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YELLOW PINE CHIPMUNKS CANNOT CLIMB QUAKING ASPENS: IMPLICATIONS FOR AVIAN NEST SITE SELECTION

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ABSTRACT.—Predation of eggs or nestlings is generally believed to be the most influential factor limiting passerine reproductive success. Thus, there should be strong selective pressures for birds to place their nests in sites that are inaccessible to predators or that are less likely to be discovered by them. We found and monitored 231 nests of 4 species of arboreal, cup-nesting birds: Western Wood-Pewee (*Contopus sordidulus*), Warbling Vireo (*Vireo gilvus*), American Robin (*Turdus migratorius*), and Yellow-rumped Warbler (*Dendroica coronata*). We determined strength of nest tree species selection by comparing nest trees and tree species availability. Western Wood-Pewees and Warbling Vireos demonstrated strong preference for placing nests in quaking aspen (*Populus tremuloides*). Yellow-rumped Warblers showed a weak preference for aspen, and American Robins demonstrated no preference. We designed a series of experiments to determine whether yellow pine chipmunks (*Tamias amoenus*), an abundant nest predator, could climb aspen trees and, if so, what factors might prevent them from doing so. Yellow pine chipmunks were unable to climb aspen but showed no difficulty in climbing and maneuvering on lodgepole pine (*Pinus contorta*) boles, which were identical in diameter to aspen boles. Refuge from chipmunks as potential nest predators is likely contributing to nest site selection for a few arboreal cup-nesting bird species where aspen trees are available.

Key words: Populus tremuloides, *quaking aspen,* Tamias, *chipmunk, nest site selection, nest predation,* Vireo gilvus, *Warbling Vireo,* Contopus sordidulus, *Western Wood-Pewee.*

The relationship between predation and nest site selection plays a critical role in the reproductive success of birds (Ricklefs 1969, Martin 1993b). Discovery of a bird nest by a predator can often equate to complete failure of that reproductive effort. Among cup-nesting passerine birds, nest predation is typically the leading cause of nest failure (Lack 1954, Nice 1957, Ricklefs 1969, Martin 1992, 1993a), and Martin (1993b) calculated that predation accounts for 80% of nest failures on average. In some systems, survival of a clutch of eggs to fledging may depend more upon the location of the nest than upon any other factor, including food availability and parental behavior (Martin and Roper 1988, Martin et al. 2000, Forstmeier and Weiss 2004), and predation pressures may constrain incubation and provisioning behavior (Martin and Ghalambor 1999, Conway and Martin 2000), further limiting reproductive success. Thus, there is strong selection on birds to deter nest predators by choosing nest sites that are inaccessible to predators or less likely to be discovered by them (Collias and Collias 1984, Martin and Roper 1988, Filliater et al. 1994). Developing a better understanding of nest predator ecology and foraging strategies can facilitate an increased understanding of nest site selection strategies.

We have spent hundreds of hours observing chipmunks, known nest predators, in quaking aspen (*Populus tremuloides*) and conifer vegetation types. During this time, we have regularly observed chipmunks climbing coniferous trees, predominately Jeffery pine (*Pinus jefferyi*), lodgepole pine (*Pinus contorta*), and white fir (*Abies concolor*), occasionally to heights well over 10 m. Chipmunks have also been observed regularly foraging in small, shrubby aspens, willows (*Salix* sp.), and other shrubs that dominate that vegetation type (e.g., *Ribes* spp. and *Symphoricarpos* sp.). Although chipmunks are predominately ground dwelling, such behavior is typical. Indeed, in a time allocation study, yellow pine chipmunks (*Tamias amoenus*) were found to spend approximately 8% of their time in conifer trees (K.M. Kuhn unpublished data). Why chipmunks ascend trees is not always clear, but several behaviors of chipmunks in trees have been observed, namely, raising an alarm or other social vocalization, gaining a higher vantage

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for vigilance, and, less frequently, finding a sunny spot for rest and insolation (T.W. Richardson personal observation). They have also been observed grooming, eating, and foraging in trees (States 1976, Kuhn personal communication), and chipmunks will prey on bird nests located in trees and shrubs when nests are accessible.

