

Fitness Consequences of Interspecific Nesting Associations among Cavity-Nesting Birds

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ABSTRACT: Interspecific aggregations of prey may provide benefits by mitigating predation risk, but they can also create costs if they increase competition for resources or are more easily detectable by predators. Variation in predation risk and resource availability may influence the occurrence and fitness effects of aggregating in nature. Yet tests of such possibilities are lacking. Cavity-nesting birds provide an interesting test case. They compete aggressively for resources and experience low nest predation rates, which might predict dispersion, but across 19 years of study we found that they commonly aggregate by sharing nest trees. Tree sharing was more common when aspen were more abundant and was somewhat more common in years with higher nest predation risk. Nest success was higher in shared trees when nest predation risk was higher than average. Ultimately, the costs and benefits of aggregating (nest tree sharing) varied across years, and we outline hypotheses for future studies.

Keywords: heterospecific aggression, resource limitation, competition, nest predation, protective association, spatial aggregation.

Introduction

Aggregation of species can incur costs and benefits from predation and competition that influence fitness and shape the extent of aggregating in nature. Less aggregation and greater dispersion should be favored when prey aggressively compete for limited resources (Orians and Wilson 1964; MacArthur and Levins 1967). Similarly, prey may avoid predators by becoming more dispersed and less conspicuous (Inmam and Krebs 1987; Martin 1988, 1993a, 1996; Martin et al. 2000; Varela et al. 2007). In contrast, among species that have mutual predators, interspecific aggregations may prove beneficial through risk dilution, earlier detection of predators, and more effective defense (Hamilton 1971; Morse 1977; Quinn and

Ueta 2008; Krams et al. 2010). In either of these cases, the costs and benefits of interspecific aggregations may be dependent on the levels of both predation risk and intensity of competitive interactions, and each can change over time (Agrawal et al. 2007; Chamberlain et al. 2014). Yet the influence of variation in both predation risk and competition on spatial associations among species and their fitness consequences is poorly understood.

Species with high levels of resource overlap and heterospecific aggression are generally unlikely to aggregate but may be more likely to do so under certain environmental conditions (Orians and Wilson 1964; MacArthur and Levins 1967; Peiman and Robinson 2010). For example, while aggressive interactions over access to shared resources can lead to increased dispersion when one species excludes another from the area around a resource, aggression is thought to be less important when resources are abundant (Brown 1975; Peiman and Robinson 2010). Thus, when resources are abundant, aggregating may become more common, even among species with high levels of resource overlap. Furthermore, if aggregating species gain benefits from reduced predation risk, the benefits of aggregating may compensate for any costs due to aggressive interactions, especially when resources are abundant or predation risk is elevated. Still, for species that experience low predation rates on average, benefits of further reductions in predation risk may be relatively unimportant, and costs of aggression should be predominant. Thus, species with low predation rates that aggressively compete for defendable resources should generally avoid aggregating unless predation risk or resource availability is particularly high.

Cavity-nesting birds provide an interesting system to test these ideas. They have low nest predation rates (Nice 1957; Martin 1995; Fontaine et al. 2007) and often compete for limited nest sites, aggressively excluding other cavity-nesting species from the areas around their nests to prevent nest takeover attempts (Short 1979; Nilsson 1984; Ingold 1994; Newton 1994; Duckworth 2006). In addition, many cavity-nesting species also overlap in foraging sites and food resources

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(e.g., Bull et al. 1986), which could exacerbate aggressive interactions. These conditions predict dispersion of species, but different cavity-nesting species have been observed nesting in the same tree (Hoyt 1948; Reller 1971; McClelland 1977; Belson 2000). However, the extent of nest tree sharing is not well described, and the costs and benefits of sharing are unstudied, especially with respect to temporal variation in nest predation risk and resource availability.

