context in trait evolution. Here, we examine a unique and poorly understood breeding behavior of birds—the use of shed snake skin in nest construction—and suggest that the evolution of this behavior is influenced by two important ecological contexts: nest morphology and the community of nest predators.

Bird nests are spectacularly diverse, from the shallow depressions scraped into the ground by many shorebirds (family: Charadriidae), to the delicate, lichen-encrusted open cup nests of many hummingbirds (family: Trochilidae), to the skillfully woven basket nests hanging from the tips of tree branches, characteristic of many weavers (genus: *Ploceus*; Hansell 2000, 2005). These different nest morphologies and placements create different ecological contexts for breeding birds by changing the strength of interactions with biotic and abiotic variables. For example, open cup nests experience higher rates of nest predation (Lack 1968; Ricklefs 1969; Martin and Li 1992) and usually interact with a different nest predator community compared with cavity nests (Remeš 2005; Czeszczewik et al. 2008; Degregorio et al. 2016). Contrasts in ecological contexts, such as different rates of nest predation between nest morphologies, likely plays a key role in shaping nest building and breeding behaviors, such as parental activity around nest sites (Martin et al. 2000; Fontaine and Martin 2006), time allocated to nest building (Rohwer et al. 2015), nest placement (Martin 1988, 1993), or the materials used to construct the nest (Schuetz 2005; Liu and Liang 2021).

Perhaps because of the variability in nest morphologies, placements, and environmental conditions during

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breeding, the context-dependent fitness benefits of many nesting materials remain unclear (Mainwaring et al. 2014; Deeming and Mainwaring 2015). A specific nesting material may award fitness benefits in some nest morphologies, breeding sites, or seasons while offering no fitness advantages in others (e.g., Dubiec et al. 2013; Liu et al. 2023). Uncertainty in the function of nesting materials is further compounded by multiple selective pressures (sexual vs. natural) operating on nest material choice (Clark and Mason 1985; Tomás et al. 2013) or if materials create trade-offs in metrics of reproductive success (Suárez-Rodríguez et al. 2014). Additionally, long-held views about the function of some nest-building behaviors can delay tests of alternative hypotheses (for an example that provides a novel view to a long-standing idea about nest morphologies, see Martin et al. 2017).

We examine a poorly understood breeding behavior of birds—the use of shed snake skin in nest construction—and suggest that the evolution of this behavior is mediated by nest morphology and predator communities. The materials used in nest construction affect conditions experienced by eggs, nestlings, and incubating parents (Hansel 2000; Deeming and Reynolds 2015). Moreover, some nesting materials are thought to signal individual quality and change parental investment in reproduction (Sergio et al. 2011; Moreno 2012). Thus, selection should favor an ability to gather materials that increase reproductive success. Surprisingly, the function of many nesting materials remains poorly understood (e.g., spider egg sacs [McCabe 1965], lichens [Hansell 1996], horse hair fungus [Aubrecht et al. 2013], wild rosemary [Rohwer et al. 2017], tree fern scales [Greeney and Halupka 2008]). For many of these materials, their availability in the landscape is uneven. This suggests that birds invest time and energy to find and gather them, that these materials are not selected at random, and that selection favors their use.

Observations of shed snake skin in bird nests have a long history, but the function of this material remains elusive. Early ideas suggested that snake skin reduced nest predation primarily from snake and lizard predators (Hume 1889; Bolles 1890; Finn 1919; Wittle 1927), by startling or repelling potential nest predators through visual or olfactory cues. Later, this predation hypothesis was questioned by observations that birds appeared to use snake skins indiscriminately (Suthard 1927; Wittle 1927) and by speculations that fragments of snake skins seemed ineffective at deterring even the smallest of predators (Skutch 1945). Throughout this early literature is the repeated anecdote that cavity-nesting species use shed snake skin more often than open cup–nesting species (Hume 1889; Finn 1919; Strecker 1926; Skutch 1945), although tests of this idea are still missing. More recently, the antipredation role of shed snake skin has received conflicting support. Shed snake skin has been reported to reduce predation in cavity nests (Medlin and Risch 2006; Liu and Liang 2021; Liu et al. 2023) but not in open cup nests (Trnka and Prokop 2011), suggesting that the efficacy of snake skin may depend on nest type or breeding location (Liu et al. 2023) or serve multiple functions beyond mitigating nest predation risk (Trnka and Prokop 2011; Liu et al. 2021). This history of research highlights how few hypotheses besides nest predation have been considered when thinking about the function of shed snake skin in bird nests. For example, snake skin may function as a signal of individual quality, offer chemical compounds to mediate interactions with microbial communities or ectoparasites in nests, or offer no fitness benefits in some ecological contexts. Regardless, the anecdotes from the early literature and conflicting evidence from recent studies suggest that the fitness benefits of shed snake skin may be most pronounced in cavity compared with open cup nests. If so, then the evolution of this behavior may be mediated, in part, by nest type.

We examined the role of shed snake skin in bird nests, using both comparative and experimental approaches. First, we reviewed the literature to explore evolutionary patterns in the use of shed snake skin in bird nests and to test a long-speculated assumption that snake skin is more frequently reported in cavity-nesting than in noncavity-nesting species. Because this comparative approach only considers whether a species has been reported to use shed snake skin in nest construction, we further explored intraspecific variation in the proportion of nests that contain snake skin, using a subset of North American species, all of which have been reported to use snake skin in nest construction. If selection has favored the use of snake skin in cavity nesters, more so than in open cup nesters, then we predicted that (i) across the avian phylogeny, there should be an association between cavity-nesting species and the use of snake skin in nest construction, and (ii) among species reported to use shed snake skin in their nests, a higher proportion of nests will contain snake skin in cavity- compared with open cup–nesting species.