Members of the genus *Tamias* are nontrivial nest predators in many systems and demonstrably affect nesting success, nest placement, and even territory selection in ground nesting birds (Ketterson et al. 1996, Forstmeier and Weiss 2004, Morton 2005). Chipmunks prey on nests of shrub and arboreal nesters as well (Craig 1998, Purcell and Verner 1999). For example, Allen's chipmunks (*Tamias senex*) were responsible for 25% of nest predations on Dusky Flycatcher nests in northern California (Liebezeit and George 2002). Callahan (1993) believed that lodgepole chipmunk (*Tamias speciosus*) specialized as an arboreal nest predator and cited anecdotal examples of the species' conifer-climbing habits from elsewhere in California (Grinnell 1908, Grinnell and Storer 1924), and believed they may be responsible for a large percentage of arboreal nest predations where the species occurs. Considering that chipmunks are predators of tree-nesting birds, we find it notable that we have never observed chipmunks climbing a mature aspen during this study.

Coniferous trees have highly textured bark, presumably providing a solid grip for climbing chipmunks. Aspens, however, have relatively smooth bark, and may present a substrate that is difficult for chipmunks to climb. Further, aspen growing under a closed canopy self-prune lower branches as they grow. Self-pruning results in a tree with few lateral branches below the crown. This lack of cover may present more exposure to predators than chipmunks are willing to risk (Lima and Valone 1986). If chipmunks are unable or otherwise unwilling to climb and forage in mature aspens, then they may not function as potential nest predators for birds nesting in that tree species. We designed a series of experiments to determine whether yellow pine chipmunks could climb aspen trees and, if so, what factors might prevent them from doing so. We also investigated the strength of nest tree species selection by comparing nest tree species use to tree species availability for 4 tree-nesting bird species.

METHODS

Experiments were conducted during October 2005 in the University of Nevada's Whittell Forest and Wildlife Area in Little Valley, Washoe County, Nevada. The research area is on the east slope of the Carson Range (39°15′10″N, 119°52′35″W, elevation 1990 m) 30 km south of Reno. Data on breeding-bird nest tree selection come from mixed aspen stands in the Lake Tahoe Basin, from 4.5 km to 41.5 km west and south of the Whittell Forest and Wildlife Area. The capture and experimental observation of the chipmunks was approved by the University of Nevada's Institutional Animal Care and Use Committee (UNR IACUC protocol A04/05-31).

With the intent of observing and quantifying chipmunk behavior on various tree bole substrates, we conducted initial pilot experiments in a rodent-proof aviary (6 × 10 m) constructed of mesh hardware cloth on a wooden frame. We had hoped to determine if the addition of fir limbs to an aspen bole would encourage chipmunks to spend more time climbing aspen. However, all but 1 of our subjects refused to climb or attempt to climb any of the boles present, despite bait, ramps, and many hours of habituation. Rather, chipmunks spent almost all of their time looking for an escape route along the aviary walls. Through subsequent pilot experiments we determined that chipmunks would attempt to climb tree boles when placed in a confined space with no alternatives for escape.

We conducted our experiments in 4 adjacent plywood arenas. Arenas were approximately 120 × 120 × 60 cm, and the walls of each arena were topped with aluminum flashing to prevent animals from escaping. In the center of each arena, we installed a 2-m-tall tree bole, stripped of limbs. The 4 boles were of the following size and species: 10-cm-diameter aspen, 10-cm-diameter lodgepole pine, 25-cm-diameter aspen, and 25-cm-diameter lodgepole pine. Height from ground was marked on the aspen boles at 5-cm increments with a permanent marker. For the trials, we captured 24 yellow pine chipmunks from habitat adjacent to the arenas, using Sherman live-traps. We weighed each subject, marked it with a numbered eartag, and released it into an arena. Each animal was subjected to a 5-minute bout per arena, and the order of the arenas was randomized. During

TABLE 1. Number of yellow pine chipmunks attempting to climb tree boles of aspen and pine. *P*-values refer to Fisher's exact test of probability.