Variation in nest predation risk and nest tree availability could influence the incidence and fitness effect of tree shar-

ing in several ways (fig. 1). First, limited availability of nest trees may force cavity-nesting birds to share trees because there are no other suitable sites. If nest site limitation forces sharing, then sharing should be more common when nest trees are more limited (fig. 1*a*). In contrast, aggression among species at nests may be more severe when either nest site or food resources are limited (Peiman and Robinson 2010), causing sharing to be less common (fig. 1*b*). In either case, greater aggression among cavity-nesting species with greater resource overlap in nest site or food resources may limit which

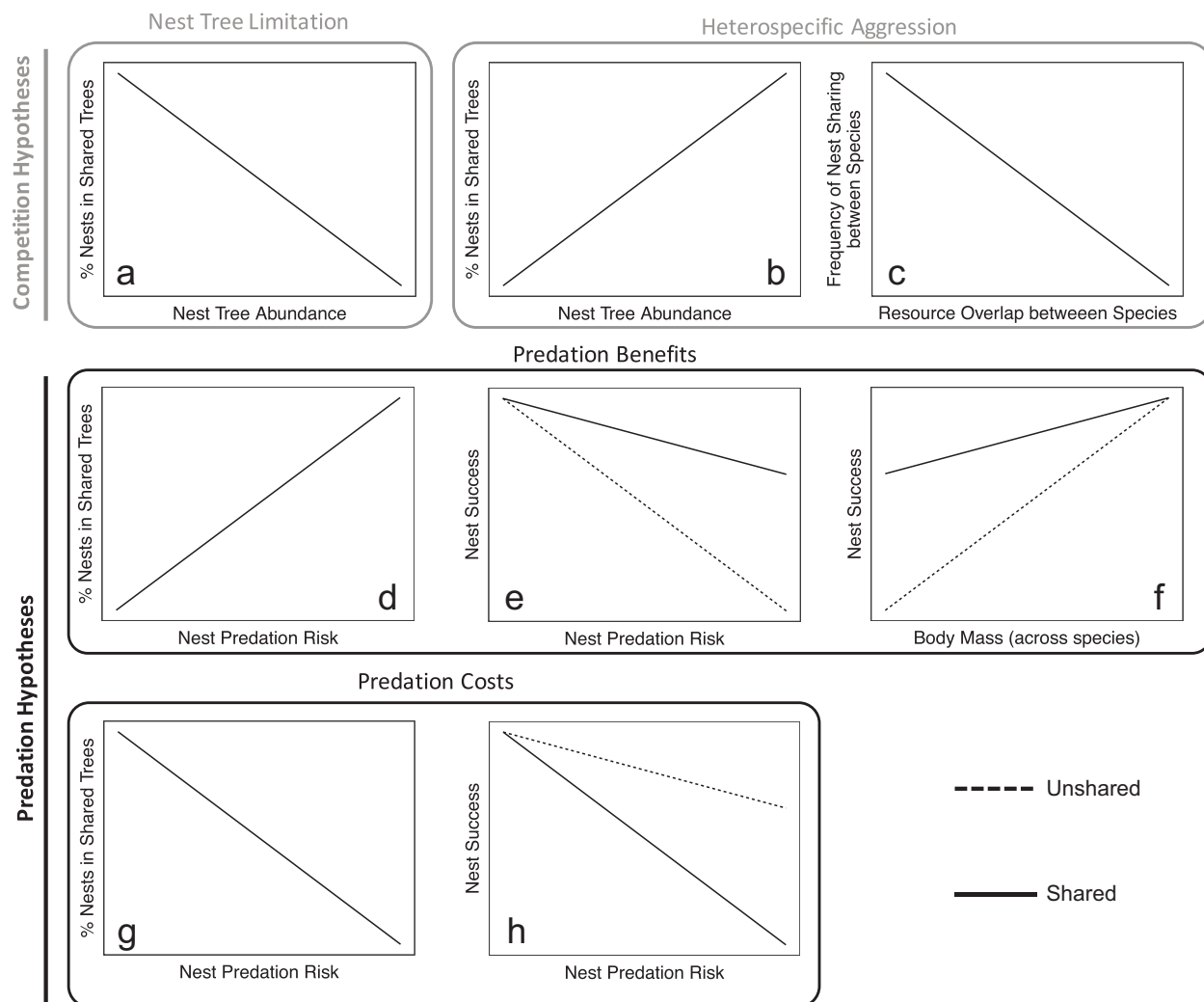


Figure 1: Hypotheses explaining how resource availability and nest predation risk could influence the occurrence and reproductive success of nest tree sharing. If sharing is a result of nest tree limitation, then the frequency of nest tree sharing should decrease when nest trees are most abundant (*a*). In contrast, if heterospecific aggression limits nest tree sharing, then (*b*) the frequency of nest tree sharing should increase when nest trees are most abundant, and (*c*) species with greater resource overlap should share trees less often because they should exhibit higher levels of aggression toward one another. Variation in nest predation risk could also influence nest tree sharing. If sharing nest trees yields increased nest success due to better detection or deterrence of predators, then shared nest trees (*d*) should be more common and (*e*) have greater benefits in years with high nest predation risk. Furthermore, if the predation benefits of tree sharing are due to better deterrence of predators, smaller species may gain more benefits from sharing nest trees (*f*). In contrast, if shared nest trees are more conspicuous to predators, tree sharing may (*g*) be less common and (*h*) experience greater costs in years with high nest predation risk.

species commonly share nest trees (fig. 1c; Brown and Wilson 1956; MacArthur 1972; Hespeneide 1973; Short 1979; Nilsson 1984). Sharing nest trees may also have benefits when nest predation risk is elevated because multiple pairs of adults can better deter potential predators and increase the likelihood of successfully fledging young (fig. 1d, 1e; reviewed in Quinn and Ueta 2008). On the one hand, this benefit may be particularly strong for small species, which may be less likely to be able to deter potential predators than larger species (fig. 1f). On the other hand, higher levels of parental activity of multiple pairs might attract predators (Skutch 1949; Martin et al. 2000) and increase costs of sharing when nest predation risk is high (fig. 1g, 1h). In contrast, when the risk of nest predation is low, energetic costs from aggressive encounters may outweigh any potential gains in nest success. In this case, breeding adults may more commonly nest alone on trees and adopt other strategies to reduce predation risk. Resolution of these alternatives requires examination of the incidence and consequences of sharing nest trees under different levels of resource availability and nest predation risk.