Next, we used a series of experimental approaches and comparisons of existing data to explore four hypotheses (predation, ectoparasites, nest microbial communities, social signaling) that might favor the use of shed snake skin in nest construction. For these hypotheses, we predicted that the addition of shed snake skin would (i) reduce nest predation, (ii) reduce the total number or diversity of ectoparasites within nests, or (iii) alter nest microbial communities in ways that reduce the likelihood of pathogenic strains impacting eggs, young, or incubating parents. For the social signaling hypothesis, we predicted increased clutch sizes in nests containing snake skin but note that this could be the result of increased parental quality or increased parental investment because of potential benefits of any of the other processes occurring above (e.g., parents investing more in nests that are less likely to fail due to reduced risk of predation). If the fitness benefits of shed snake skin are higher in cavity compared with open cup nests, we predicted that any effects of shed snake skin in these experiments should be most detectable in cavity compared with open cup nests and help explain the evolutionary patterns observed in our comparative data.

Methods

Comparative Data of Shed Snake Skin in Bird Nests

We searched the Birds of the World database (Billerman et al. 2020) to find species that use shed snake skin in nest construction using the following search terms: "snake skin," "snakeskin," and "reptile skin." We searched the literature (primarily through Google Scholar) using the same search terms, coupled with "bird nests" and "bird nest." Finally, we searched the references within articles investigating shed snake skins in bird nests. For all species reported to use shed snake or reptile skin in nest construction, we recorded the following information: the type of nest constructed (e.g., open cup, dome, cavity; following nest categories of Hansell 2000), placement of the skin within the nest (i.e., inner vs. outer nest walls where snake skin either does or does not contact eggs, young, and incubating parents), and, if provided in the accounts, information about which member of the pair was responsible for nest construction or for finding and bringing shed snake skin to the nest (see the data file fromVanya23Mar2023.csv in the Dryad Digital Repository at https://doi.org/10.5061/dryad.hdr7sqvpq; Rohwer et al. 2024). For species reported to use shed snake skin in nest construction, categorizing nest morphology was straightforward, as we did not encounter any ambiguous or intraspecific variation in nest morphologies. We attribute this to the majority of these species being fairly well studied and/or relatively stereotyped in their nest-building behaviors and final nest morphology. Regardless, this was a challenging dataset to assemble, both because many bird nests are either unknown or poorly described (Sheard et al. 2023) and because snake skin use is a trait that can show intraspecific variation (or fail to be noticed by observers); the absence of a species from the list of those that use snake skin does not mean that species lacks the trait. We describe methods of handling this uncertainty below but note that the bias likely runs counter to our prediction. That is, we predicted that snake skin use is associated with cavity nests. These nests, however, are more difficult for human observers to access, and thus it seems likely that a greater proportion of cavity nesters unknowingly use snake skin than do open cup nesters.

To identify potential gains and losses over evolutionary time in the use of shed snake skin in bird nests, we used a maximum clade credibility phylogeny created from a set of possible trees from https://birdtree.org (Jetz et al. 2012). We used the Hackett backbone (Hackett et al. 2008) and a set of taxonomically complete phylogenies to create this maximum clade credibility tree. Our results remained qualitatively unchanged when we experimented with alternative topologies obtained from the Open Tree of Life project (McTavish et al. 2021). We implemented two methods of ancestral state reconstruction to quantify the evolutionary dynamics of snake skin use in birds. The first was an Mk model (Pagel 1994), implemented in R (R Core Team 2022) using the castor package (Louca and Pennell 2020), which allows for uncertainty in the tip states. To derive these measures of uncertainty, we did the following. First, for non-snake-skin-using species, we used the length of each breeding account (i.e., number of words) in the Birds of the World (Billerman et al. 2020) as a proxy of how well studied that species' breeding biology is. We took the natural logarithm of account length to derive a normal distribution, then scaled these values from 0.5 to 1. These values became the measure of certainty in the tip state, such that species with the shortest breeding accounts were essentially an even split between not using and using snake skin. Second, for species in the Jetz et al. (2012) taxonomy that we could not readily match to accounts in Birds of the World, we set their probability of being in the non-snake-skin-using state to the mean (0.78) of the other such species. Last, for all species reported to use snake skin in their nest, we set the probability of being in that state to 0.99.

Our second ancestral state reconstruction approach was a precursor model (Marazzi et al. 2012), implemented in the corHMM package (Boyko and Beaulieu 2021) in R. Here, shifts to the state of using snake skin are permitted only once a precursor trait has originated (and only one shift in state is allowed per branch). The variable of interest in this model then becomes the hidden precursor state. Because non-snake-skin-using species can still be inferred to possess the precursor trait reflecting, for example, poorly studied species that are related to species known to use snake skin, this approach offers another method to account for tip-level uncertainty in the use of snake skin.