	Quaking aspen		Lodgepole pine		
	Successful	Unsuccessful	Successful	Unsuccessful	*P*
Large boles (25 cm)	0	17	13	0	<0.0001
Small boles (10 cm)	0	16	18	0	<0.0001

the bouts, we noted climbing attempts and successful climbs of the boles, as well as time spent on the bole itself. Heights of attempts were estimated for aspen boles based on the markings on the bole. We discovered that chipmunks would reliably attempt to ascend the boles when we challenged them by scraping a meterstick in the soil at the bottom of the arena. At the end of any bout during which the subject did not attempt to climb the bole, we challenged the subject in this manner until either it attempted to climb the bole or 2 minutes had transpired. Each trial was assigned a binary score indicating whether the animal was successful or unsuccessful in attempting to climb the substrate. We defined "success" as a controlled ascent on the substrate above 1 m without slipping and falling to the ground. These data were compared by bole size class using a Fisher's exact probability test.

Nest site preference was determined based on data collected from June through August 2003 and 2004, as part of another study (Richardson 2005). In short, all bird nests were found and monitored in 6 study areas in a mixed aspen vegetation type (68.7 ha total). Only arboreal cup nests known to have contained at least 1 conspecific egg were included in these analyses. For each nest, all trees within an 11.3-m-radius plot were tallied. Data on tree species that birds selected for nest sites were pooled by species and compared against available tree species using a Fisher's exact probability test. Statistical tests were performed with SAS statistical software (PROC FREQ; SAS 1999). Significance was assumed at $\alpha = 0.05$. Data are presented as means with standard deviations.

RESULTS

Of the 24 yellow pine chipmunks captured and subjected to trials, 2 escaped before data were taken. Nine animals escaped prior to exposure to all 4 substrates, or refused to attempt to climb at least 1 of the boles. Thirteen animals completed all 4 trials and climbed or attempted to climb each of the 4 boles. Yellow pine chipmunks were able to climb and maneuver on the pine boles with no apparent difficulty. Many of the animals quickly climbed up the pine boles as soon as they were released and hid on the back of the bole, in the manner of tree squirrels (*Sciurus*, *Tamiasciurus*), for the duration of the bout. Chipmunks spent a mean of 97 ± 123 seconds ($n = 12$) on the 10-cm pine bole and 208 ± 109 seconds ($n = 16$) on the 25-cm pine bole. Chipmunks descended pine boles headfirst, and the animals appeared to have no difficulty stopping, clinging to side of the bole for ≥5 minutes, climbing from a stopped position, turning around to face downwards, circling the bole to keep hidden, or leaping from a static stance on the side of the boles. Subjects never slipped or fell from a pine bole. Every chipmunk that attempted to climb a pine bole ascended with apparent ease (Table 1).

Chipmunks were considerably less successful when they attempted to climb aspen boles. In 102 of 105 attempts to climb an aspen bole, the animal slipped and fell immediately (10-cm bole, 36 instances; 25-cm bole, 66 instances). Mean maximum heights that chipmunks attained before falling were 44 ± 13 cm on the 10-cm aspen bole ($n = 17$) and 56 ± 27 cm on the 25-cm aspen bole ($n = 16$). In 2 instances chipmunks managed to cling to low (20–25-cm) branch scars on the 25-cm bole for 1–2 seconds before dropping to the ground. In 1 instance a chipmunk was able to climb up approximately 30 cm and cling to a rough section of bark on the 25-cm bole for 16 seconds before dropping to the ground. This subject slipped and fell on 3 subsequent attempts. Two chipmunks stood on their hind legs with their forelimbs on the aspen boles, looking up for 1–3 seconds before dropping down to a 4-legged stance. Two other subjects refused to attempt to climb the aspen boles despite 2