We used 19 years of nesting data to test these *a priori* hypotheses and consider additional alternatives in the discussion section. First, we provide a general description of the incidence and habitat characteristics associated with nest tree sharing in a community of cavity-nesting birds. Specifically, we assess whether species were more likely to share trees with other species that have less resource overlap. Second, we examine whether variation in nest predation risk and aspen abundance across years explains variation in the prevalence of shared nest trees. Because aspen are preferred nesting trees (Li and Martin 1991; Martin et al. 2004; Martin 2014), years with high aspen abundance may reflect high nest tree availability, although greater aspen abundance could also correlate with higher food availability. Finally, we examine how sharing a nest tree influences reproductive success and whether reproductive consequences change with variation in nest predation risk across years. Ultimately, the well-documented interference competition for nest sites and low predation rates among cavity nesters raises questions about why nest tree sharing occurs. Understanding how predation risk and interference competition shape nest tree sharing can provide new insight into the role of environmental variation for other interspecific associations and their fitness consequences.

Material and Methods

Study Areas and Species

We studied cavity-nesting birds at a midelevation (2,350 m) mixed forest field site in Arizona (34°N) from 1993 to 2011. This site provided an excellent system to address our questions because both nest predation risk and the abundance of

the preferred nest tree species (quaking aspen [*Populus tremuloides*]) varied across years (Li and Martin 1991; Martin 2014).

We found and monitored cavity nests for five common woodpeckers (downy woodpecker [*Picoides pubescens*], hairy woodpecker [*Picoides villosus*], Williamson's sapsucker [*Sphyrapicus thyroideus*], red-naped sapsucker [*Sphyrapicus nuchalis*], and northern flicker [*Colaptes auratus*]) and five common passerines (house wren [*Troglodytes aedon*], red-breasted nuthatch [*Sitta canadensis*], white-breasted nuthatch [*Sitta carolinensis*], western bluebird [*Sialia mexicana*], and mountain chickadee [*Parus gambeli*]). All woodpeckers and one species of passerine (red-breasted nuthatch) are capable of excavating new cavities. However, both excavating and nonexcavating species make regular use of previously existing cavities (Martin 1993b).