To test whether the use of shed snake skin is associated with cavity nesting, we fitted a phylogenetic logistic regression (Ives and Garland 2020) in the package phylolm (Ho and Ane 2014) in R. This approach allows for analyses of binomial-dependent variables with either continuous or discrete independent variables when the residual variation in the dependent variable is phylogenetically correlated among species (Ives and Garland 2020). For our model, the dependent variable was the presence/absence of snake skin in nest construction, and the independent variable was nest type. We used data from van der Hoek et al. (2017) to identify cavity-nesting species. Van der Hoek et al. (2017) defined a cavity nest as one that a bird can enter and descend or move laterally such that it is not visible from the outside. This dataset assigned cavity nesters as species that nest in tree, cactus, and palm cavities; tree knotholes; or hollow stumps, but not tunnels excavated in earthen banks. For species showing variability in nest descriptions, at least one description had to be within a tree/cactus/palm cavity to be considered a cavity nester. Because this dataset only contains information on whether a species is a cavity nester, our independent variable was simply whether a species nested in cavities or not; all other nest types, including open cup, dome, and so on, were lumped as "noncavity." Here, to account for uncertainty in our knowledge of snake skin use, we flipped the state of 12 non-snake-skin users (equivalent to adding 20% more positive classes to the regression model) by multiplying 1 minus the species' prior, described above, by its inverse of the average phylogenetic distance to all other snake skin users and using the resulting product as a probability vector when sampling species from the potential pool of those to flip. Thus, poorly known species and species related to those that are known to use snake skin are the ones with the best chance of being shifted into the positive, snake-skin-using class. We repeated this process 100 times, each time saving the coefficient of the relationship between snake skin use and cavity nesting and the P value of this variable from the model.

Proportion of Nests with Shed Snake Skin

We used digitized nest record cards from the Western Foundation of Vertebrate Zoology (https://collections.wfvz.org/) to evaluate the proportion of nests, within a species, that contained shed snake skin. We examined only species that had been reported to use shed snake skin from our comparative data above. For each species, we considered only cards that provided a verbal description of nesting materials (see examples in fig. S1; figs. S1–S16 are available online) and then calculated the per-species proportion of cards that mentioned the presence of shed snake or reptile skin in the nest description. We included species with at least 20 usable nest record cards, but all species included contained more than 100 nest record cards except one (Blue Grosbeak, *Passerina caerulea*), which had 28. The number of species with sufficient data for this analysis are modest ($n = 5$ species of cavity nesters, $n = 4$ species of open cup nesters), and for each species nest record cards come from across their breeding ranges.

These criteria rely on observers to notice shed snake skin in a nest and record it on the nest card, thus likely underestimating the proportion of nests within species that use shed snake skin. This potential bias is likely more pronounced in cavity-nesting species because nearly all cavity nests in this dataset come from natural cavities (not nest boxes) that are typically more difficult to access and describe the materials used in construction.

While data were normally distributed, we used Wilcoxon sign rank tests to account for small sample sizes and ANOVAs with phylogenetic controls implemented in R (R Core Team 2022) to evaluate differences between cavity and open cup nesters in the proportion of nests containing shed snake skins.

Experimental Procedures

All experimental procedures described below were performed near Ithaca, New York, from April to August 2021. Several species of birds that use shed snake skin in nest construction breed locally. For all experimental procedures we used shed snake skins acquired from local snake breeders. These sheds were dominated by corn snakes (*Pantherophis guttatus*) but also included some ball pythons (*Python regius*) and king snakes (*Lampropeltis* spp.); none of these species occur within the study site. While sheds from captive snakes have the potential to lack properties found in local sheds from wild snakes (i.e., scent may differ among captive vs. wild sheds), we note that sheds from both corn and king snakes are likely used by birds where these snakes occur. To our knowledge, no studies have quantified the types of snake skins used by birds relative to the diversity and abundance of snakes within a region.

Nest Microbiotas. Cup and cavity nests may differ in their nest microbiotas (Godard et al. 2007; Peralta-Sánchez et al. 2012; Campos-Cerda and Bohannan 2020), such that one nest type may be more affected by potentially pathogenic bacteria that affect eggs, young, or incubating parents or lack beneficial bacteria that help colonize the digestive tracts of young birds (Shawkey et al. 2009; Teyssier et al. 2018). Shed snake skin could ameliorate challenges associated with nest microbiotas through their emission of chemical compounds. We tested the hypotheses that (i) nest microbiotas differed consistently between cavity- and open cup–nesting species and (ii) that the addition of shed snake skin reduced the diversity of microbiota communities in bird nests. We tested these hypotheses using three approaches. First, we explored possible differences in nest microbiotas in a diversity ($n = 11$ passerine species) of active, unmanipulated cavity and open cup nests (table S1; tables S1–S24 are available online). We included a species if we were able to sample microbial communities from at least three different nests. All nests were sampled early in incubation (between days 1 and 3) to control for potential changes in microbiotas with incubation stage (Cook et al. 2005; Campos-Cerda and Bohannan 2020). This approach informed whether nest morphologies differed in microbial diversity and composition in ways that could exert consistent selection pressures between nest types, potentially explaining patterns across species in the use of shed snake skin. Our second approach explored how nest microbiotas might vary with nest placement within a single open cup–nesting species, American Robins (*Turdus migratorius*). We compared active, unmanipulated robin nests that were constructed in "unprotected" sites, which were located in shrubs or trees, with robin nests constructed in "protected" sites, which were found under bridges, porches, eaves of houses, and other sheltered sites. The logic here was that protected nests that were covered from above and from at least one side might provide an ecological setting more similar to cavity nests, providing insight into how nest placement might affect nest microbiotas while controlling for the species that built the nest. All robin nests were swabbed in early incubation, like our across-species approach described above. Our third approach experimentally tested whether the addition of shed snake skin influenced nest microbial diversity throughout the duration of incubation, using two species of cavity-nesting birds that have not been reported to use shed snake skin in nest construction: Tree Swallows (*Tachycineta bicolor*) and Eastern Bluebirds (*Sialia sialis*). We swabbed nest interiors in early incubation, between days 1 and 3, then added a piece of snake skin, 20–30 cm long, to half the nests while the other half received no snake skin. Snake skins were added to the nest interior adjacent to the eggs. We alternated treatments to account for nest microbiotas changing as the breeding season progressed. Finally, we swabbed nests again in late incubation (1–3 days prior to hatch) to test whether the presence of shed snake skin altered nest microbiota throughout the incubation period. For all approaches, we evaluated metrics of alpha (Shannon index and Faith's phylogenetic diversity) and beta (Bray-Curtis dissimilarity) diversity in microbial communities using 16S ribosomal RNA amplicon sequencing.