TABLE 2. Nest site preference of arboreal cup-nesting birds breeding in mixed aspen-conifer stands, Lake Tahoe, California and Nevada, 2003–2004. *P*-values refer to Fisher's exact test of probability

	Aspen		Non-aspen		
	Nest tree	Trees available	Nest tree	Trees available	*P*
Western Wood-Pewee	51	1268	1	195	0.007
Warbling Vireo	91	2368	0	381	<0.001
American Robin	66	2004	6	195	1.000
Yellow-rumped Warbler	11	380	5	83	0.189

minutes of being challenged; both of these subjects readily climbed the 25-cm pine bole. Ultimately, none of the subjects was able to successfully climb either aspen bole (Table 1).

We found and monitored 241 arboreal, open-cup nests of 11 bird species. Most of these (96%) belonged to 4 species: Western Wood-Pewee (*Contopus sordidulus; n* = 52), Warbling Vireo (*Vireo gilvus; n* = 91), American Robin (*Turdus migratorius; n* = 72), and Yellow-rumped Warbler (*Dendroica coronata; n* = 16). Nests were located in Jeffery pine, lodgepole pine, white fir, red fir (*Abies magnifica*), incense cedar (*Calocedrus decurrens*), quaking aspen, Scouler's willow (*Salix scouleriana*), and mountain alder (*Alnus incana*). Western Wood-Pewees and Warbling Vireos both demonstrated a strong preference for aspen relative to the tree species available on their territories ($P < 0.01$; Table 2). American Robins ($P = 1.0$) and Yellow-rumped Warblers ($P = 0.19$) did not demonstrate a significant preference for aspen (Table 2).

DISCUSSION

Yellow pine chipmunks have difficulty climbing aspen, apparently because of its smooth bark. Anecdotal evidence from Elliot (1978) suggests that the smooth bark of beech (*Fagus grandifolia*) presents a similar obstacle for eastern chipmunks (*Tamias striatus*). Smooth bark and thin, unbroken, persistent periderm is typical of healthy aspen, and it is only because of pathogenic fungi, lichens, or mechanical injury that one finds rough bark on an aspen bole (Kaufert 1937). An exception is the inverted "V" of rough bark found directly above each limb or limb scar, known as a branch bark ridge (Shigo 1985). Mechanical injuries to aspen bark can come from many sources, including gnawing by animals, climbing by large, clawed animals, woodpecker excavations, graffiti, harsh weather, falling trees and branches, and directional stress from wind or from growing on a steep hillside. Such wounds can accumulate on an old, decadent tree. However, on most healthy aspen, areas of rough bark are limited to within a few meters of the ground or restricted to 1 side of the tree, and aspen boles often have relatively large spans of smooth bark in between these rough areas. What limited success chipmunks demonstrated at climbing aspen boles in the arenas was due to the availability of limb scars, bark branch ridges, and other sections of rough bark. Though yellow pine chipmunks may not be able to surmount the average span between sections of rough bark, it should be noted that they are a relatively small chipmunk species (40–50 g). Other chipmunk species are larger, have a broader reach, can jump higher, and may possibly be better adapted for climbing (but see Grinnell and Storer 1924:180). Thus, our results may not apply equally to all chipmunk species.