Data Collection

Nests were found using parental behavior and systematic search and monitored every 2–4 days (Martin and Geupel 1993). Nests were designated as being in a shared tree when two nests were simultaneously active in the same tree. Nests were considered successful when at least one nestling was confirmed to have fledged or the nest became inactive within 2 days of the end of the average nestling period for that species (Martin and Geupel 1993).

After nests became inactive, various characteristics of the cavity, nest tree, and nest patch were recorded. We recorded the height, visibility (crypsis), and type of cavity (old, freshly excavated, natural) for each nest. The status (live vs. dead) and number of additional cavities on each tree seen from the ground were also recorded. At the patch level, the number and species of trees were counted within 11 m of a nest tree. Each year starting in 1995, we also estimated the abundance of most cavity-nesting species across our site using the plot-mapping technique (Christman 1984; Martin 2014) and the abundance of aspen by following the fates of permanently marked trees (Martin 2007, 2014). See the appendix (available online) for more detailed methods.

Statistical Analyses

Occurrence of Shared Nest Trees. We tested whether resource overlap explained which species were more likely to share nest trees by examining differences in mass and phylogenetic distances. Because small entrance holes can exclude potential nest predators and larger nest site competitors, species are thought to prefer cavities with the smallest possible entrances (Short 1979; Nilsson 1984; Martin et al. 2004). Thus, we used differences in body mass between species to indicate overlap in nest site resources. We used phylogenetic distance between species as a more general proxy for ecolog-

ical differences between species, including food and nest site resource overlap. We include matrices containing these variables in two separate partial Mantel tests, which controlled for differences in preferences for live or dead aspen (Martin 2014). We used species masses from our site published elsewhere (Li and Martin 1991). Phylogenetic distances were obtained from a majority-rules consensus tree constructed from 1,000 trees using the program Mesquite (Maddison and Maddison 2011). Phylogenetic trees were downloaded from <http://www.birdtree.org> (Jetz et al. 2012) using the Hackett et al. (2008) backbone.

Resource overlap and interference competition might also influence the vertical distance between nests on shared trees. To test this idea, we used a linear mixed model with the distance between each nest as the response variable, the difference in mass and the number of cavities in the tree as explanatory variables, and year as a random effect. We limited this analysis to trees with at least one unoccupied cavity.

To characterize any differences in the habitat around shared nest trees, we used a logistic mixed model with sharing as the response variable. We included the abundance of live aspen, dead aspen, live conifers, and other live deciduous tree species within 11 m of the nest tree, as well as the total number of cavities in the nest tree, nest height, nest crypticity, status of the nest tree (dead vs. alive), and type of cavity as explanatory variables. Year and species were included as random effects.

Proportion of Shared Nest Trees over Time. We used linear models to test for the effect of aspen abundance and nest predation risk on the proportion of nests shared each year. We included the number of aspen still standing as an explanatory variable and controlled for the total density of cavity nesters and the density of woodpeckers in the previous year because this may affect cavity availability and quality (Norris and Martin 2010). Finally, we included average annual nest predation rates to test the role of predation risk. We estimated nest predation rates using the logistic exposure method, including year as a fixed effect and species as a random effect (Shaffer 2004).

Reproductive Success

We used the logistic exposure method (Shaffer 2004) to examine whether nest tree sharing influenced reproductive success. Because nest site characteristics can strongly influence reproductive success, we first ran a model without tree sharing to find the best predictors of nest success to include in subsequent models. We chose to use an information-theoretic approach based on the Akaike information criterion (AIC) because traditional hypothesis testing based on *P* values in logit models containing interaction terms can be problematic (Berry et al. 2010). We created a set of candidate models based on the hypotheses that there is an effect

of nest tree sharing on nest success and that this effect may vary with mean annual nest predation risk, body mass, or both. Random effects for year and species were included in all models.

Additional methodical details are included in the appendix. Data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b71g0gr> (Mouton and Martin 2018).