Nest Ectoparasites. We tested whether the addition of shed snake skin reduced the abundance or diversity of nest ectoparasites by collecting the Tree Swallow and Eastern Bluebird nests used in the microbiome analyses above. We hypothesized that shed snake skin could emit chemical compounds that either repelled adult parasites from depositing eggs or impeded the growth and development of larval parasites in nests supplemented with snake skin. We focused only on cavity nesters because our comparative data (see below) suggested that beneficial effects of shed snake skin should be most pronounced in cavity-nesting species. Only nests that survived until at least 4 days after hatching were included in analyses, as many nest ectoparasites rely on nestlings for blood meals and development (Bennett and Whitworth 1991). After a nest fledged or became inactive, we collected (within 1 week of fledging/inactivity), froze (−20°C), and then carefully dissected each nest. We counted the number and diversity (to the family level) of ectoparasites to evaluate possible differences in ectoparasite communities between nests with and without shed snake skin. We used generalized linear models in R (R Core Team 2022) with a negative binomial distribution to test whether the addition of shed snake skin reduced the number or diversity of ectoparasites within nests.

Social Signaling. Cavity nesters may be more likely to signal aspects of quality through the size or composition of their nests because cavity nests are typically more concealed than open cup nests. Thus, any increase in nest size or use of unique or conspicuous nesting material may be less constrained by nest predation (Moreno 2012). We explored whether shed snake skin in nests may signal individual quality and result in increased reproductive investments by parents (Soler et al. 2001; Moreno 2012) by comparing clutch size from nest record cards of the Western Foundation of Vertebrate Zoology. We predicted larger clutch sizes in nests with versus without snake skin. We tested this prediction in six species, all of which had a minimum of five nests in each category of with or without snake skin. We tested for differences in clutch size using Wilcoxon signed rank tests in all species, as clutch size data were not normally distributed. We emphasize that clutch size represents a single metric of reproductive investment from females only and ignores possible increases in reproductive investment from males. Thus, these data should be viewed as an exploratory analysis of this hypothesis.

Nest Predation. Cavity and open cup nests differ in their risk of nest predation, such that cavity nests are typically safer than open cup nests (Lack 1968; Ricklefs 1969; Martin and Li 1992). Moreover, cavity and open cup nests may be targeted by different nest predators (Thompson et al. 1999; Czeszczewik et al. 2008; Degregorio et al. 2016), making the effect of shed snake skin more pronounced in one nest type over another. We tested whether the addition of shed snake skin reduced the risk of predation in cavity and open cup nest morphologies using an artificial nest experiment. We used nest boxes as cavity nests and inactive American Robin nests as open cup nests. We emphasize that these experiments are meant to examine how shed snake skin might change the relative risk of predation between nest types and do not reflect predation risks of real nests.

We hung nest boxes 4–5 m high and placed inactive robin nests (open cup nests) at variable heights to ensure more realistic nest placement locations. Because inactive robin nests were salvaged from outside the study area, we relocated them to within our study site to control for potential variation in nest predator communities. We alternated the placement of open cup and cavity nests to control for spatial variation in predator communities and predation rates and alternated treatments so that nests with and without shed snake skin were evenly distributed across the study site. Nests were separated by at least 50 m. For both cavity and open cup nests, control treatments had a grass lining and received two Japanese quail eggs, and experimental treatments were identical to controls but supplemented with a piece of shed snake skin 20–30 cm long, a length commonly reported in nests of Great Crested Flycatchers (*Myiarchus crinitus*; Taylor and Kershner 1991). All nest boxes had 3.8-cm entrance hole diameters, and shed snake skin was placed inside the box, near the eggs but never obscuring them. We checked all nests at least once every 3 days for signs of predation, for a total trial period of 14 days, which is similar to the incubation period of many species at the study site. We considered a nest to have been depredated if any damage occurred to at least one egg; partial predation events (one egg damaged or missing) were classified as a depredated nest. Signs of predation included puncture holes through egg shells, broken eggs, missing eggs, and so on. Throughout the duration of the experiment (May and June 2021), we placed 30 motion-activated trail cameras to record nest predators and to examine differences in predator communities between open cup and cavity nests. Cameras were divided between nest type (15 with cavity nests, 15 with open cup nests) and were moved to other nests of the same category once a nest became depredated. We tested for differences in survival probabilities of nests with and without shed snake skin using Cox proportional hazards regression in the survival package (Therneau 2023) in R (R Core Team 2022).

Results

Comparative Data

We found 78 species of birds, spanning 22 families, that have been reported to use shed snake skin in nest construction (fig. 1; table 1; for species list, see the data file fromVanya23Mar2023.csv at https://doi.org/10.5061/dryad.hdr7sqvpq). Species reported to use shed snake skin are almost exclusively passerines. The one exception, Greater Roadrunner (*Geococcyx californianus*; family: Cuculidae), appears to rarely use snake skin (see fig. 2 and the supplemental PDF) and was omitted from our ancestral reconstruction analyses and our phylogenetic logistic regressions below. Passerines reported to use snake skin come from all major landmasses (Australia, Africa, the Americas, Europe, Asia) except Antarctica. We present the results of the Mk model of ancestral state reconstruction in the main text and present the results of the corHMM precursor model in the supplemental PDF. After accounting for uncertainty in our knowledge of nest materials and after allowing transition rates to vary between states (this model had a lower AICc [Akaike information criterion corrected for small sample sizes] score than one with equal or symmetric transition rates), the best supported model inferred that the ancestral bird did not use snake skin in its nest and that this behavior has originated 21 times (all within passerines) and been lost 130 times (fig. 1).