Even if larger chipmunks were able to link up sections of rough bark to make an ascent of a typical aspen tree, they might not do so because of their extreme vulnerability to danger during the ascent, the descent, and while foraging on the bole. This vulnerability is from 2 main risks: injury from falls and predation. During the summer of 2004, T.W. Richardson observed a chipmunk of undetermined species ascend an aspen snag with no bark, that was leaning approximately 50° against a mature aspen (59 cm dbh). When the chipmunk reached the top of the snag, it jumped to the aspen and rested momentarily in the crotch of a lateral branch. It then leapt laterally to another branch at the same height, appeared to slip, and then fell to the ground, 8.25 m below. Although this animal scurried off, apparently unfazed, such falls could be injurious or lethal. The other risk, not mutually exclusive, is predation. There is a growing body of evidence

that squirrels and other animals attempt to balance the potential benefits of foraging with the risks of becoming food themselves (Lima and Dill 1990, Lima 1998). The lack of cover presented by an aspen bole, in combination with the animal's compromised agility on that substrate and its inability to use the opposite side of the bole for cover when threatened, may prevent most chipmunks from attempting to climb aspen. Unfortunately, because none of our subjects were able to climb aspen boles, we were unable to test the importance of cover or behavior when chipmunks were threatened while climbing aspen.

Our results may have implications for fine-scale nest site selection in birds nesting in mixed aspen stands, for at least a few species. Our results clearly demonstrate that, on our study sites, Western Wood-Pewees and Warbling Vireos prefer to locate nests in aspen trees. Both of these species are known to nest in pure or nearly pure coniferous vegetation types (Chace et al. 1997, Bemis and Rising 1999, Gardali and Ballard 2000, Smith et al. 2004); however, natural selection may favor the placement of nests in aspen trees where they are available. Additionally, north of our study area, Smith et al. (2005) found that success for Warbling Vireo nests placed in aspen was higher than success for nests in lodgepole pine; however, this result was not statistically significant and no distinction was made between predation and other causes of nest failures. Yellow-rumped Warblers appeared to demonstrate a slight preference for placing their nests in aspens relative to available tree species; however, this preference was not significant. This bird species is primarily associated with conifers throughout its range, and a literature review revealed that Yellow-rumped Warblers typically place their nests on horizontal branches of conifers (Hunt and Flaspohler 1998). These warblers occurred at relatively low densities at our aspen study sites and possibly represent peripheral breeding populations in suboptimal habitat for the species. Thus, selection pressures to place nests in aspen may be relatively weak for this species on these sites or may be overridden by other selective pressures or by the inherent nest site preferences of the species. American Robins may be large enough to defend their nests from chipmunks; therefore, predation by chipmunks is a rare occurrence. Chipmunk predation on American Robin nests has not been documented so far as we are aware (Sallabanks and James 1999). It has been suggested, though rarely observed, that American Robins are able to defend their nests from slightly larger predators such as western gray squirrels (*Sciurus griseus*) and Blue Jays (*Cyanocitta cristata*) because of robins' large size and aggressive nature (Howell 1942, Gottfried et al. 1985, Schmidt and Whelan 1998).

Filliater et al. (1994) discussed the difficulty that birds face in choosing a nest site amid a rich guild of potential nest predators. Such is likely the case for birds breeding at our study sites, and we do not wish to overstate the nest site selection pressures contributed by chipmunks in these aspen stands. Further, predation alone may not explain the selection of aspen as nesting substrates at these sites. For example, birds may be selecting aspen at the nest patch or territory scale for reasons related to foraging tactics (Whelan 2001), the abundance of invertebrate prey found in aspen (Schimpf and MacMahon 1985), or fewer potential predators (Sieving and Willson 1998, Willson et al. 2003). The birds may be selecting aspen as nesting trees simply because they are the most abundant species within those preferred patches or territories, conforming to the potential-prey-site hypothesis. This hypothesis predicts that nest predator efficiency decreases as the number of potential nest sites increases (Bowman and Harris 1980, Martin 1993b). A nest placed in an aspen tree within a pure aspen stand is surrounded by other potential nest sites, thereby greatly increasing the number of locations a predator might search before locating the nest.