Results

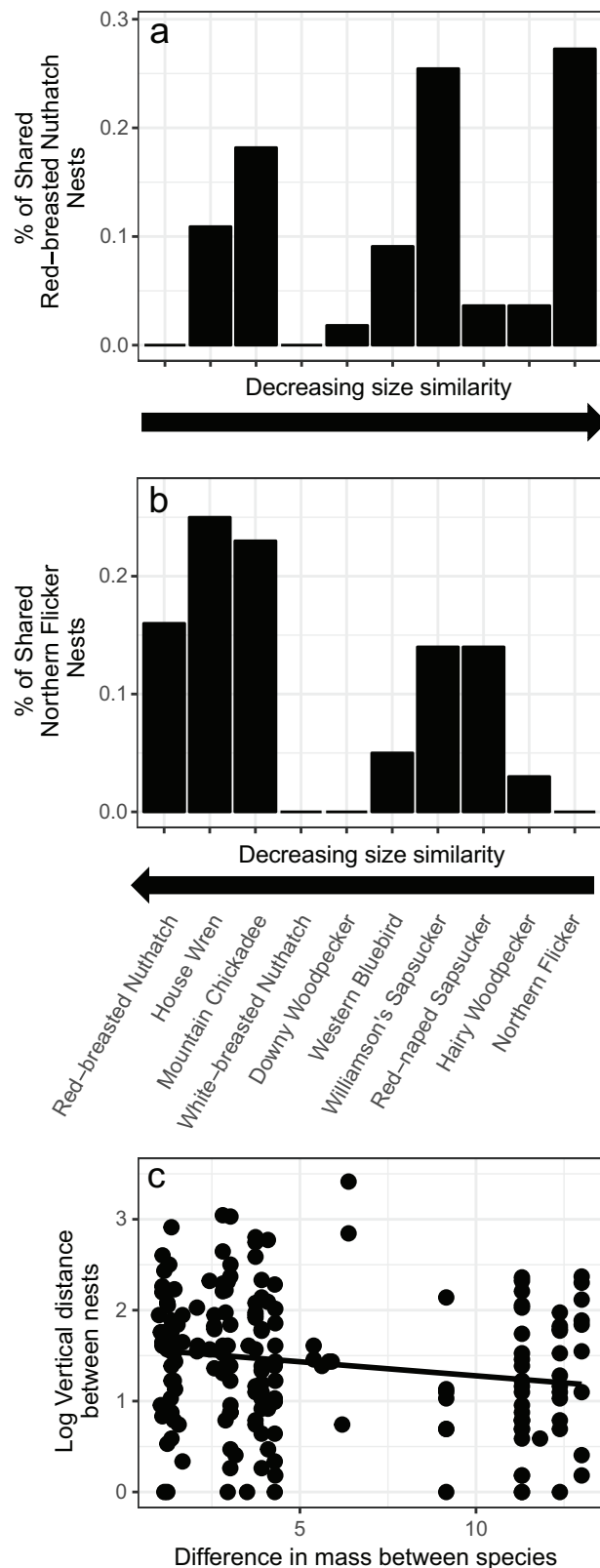
Occurrence of Shared Nest Trees

We found 5,966 nests overall, of which 841 were located in shared nest trees. The proportion of nests occurring in shared nest trees varied between 0% and 30.9% across years (mean = 15.1%). Most shared nest trees included exactly two nests (85%), although there were trees with larger numbers of nests (15%). Unoccupied visible cavities were observed in 50.9% of unshared nest trees and in 68.8% of shared nest trees. No cases of intraspecific sharing were observed. The number of nests shared by all pairs of species increased with both the mass ratio (greater ratio reflects greater difference) between species (partial Mantel test: $r = 0.364$, $P = .046$; figs. 2a, 2b, A1; fig. A1 is available online) and their phylogenetic relatedness (partial Mantel test: $r = 0.358$, $P = .001$). Nests in shared trees were closer in vertical distance on the trunk of the tree with greater differences in masses between species (mass ratio: $b = -0.032$, $t = -2.551$, $P = .011$; number of cavities in tree: $b = 0.014$, $t = 1.755$, $P = .085$, $n = 212$; fig. 2c).