We found robust support for the long-speculated idea that cavity-nesting species use shed snake skin more often than non-cavity-nesting species (phylogenetic logistic regression: slope $= 1.98 \pm 0.34$ SE, $P < .001$, $\alpha = 0.21$ [95% confidence interval: 0.02–0.48], 100 bootstraps). Because the use of snake skin may be entirely lacking in nonpasserines, we reran this analysis using only passerines and recovered the same qualitative result, albeit with an even steeper slope—cavity nesters have a significantly elevated probability of using snake skin in their nests (slope $= 2.52 \pm 0.30$ SE). Because our question concerns the use of snake skin in bird nests in general, we focus on our results across all birds for the remainder of the article. The mean of the 100 simulated datasets where 20% more positive classes were added was 1.64 (±0.08), and the P values of all of these augmented relationships were below .001. Of the 78 species reported to use snake skin, nearly half are cavity nesters (~44%; 34 cavity, 44 noncavity), despite cavity-nesting species comprising only ~17% of the species in the Jetz et al. (2012) phylogeny (1,702 cavity, 8,291 other).

Cavity- and non-cavity-nesting species differ in where they place shed snake skin in the nest, but these differences are likely constrained by nest morphology. Cavity nesters typically place shed snake skin inside the cavity within the nest lining, such that snake skins are near or touching the eggs, young, or incubating parent (although skins occasionally extend beyond the entrance hole), whereas placement is less predictable in other nest types. Open cup nesters typically place shed snake skins in the exterior nest walls, away from the eggs and young, and species that construct dome/enclosed nest types place snake skins within the nest lining and outer nest walls. These differences in placement between cavity and noncavity nesters suggests that the fitness benefits of using shed snake skin do not require skins to be in direct contact with the eggs or young or that the optimal placement of shed snake skin differs between nest morphologies.

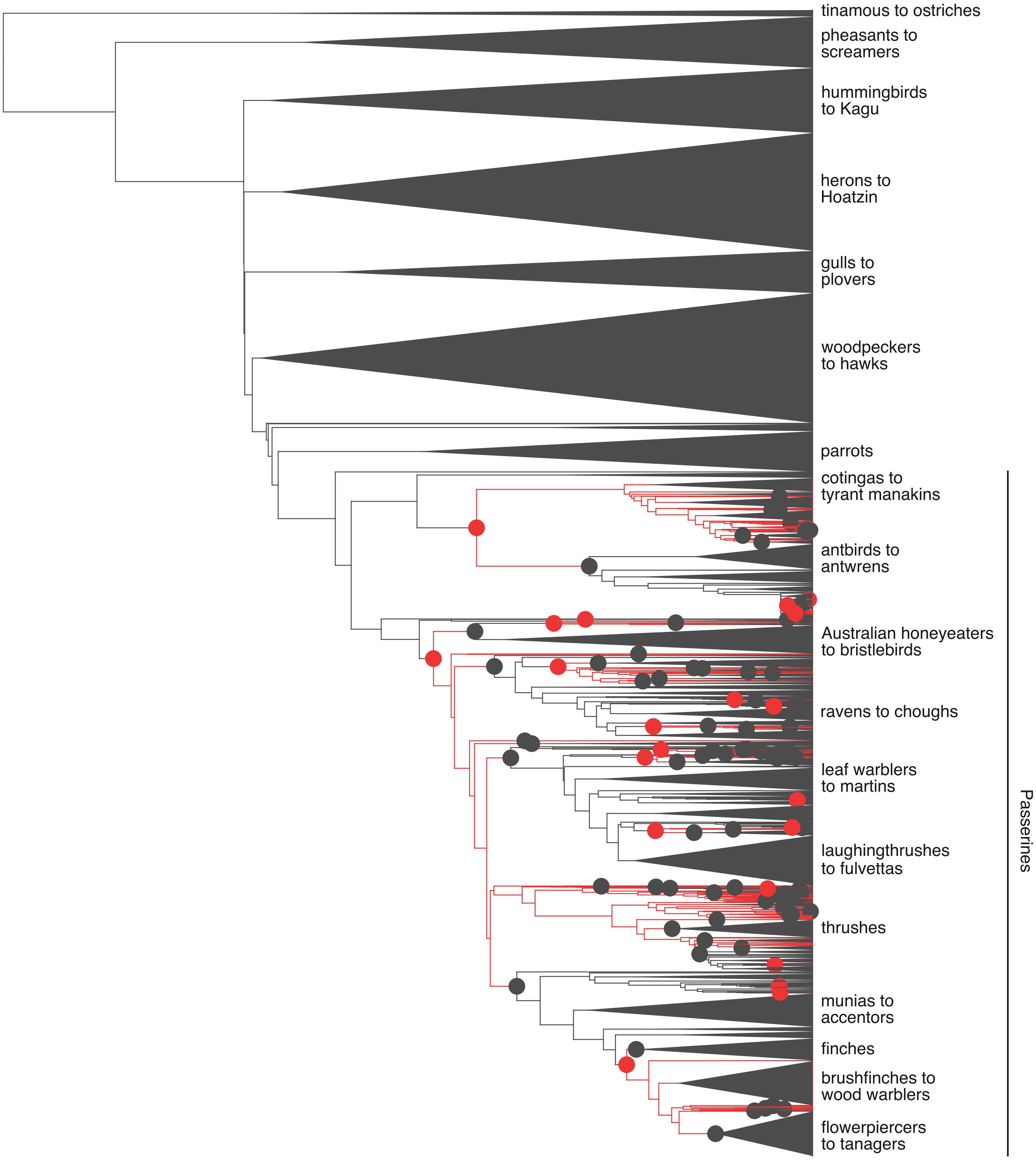

Figure 1: The use of shed snake skin in nest construction is overwhelmingly restricted to passerines and is disproportionately observed in cavity-nesting species. Red circles indicate suspected gains of this behavior; gray circles indicate suspected losses. Phylogeny labels are not comprehensive but are meant to orient readers; labels within the passerines highlight lineages where the use of shed snake skin remains largely unreported.