Nest predation by chipmunks is unlikely the sole cause of these birds' nest site preferences but almost certainly contributes selective pressures for placement of nests in aspen trees. It is significant that yellow pine chipmunks cannot climb aspen trees. Placing a nest in a mature aspen tree virtually guarantees that the nest contents will be safe from chipmunk predation. In other systems, smooth bark has been demonstrated to decrease or prevent nest predation by snakes, putatively explaining increased nesting success for a number of bird species (Rudolph et al. 1990, Hooge et al. 1999, Saenz et al. 1999, Mullin and Cooper 2002). A similar dynamic involving chipmunks as potential

nest predators is likely contributing to nest site selection for some arboreal cup-nesting birds where aspen trees are available.

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LITERATURE CITED

BEMIS, C., AND J.D. RISING. 1999. Western Wood-Pewee (*Contopus sordidulus*). *In:* A. Poole and F. Gill, editors, Birds of North America, No. 451. Academy of Natural Science of Philadelphia, American Ornithologists' Union, Washington, DC.

BOWMAN, G.B., AND L.D. HARRIS. 1980. Effect of spatial heterogeneity on ground-nest predation. Journal of Wildlife Management 44:806–813.

CALLAHAN, J.R. 1993. Squirrels as predators. Great Basin Naturalist 53:137–144.

CHACE, J.F., A. CRUZ, AND A. CRUZ, JR. 1997. Nesting success of the Western Wood-Pewee in Colorado. Western Birds 28:110–112.

COLLIAS, N.E., AND E.C. COLLIAS. 1984. Nest building and bird behavior. Princeton University Press, Princeton, NJ.

CONWAY, C.J., AND T.E. MARTIN. 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54:670–685.

CRAIG, D.P. 1998. Chipmunks use leverage to eat oversize eggs: support for the use of quail eggs in artificial nest studies. Auk 115:486–489.

ELLIOT, L. 1978. Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. Smithsonian Contributions to Zoology 265:1–107.

FILLIATER, T.S., R. BREITWISCH, AND P.N. NEALEN. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96:761–768.

FORSTMEIER, W., AND I. WEISS. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. Oikos 104:487–499.

GARDALI, T., AND G. BALLARD. 2000. Warbling Vireo (*Vireo gilvus*). *In:* A. Poole and F. Gill, editors, Birds of North America, No. 551. Academy of Natural Science of Philadelphia, American Ornithologists' Union, Washington, DC.

GOTTFRIED, B.M., K. ANDREWS, AND M. HAUG. 1985. Breeding robins and nest predators: effect of predator type and defense strategy on initial vocalization patterns. Wilson Bulletin 97:183–190.

GRINNELL, J. 1908. The biota of the San Bernardino Mountains. University of California Publications in Zoology 5:1–170.

GRINNELL, J., AND T.I. STORER. 1924. Animal life in the Yosemite. University of California Press, Berkeley.

HOOGE, P.N., M.T. STANBACK, AND W.D. KOENIG. 1999. Nest-site selection in the Acorn Woodpecker. Auk 116:45–54.

HOWELL, J.C. 1942. Notes on the nesting habits of the American Robin (*Turdus migratorius* L.). American Midland Naturalist 28:529–603.

HUNT, P.D., AND D.J. FLASPOHLER. 1998. Yellow-rumped Warbler (*Dendroica coronata*). *In:* A. Poole and F. Gill, editors, Birds of North America, No. 376. Academy of Natural Science of Philadelphia, American Ornithologists' Union, Washington, DC.

KAUFERT, F. 1937. Factors influencing the formation of periderm in aspen. American Journal of Botany 24: 24–30.

KETTERSON, E.D., V. NOLAN, JR., M.J. CAWTHORN, P.G. PARKER, AND C. ZIGENFUS. 1996. Phenotypic engineering: using hormones to explore the mechanistic and functional bases of phenotypic variation in nature. Ibis 138:70–86.

LACK, D. 1954. The regulation of animal numbers. Clarendon Press, Oxford, U.K.

LIEBEZEIT, J.R., AND T.L. GEORGE. 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed Ponderosa Pine forest. Condor 104:507–517.