Nests in shared trees were less cryptic ($b = -0.271$, $z = -2.546$, $P = .010$; table A1; tables A1–A3 are available online), less likely in natural cavities than either old ($b = 1.673$, $z = 5.036$, $P < .001$; table A1) or freshly excavated ($b = 1.066$, $z = 2.997$, $P = .002$; table A1) cavities, and marginally higher than solitary nests ($b = 0.207$, $z = 1.833$, $P = .066$; table A1). Shared nest trees also had more observed cavities ($b = 0.467$, $z = 7.931$, $P < .001$; table A1) and were marginally more likely to be in patches with greater density of aspen snags ($b = 0.034$, $z = 1.929$, $P = .053$; table A1) than unshared nest trees. Similar patterns existed when considering only nonexcavating species, but only the number of cavities in a tree explained tree sharing for excavating species ($b = 0.406$, $z = 4.839$, $P < .001$; table A1).

Proportion of Shared Nests over Time

The proportion of nests in shared trees increased with the number of standing aspen in that year ($b = 0.667$, $t = 4.371$, $P = .001$; table A2; fig. 3a), decreased with woodpecker density in the previous year ($b = -0.303$,



$t = -2.395$, $P = .035$; table A2; fig. 3b), and marginally increased with annual nest predation rates ($b = 0.093$, $t = 2.118$, $P = .057$; table A2; fig. 3c).

Reproductive Success

Overall, 79.7% and 90.5% of solitary and shared nests fledged young, respectively. Among the nest site characteristics that predicted whether a nest tree would be shared, only cavity type explained the probability that a nest succeeded (nest height: $P = .893$; number of observed cavities: $P = .142$; nest crypsis: $P = .924$; number of dead aspen within 11 m: $P = .978$; old vs. natural cavities: $P = .015$; fresh vs. natural cavities: $P = .129$). We found strong support for larger increases in nest success in shared trees in years with above average nest predation risk (AIC weight: 0.995, fig. 4; table A3). Models suggesting greater benefits of tree sharing in species with smaller body mass also had some support (AIC weight: 0.626; fig. 4; table A3).

Discussion

Theory predicts higher dispersion and less aggregation among species with high resource overlap and low average predation rates. Mixed-species aggregations may be particularly rare and costly when species show high levels of heterospecific aggression and exclude each other from the area around resources. Cavity-nesting birds are generally thought to fit these criteria, yet here we show that they regularly nest together on the same tree. These results raise the following question: Why does nest tree sharing occur? That the extent of nest tree sharing fluctuated over time with variation in resource levels and nest predation risk points to several possible explanations.

Benefits due to reducing predation risk may promote nest tree sharing. In theory, nesting in close proximity to other birds could provide earlier detection and more effective deterrence of approaching predators. We found that nests in shared trees had higher probabilities of fledging young than solitary nests in years with higher than average levels of nest predation risk (fig. 4; table A3). Furthermore, we found that nest tree sharing was somewhat more com-

Figure 2: Mass differences between species explained the frequency of sharing between a given species pair. For example, (a) relatively small birds such as the red-breasted nuthatch (10 g) tended to share more often with larger species (larger species toward right side of figure), while (b) larger species such as the northern flicker (130 g) tended to share more often with relatively smaller species on average (smaller species toward left side of figure). Note that hairy woodpeckers and red-naped sapsuckers mostly nest in live aspen, explaining their lower sharing with red-breasted nuthatches, which primarily use dead aspen (Martin 2014). Greater differences in mass between two species sharing a nest tree was associated with closer vertical distances between the two cavity entrances on the tree (c).