Table 1: Bird families ($n = 22$) reported to use shed snake skin in nest construction

Family	Species count	Fraction cavity nesters
Acrocephalidae	1	.00
Alaudidae	2	.00
Cardinalidae	5	.00
Climacteridae	1	1.00
Cuculidae	1	.00
Donacobiidae	1	.00
Estrildidae	1	.00
Furnariidae	13	.08
Laniidae	1	.00
Malaconotidae	2	.00
Maluridae	1	.00
Muscicapidae	7	.14
Nectariniidae	2	.00
Oriolidae	1	.00
Paradisaeidae	2	.00
Paridae	3	1.00
Pomatostomidae	1	.00
Pycnonotidae	1	.00
Sittidae	1	1.00
Sturnidae	9	.89
Troglodytidae	4	.75
Tyrannidae	18	.89

Note: "Species count" summarizes the number of species within each family reported to use snake or reptile skin in nest construction, and "fraction cavity nesters" summarizes the fraction of these species, per family, that nest in cavities.

Proportion of Nests with Shed Snake Skin

Nest record cards for a subset of nine species, all of which are reported to use shed snake skin in nest construction, revealed that the proportion of nests containing snake skin are, on average, 6.5 times higher in cavity than in open cup nesters (fig. 2). This analysis was limited to species for which sufficient nest record cards existed and shows phylogenetic nonindependence (without phylogenetic controls: Wilcoxon test $P < .060$; with phylogenetic controls: ANOVA $F = 4.82$, $P = .185$). Broadly, breeding ranges of cavity- and open cup–nesting species in this analysis overlap, so access to snake skins is unlikely to drive this pattern.

Experiments

We tested four hypotheses for the fitness benefits of incorporating shed snake skin in bird nests: predation, ectoparasites, microbiota, and social signaling. We found no support for the ectoparasite, microbiota, or social signaling hypotheses. Instead, our data supported the predation hypothesis (fig. 3), but only in cavity nests. Cavity nests that received shed snake skin were more likely to survive the 14-day trial period compared with cavity nests without snake skin (Cox regression: $z = -2.79$, $P = .005$). By contrast, open cup nests, both with and without snake skin, had similar survival probabilities (Cox regression: $z = -0.43$, $P = .672$; fig. 3); nest height had no effect on the survival of open cup nests (Cox regression: $z = 0.24$, $P = .813$). Our camera trap data revealed different predator communities between nest types (Fisher's exact test $P < .001$; table 2). Open cup nests were visited by both small mammal and avian nest predators, whereas cavity nests were visited only by small mammals. See the supplemental PDF for detailed results and statistical summaries of analyses exploring microbiome, ectoparasite, social signaling, and nest predation hypotheses.

Discussion

By combining comparative and experimental approaches, we provide new insights into the fitness benefits and ecological context favoring the use of shed snake skin in bird nests and the likely evolutionary history of this unique behavior. Shed snake skin was effective at reducing predation in cavity, but not open cup, nests (fig. 3). At our study site, the suite of nest predators visiting open cup nests was more diverse than the predator community visiting cavity nests, a pattern that seems robust across localities (Thompson and Burhans 2003; Remeš 2005; Czeszczewik et al. 2008;

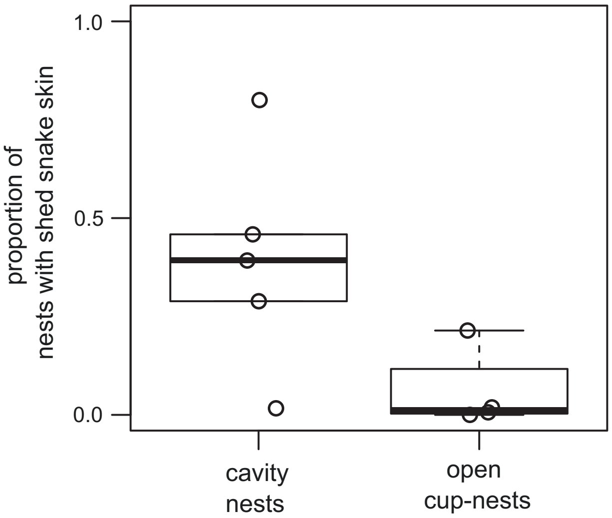

Figure 2: Among species reported to use shed snake skin in nest construction, the proportion of nests with snake skin is, on average, ~6.5 times higher in cavity- than in open cup–nesting species. Each circle represents a species. Cavity nesters include, from top to bottom, Great Crested Flycatcher, Bewick's Wren, Tufted Titmouse, House Wren, and Ash-throated Flycatcher. Open cup nesters include, from top to bottom, Blue Grosbeak, Northern Cardinal, Indigo Bunting, and Greater Roadrunner.