LIMA, S.L. 1998. Stress and decision making under risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215–290.

LIMA, S.L., AND L.M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

LIMA, S.L., AND T.J. VALONE. 1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. Animal Behaviour 34:536–544.

MARTIN, T.E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 *in* J.M. Hagan and D.W. Johnston, editors, Ecology and conservation of neotropical migrants. Smithsonian Institution Press, Washington, DC.

_____. 1993a. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897–913.

_____. 1993b. Nest predation and nest sites: new perspectives on old patterns. BioScience 43:523–532.

MARTIN, T.E., AND C.K. GHALAMBOR. 1999. Males helping females during incubation. I. Required by microclimate or constrained by nest predation? American Naturalist 153:131–139.

MARTIN, T.E., AND J.J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

MARTIN, T.E., J. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London. Series B, Biological Sciences 267:2287–2293.

MORTON, E.S. 2005. Predation and variation in breeding habitat use in the Ovenbird, with special reference to breeding habitat selection in northwestern Pennsylvania. Wilson Bulletin 117:327–335.

MULLIN, S.J., AND R.J. COOPER. 2002. Barking up the wrong tree: climbing performance of rat snakes and

its implications for depredation of avian nests. Canadian Journal of Zoology 80:591–595.

NICE, M.M. 1957. Nesting success in altricial birds. Auk 74:305–321.

PURCELL, K.L., AND J. VERNER. 1999. Predators of open and cavity nesting birds in oak woodlands. Wilson Bulletin 111:215–256.

RICHARDSON, T.W. 2005. Avian species richness, abundance, and nesting success in aspen habitats of the Truckee River Watershed, final report: 2002–2004. Biological Resources Research Center, University of Nevada, Reno.

RICKLEFS, R.E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

RUDOLPH, D.C., H. KYLE, AND R.N. CONNER. 1990. Red-cockaded Woodpeckers vs rat snakes: the effectiveness of the resin barrier. Wilson Bulletin 102:14–22.

SAENZ, D., C.S. COLLINS, AND R.N. CONNER. 1999. A bark-shaving technique to deter rat snakes from climbing Red-cockaded Woodpecker cavity trees. Wildlife Society Bulletin 27:1069–1073.

SALLABANKS, R., AND F.C. JAMES. 1999. American Robin (*Turdus migratorius*). *In:* A. Poole and F. Gill, editors, Birds of North America, No. 462. Academy of Natural Science of Philadelphia, American Ornithologists' Union, Washington, DC.

SAS. 1999. SAS online documentation, version 8. SAS Institute, Cary, NC.

SCHIMPF, D.J., AND J.A. MACMAHON. 1985. Insect communities and faunas of a Rocky Mountain subalpine sere. Great Basin Naturalist 45:37–60.

SCHMIDT, K.A., AND C.J. WHELAN. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. American Naturalist 152:393–402.

SHIGO, A.L. 1985. How tree branches are attached to trunks. Canadian Journal of Botany 63:1391–1401.

SIEVING, K.E., AND M.F. WILLSON. 1998. Nest predation and avian species diversity in northwestern forest understory. Ecology 79:2391–2402.

SMITH, J.I., M.D. REYNOLDS, AND G. LEBUHN. 2004. Warbling Vireo nesting ecology in the northern Sierra Nevada. Western Birds 35:32–41.

_____. 2005. Warbling Vireo reproductive success and nest-site characteristics in northern Sierra Nevada, California. Journal of Field Ornithology 76:383–389.

STATES, J.B. 1976. Local adaptations in chipmunk (*Eutamias amoenus*) populations and evolutionary potential at species' borders. Ecological Monographs 46:221–256.

WHELAN, C.J. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. Ecology 82:219–231.

WILLSON, M.F., T.L. DE SANTO, AND K.E. SIEVING. 2003. Red squirrels and predation risk to bird nests in northern forests. Canadian Journal of Zoology 81: 1202–1208.

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