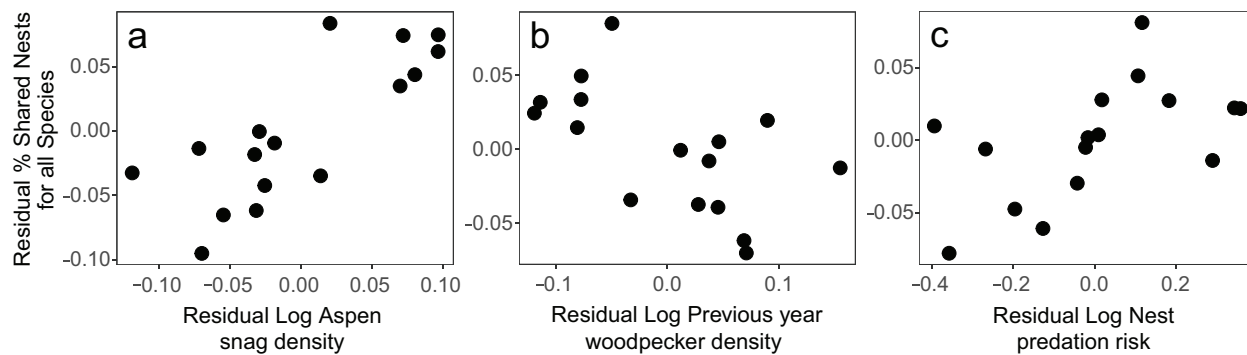


Figure 3: Partial regression plots showing residual frequency of nests in shared nest trees as a function of (a) snag density, (b) woodpecker density in the previous year, and (c) nest predation risk.

mon in years when nest predation risk was high (fig. 3; table A2). Together, these results point to the possibility that cavity-nesting birds may plastically respond to cues about nest predation risk early in the breeding season (e.g., Hua et al. 2013) by sharing nest trees to mitigate that risk. Alternatively, these patterns may reflect higher breeding densities in relatively safer areas in high-risk years, which results in greater overlap in habitat selection, increased sharing, and higher nest success. Furthermore, benefits in nest success rates might be offset by costs in the quality or quantity of young produced or parental condition from increased aggressive interactions with neighbors to thereby explain why sharing is less common than solitary nesting. Thus, ultimately, studies examining spatial patterns of predation risk and experiments using more comprehensive metrics of reproductive success and parental condition are needed to fully understand the fitness consequences of nest tree sharing.

Several pieces of evidence suggest a role for interference competition in shaping the extent of tree sharing among species. Shared nest trees were more common in years when aspen were more abundant (fig. 3; table A2), and aggressive interactions over resources, either nest sites or food, should be less intense (Peiman and Robinson 2010). Thus, it seems that shared nest trees were most prevalent in situations where preferred nest trees were most abundant, conflicting with the idea that limited nest trees may force nest tree sharing due to a lack of alternative options. Instead, interference competition may be more severe when nest site or food resources are scarce, making it especially costly to share nest trees under those conditions (Peiman and Robinson 2010). Nonetheless, the degree to which aspen abundance reflects nest site or food availability is unclear and should be addressed in future studies.

Given that aggressive interactions should be more intense among species with greater nest site or food overlap (MacArthur and Levins 1967; Peiman and Robinson 2010), interference competition may also limit which species share

nest trees. Indeed, shared nest trees were less common among species with similar body sizes and those that were more closely related phylogenetically. However, increased nest tree sharing among dissimilar species could also arise because smaller, more vulnerable passerines prefer to nest with larger species that provide the best protection from nest predators. Indeed, we did find some support for the idea that smaller species benefited more from tree sharing than larger species, although the effect seems to be fairly negligible, especially in years with low predation risk (fig. 4; table A3). However, the result that species pairs with more similar body sizes tended to nest farther apart on shared nest trees emphasizes a role for interference in shaping which species will nest together because higher levels of aggression between more similar species may favor increased dispersion even on the same tree (fig. 2c; Duckworth 2006). Thus, our results are consistent with the idea that interference competition over cavities or food resources limits tree sharing among cavity nesters. Nonetheless, direct measures of aggressive behavior at various spatial scales are lacking, and studies assaying heterospecific aggression at different levels of food and nest site availability and at various spatial scales are needed.