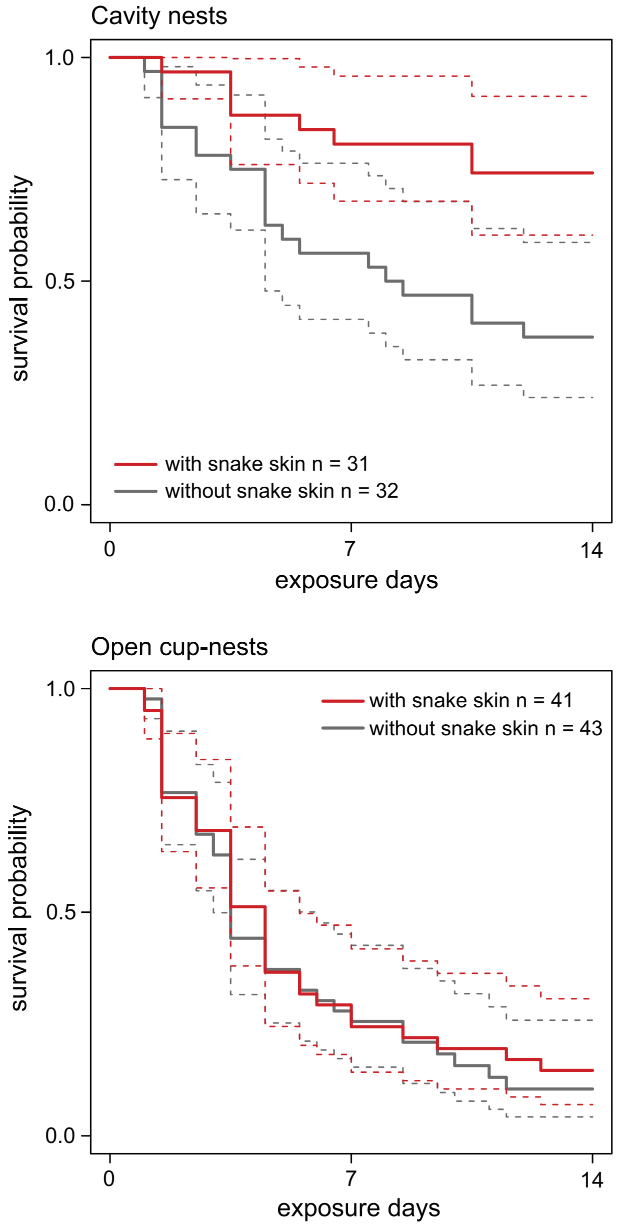

Figure 3: The presence of shed snake skin increased the probability of nest survival in artificial cavity, but not artificial open cup, nests. Dashed lines represent the 95% confidence interval around the averaged survival probability for each treatment.

Degregorio et al. 2016). Thus, shed snake skin appears effective at reducing predation from some, but not all, nest predators, and the efficacy of this material depends on nest type (i.e., cavity vs. open cup) and the associated community of nest predators. Similarly, across the avian phylogeny, the use of shed snake skin is almost exclusively observed in passerines, and within this lineage cavity nesters are disproportionately observed to use snake skin in nest construction (fig. 1). This finding supports a long-standing but until now untested supposition that cavity-nesting species use snake skin more often than open cup–nesting species. Moreover, that the proportion of nests containing snake skin was, on average, ~6.5 times higher in cavity than in open cup nesters (fig. 2) further suggests that the fitness benefits of using shed snake skin in nests may be higher in cavity- compared with open cup–nesting species.

Our finding that shed snake skin reduced nest predation in cavity but not open cup nests helps reconcile conflicting evidence from previous studies (snake skin reduced nest predation: Medlin and Risch 2006; Liu and Liang 2021; no effect of snake skin on predation: Trnka and Prokop 2011). This context-dependent effect of a nesting material suggests that these differences are driven by different nest predator communities. Cavity nests limit the diversity of predators to small-bodied species, many of which are routinely eaten by snakes (Reynolds and Scott 1982; Rodríquez-Robles 1998; Rodríquez-Robles et al. 1999) and are fearful of the sight or smell of shed snake skin in bird nests (Apfelbach et al. 2005; Borgo et al. 2006; Wang et al. 2018; Watanabe et al. 2022). This contrasts with nest predator communities of open cup–nesting birds, which are more diverse and often include predators that lack a strong evolutionary history of fearful interactions with snakes. The restricted predator community visiting cavity nests likely facilitates selection for reproductive behaviors, such as gathering shed snake skin, that mediate interactions with this narrower suite of nest predators. Remarkably, many species of cavity-nesting birds will hiss when disturbed at the nest, mimicking the sound of snakes, a behavior that likely evolved to frighten potential nest predators (Sibley 1955; Rowe et al. 1986; Zub et al. 2017; Møller et al. 2021). These contrasts in nest predator communities between cavity- and open cup–nesting species and the evolutionary history these predators have of interacting with snakes likely explains the unequal fitness benefits of snake skin between these two nest morphologies.

Our data offered no support for alternative hypotheses that shed snake skin changed nest microbial communities

Table 2: Nest predator communities

	Predator type	
	Bird	Small mammal
Cavity nests	0	11
Open cup nests	13	8

Note: Communities of nest predators differed between open cup and cavity nests, as recorded from motion-activated cameras or direct observations during nest checks. Bird predators included Blue Jays and American Crows; small mammal predators included northern/southern flying squirrels, eastern chipmunks, white-footed/deer mice, American red squirrels, and eastern gray squirrels.