Variation in cavity quality may also play an important role in the extent of tree sharing. Woodpeckers are thought to excavate high-quality cavities that other species use, but they deteriorate over time such that more recently excavated cavities provide the greatest benefits (Aitken et al. 2002; Martin et al. 2004). When they are available, recently excavated woodpecker cavities may provide an alternate way to mitigate nest predation risk without incurring costs due to aggressive interactions with neighbors. Indeed, we found that in years following relatively higher densities of woodpeckers, when more high-quality cavities were likely available, fewer nests were in shared nest trees. However, freshly excavated cavities did not have higher nest success than old or natural cavities in our system (see “Results”). Still, we could not distinguish the ages of cavities excavated in previ-

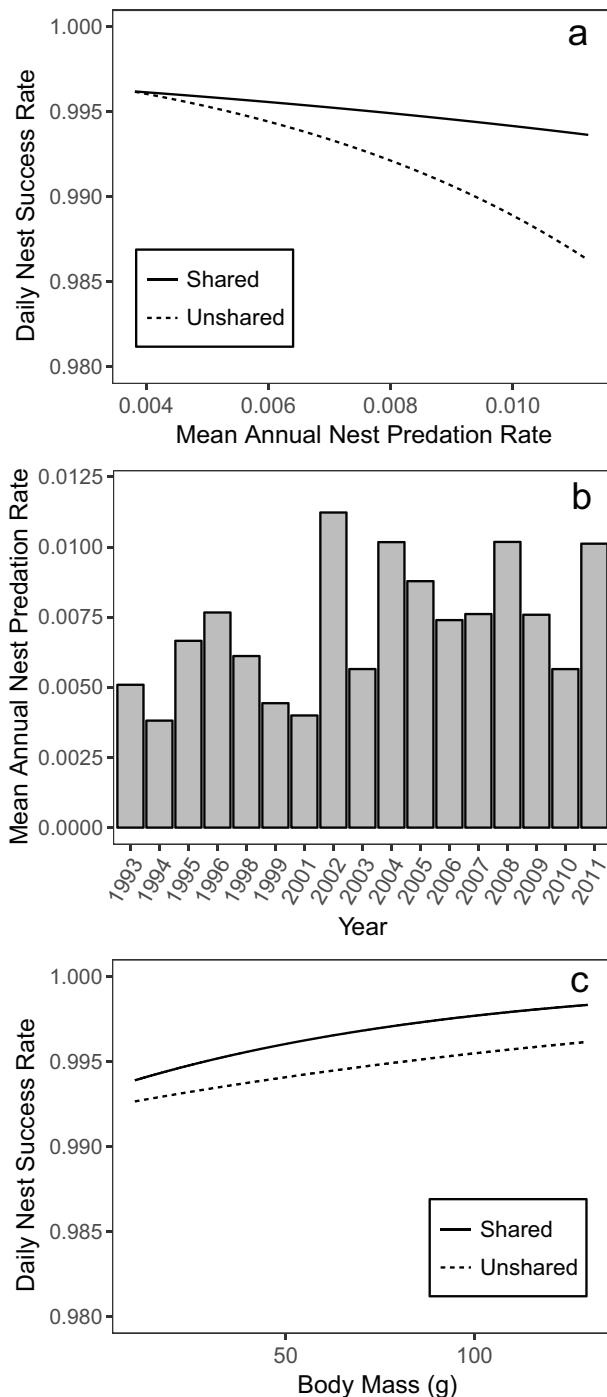


Figure 4: *a*, Predicted daily nest success rate for nests in shared and unshared nest trees as a function of mean annual nest predation rates. *b*, Mean annual nest predation rates by year. *c*, Predicted daily nest success rate for nests in shared and unshared nest trees as a function of species body mass. Predictions are from the highest supported model and are based on mean values for all habitat covariates. Predictions for body mass are from a high nest predation year.

ous years, and so the trade-offs between cavity quality and nest tree sharing remain unclear.

Overall, we show that despite the well-documented aggression among cavity-nesting birds for nest sites, sharing nest trees can be common under certain environmental circumstances and that nest success seems to be higher for nests in shared trees than in unshared trees. We discuss several possible explanations for these phenomena, but ultimately experiments are needed to tease them apart. Our results highlight the need to consider how environmental variation may influence mixed-species associations in other taxa. Indeed, examination of environmental variation that can shift the balance between the costs and benefits of aggregating may help both identify other unlikely associations among species and suggest the mechanisms that underlie them.

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