or nest ectoparasite loads (see the supplemental PDF). While we did not test temperature or humidity hypotheses, shed snake skin seems unlikely to notably modify these conditions within the nest. In some contexts, shed snake skin may function as a social signal, as proposed by Trnka and Prokop (2011) and as observed in displays of at least two bowerbirds (Frith and Frith 2020*a*, 2020*b*). Some open cup–nesting species use remarkable quantities of shed snake skin (i.e., Black-capped Donacobius, *Donacobius atricapilla*; see photos in Almeida et al. 2014) or appear to incorporate shed snake skin into their nests reliably (i.e., Oriental Magpie-Robin, *Copsychus saularis*; Western Foundation of Vertebrate Zoology nest record cards), suggesting that this material is important, but its function—predator deterrent or otherwise—remains unknown. While snake skin has the potential to signal individual quality (Moreno 2012), this signal should influence the magnitude of reproductive investment of parents or the opportunity for extrapair copulations, as pair formation has already occurred in most passerines by the time nest construction begins. Generating predictions for which member of the pair should increase its reproductive investment in response to the addition of shed snake skin to the nest is difficult because data for which member of the pair (male, female, or both) contributes snake skin to the nest are rarely known (see the data file fromVanya23Mar2023.csv at https://doi.org/10.5061/dryad.hdr7sqvpq). Our nonexperimental exploration of this hypothesis revealed no differences in clutch sizes across six species between nests with and without snake skin. Similarly, Liu et al. (2021) reported no differences in egg size or mass, clutch size, number of young hatched, or nestling growth rates between nests with and without snake skin in a population of Crested Mynas in China. We look forward to further tests of shed snake skin in nests as a potential signal of individual quality.

How does shed snake skin reduce nest predation risk? The amount of snake skin used in nests, both within and across species, often varies from small fragments to long, intact sheds. These differences could be driven by the availability of materials or could suggest that even small amounts of shed snake skin are effective at reducing predation. Recent experimental work exploring how snake skin might reduce nest predation suggested that a nest predator, Swinhoe's striped squirrels (*Tamiops swinhoei*), used visual, not olfactory, cues (Liu and Liang 2021). Surprisingly, although the presence of snake skin reduced predation, predation rates seemed independent of the amount of shed snake skin added to nest boxes (Liu and Liang 2021). This work on a largely diurnal mammal suggests that the ecology of nest predators may inform what cues are most effective for reducing predation (Watanabe et al. 2022). If predators are nocturnal, olfactory cues may be equally effective, especially given low light conditions inside many cavities and the keen sense of smell that many nest predators possess (Kats and Dill 1998; Borgo et al. 2006). While shed snake skins surely emit odors (Clucas et al. 2008), missing from these ideas are dissipation rates of snake skin scent, links between the amount of snake skin within a nest and the associated snake odor of the nest, and additional tests of the cues different nest predators use (visual vs. olfactory).

Use of shed snake skin is almost exclusively observed in passerines. We suspect that the relatively enhanced cognitive capacities in passerines (Lefebvre et al. 2002, 2004), which presumably facilitated their diversification in nest morphologies (Collias 1997; Hall et al. 2013), has also facilitated the evolution of behaviors like recognizing shed snake skin and incorporating it into their nests. Still, several groups of passerines have not been reported to use shed snake skin in nest construction (fig. 1). Why this behavior evolves in some groups and not others is poorly known, but body size, nest placement, and nest morphology may offer some clues. Relatively larger birds (Turdidae, Corvidae, genus *Philemon*) probably defend their nest sufficiently well that they need not rely on nesting material to do this. Groups that construct elaborate nests or place their nests in difficult-to-access locations, like the tips of branches (genus: *Icterus*; genus: *Ploceus*) may rely on nest structure and placement more than nest materials for coping with nest predation (Street et al. 2022). Finally, several groups of primarily open cup–nesting birds (Parulidae, Motacillidae, Thraupidae, Thamnophilidae) may simply never gain sufficiently high fitness benefits from using shed snake skin relative to the costs of finding and incorporating this material to allow this behavior to evolve. These speculations highlight the need for further study, which will surely reveal more species that use shed snake skin in nest construction and more life history traits associated with this behavior.

The passerines that use shed snake skin in nest construction are relatively small-bodied birds, which makes them less capable of defending their nests against potential predators. Reproduction ties birds to the nest site, forcing them to solve challenges associated with breeding in novel ways. The diversification of nest morphologies (Fang et al. 2018; Street et al. 2022) and nest placements (Martin 1988, 1993) in passerines represents two ways of overcoming challenges associated with reproduction, and the materials used in nest construction represents another. Constrained by their small body size, passerines have evolved unique behaviors, such as incorporating shed snake skin into their nests, to overcome challenges associated with reproduction. Data presented here offer three independent lines of evidence that the use of shed snake skin in nest construction is strongly associated with cavity nest morphologies. Cavity nests change the suite of potential nest predators such that only relatively small-bodied species can enter these nest sites. We hypothesize that the long history of snakes as major predators of animals that frequently depredate bird nests (Greene 1983; Rodríguez-Robles et al. 1999; Öhman and Mineka 2003; Klein et al. 2021) has inadvertently provided passerines with an effective deterrent against some, but not all, nest predators. Our experimental results show that the benefits of using shed snake skin in nest construction are most strongly awarded to cavity-nesting birds. These unequal fitness benefits between cavity- and open cup–nesting species likely explains why, across passerines, cavity-nesting birds show this behavior more frequently and use snake skin more often in nest construction compared with open cup–nesting birds.

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Statement of Authorship

V.G.R. and E.T.M. conceived the project, R.L.B. and M.N.V. provided access to field sites, and V.G.R., E.T.M., and J.L.H. gathered, curated, and analyzed data. V.G.R. drafted the original manuscript, and all authors helped with edits and revisions.

Data and Code Availability

All data and code associated with this study have been uploaded to the Dryad Digital Repository (https://doi.org/10.5061/dryad.hdr7sqvpq; Rohwer et al. 2024).

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