# SPECIAL SECTION: CAVITY NESTERS AND KEYSTONE PROCESSES

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# EMERGING CONCEPTS AND RESEARCH DIRECTIONS IN THE STUDY OF CAVITY-NESTING BIRDS: KEYSTONE ECOLOGICAL PROCESSES

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The papers in this special section of *The Condor* derive from a symposium entitled ''The Ecology of Cavity Nesters: Keystone Processes,'' which we organized for the Third North American Conference, held in September 2002 in New Orleans, Louisiana. The purpose of this symposium was to examine the current state of knowledge about cavity-nesting birds, ubiquitous in the world's forests, and discuss directions for future research and conservation. The unifying theme of the symposium, and what we believe is a key paradigm in understanding ecological systems, is the concept of keystone interactions and processes. Keystone species are those that exhibit disproportionate influence over the structure and function of their community due to some life-history trait or interactions with other species (Paine 1969). Keystone processes, then, may be defined as the interactions between one or more keystone species with both biotic and abiotic factors, that influence resource creation, use, and exchange for many species. Our symposium covered a broad range of species and processes involving cavity-nesting birds. The papers that follow were developed from the presentations included in the symposium.

Although it has been recognized for decades that primary cavity nesters (i.e., excavators) provided resources that facilitate the survival and viability of many organisms in forest communities, investigations into how these connections and interactions work have been rare. Notable exceptions include groundbreaking explorations into fungus–bird interactions implemented by Shigo and Kilham (1968), Conner et al. (1976), and Jackson (1977).

Generally, research on hole-nesting birds has focused on one or two cavity-nesting species per study (e.g., the Pileated Woodpecker [*Dryocopus pileatus*]; Bull and Holthausen 1993) or one aspect of forest ecology (e.g., snag density; Conner 1978, Mannan et al. 1980, Lewis 1998). Studies of woodpeckers and other cavity nesters have tended to focus particularly on nest-site selection (e.g., Raphael and White 1984, Zarnowitz and Manuwal 1985, Swallow et al. 1986). While this is certainly an important aspect of a bird's habitat needs, these data were generally not considered within the broader ecological context of how cavities came to be and their ultimate role in supporting a functioning ecosystem. Except for the early series of investigations into fungus–bird interactions cited above, researchers have only recently begun to explore the complex relationships among microorganisms, fungi, insects, primary and secondary cavity users, and the processes that create suitable habitat for all groups.

## EMERGING THEMES IN CAVITY-NESTER ECOLOGY

Martin and Eadie (1999) offered a theoretical framework for examining the complex interactions of cavity-nester ecology: the nest web, a hierarchical community structure that is similar to a food web but maps the interdependence of members of the cavity-nesting community. Based on 7 years of data on almost 2000 cavity nests, Martin et al. (2004) demonstrate the im-

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portance of interactions within the nest-web community of the forests of interior British Columbia. This cavity-dependent community was composed of five groups based on nest-site characteristics: (1) large woodpeckers (Pileated Woodpecker), (2) medium-sized woodpeckers (e.g., Hairy Woodpecker [*Picoides villosus*]), (3) weak excavators (e.g., Downy Woodpecker [*P. pubescens*]), (4) Northern Flickers (*Colaptes auratus*), the most abundant excavator, and the larger secondary cavity nesters, and (5) the most aggressive and most abundant secondary cavity nesters (e.g., European Starling [*Sturnus vulgaris*]). Martin et al. (2004) found that cavity resources were channeled primarily through the preferred cavity tree, quaking aspen (*Populus tremuloides*), and then through cavities excavated by Northern Flickers. These cavities were exploited by >22 species of secondary cavity nesters, including mammals. The determination of this hierarchical resource structure allowed for the identification of the Northern Flicker as the principal keystone species in this system, and the limiting resource as quaking aspen cavity trees.

Saab et al. (2004) have collected extensive data on the factors that influence cavity occupancy related to time after fire in western forests. These authors look at the dynamics of cavity use from a somewhat different perspective. Specifically, Saab et al. (2004) examine patterns from the temporal perspective and model cavity nester use over time, as opposed to using the snapshot approach and diagramming the way cavities pass among species groups (Martin et al. 2004). Saab et al. (2004) explore the influence of several variables potentially affecting postfire occupancy by cavity-nesting birds, including the length of time since fire, the proximity of unburned forest, and tree characteristics within the burn site (e.g., tree height and diameter). These factors are examined for their effects on both strong cavity excavators (e.g., Hairy Woodpecker) and a weak excavator, Lewis's Woodpecker (*Melanerpes lewis*). Saab et al. (2004) document a succession of use by cavity nesters, especially in relation to time since fire. This modeling effort also indicated that strong excavators occupied cavities longer in the larger burned area. These patterns suggest that woodpecker populations may depend substantially on forest landscape structure as well as individual tree characteristics and that these are ephemeral habitats that change rapidly after fire. Importantly, occupancy of cavity excavators declined more rapidly in the smaller, patchier burned area, possibly due to colonization by predators from adjacent undisturbed habitat. Data provided by Saab et al. (2004) suggest that periodic stand-replacement fires are needed to provide high-quality habitat on a continuous basis for several important keystone woodpeckers using western conifer forests. What proportion of the landscape should be composed of recently burned areas to sustain viable populations of primary keystone excavators is not known.

One pattern that seems to be emerging from intensive studies elucidating the keystone linkages in a number of diverse ecosystems is that most often only one, or sometimes two, species of primary excavator supply the bulk of the cavities that support the entire nest webs in those systems. Specifically, Martin et al. (2004) documented that the Northern Flicker furnished most cavities used by the variety of secondary cavity nesters in the mixed interior forests of British Columbia. In this system, a distant second in importance was the Pileated Woodpecker, which especially provided cavities for the larger species of the nest web. In the burned ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) forests of Idaho, data collected by Saab et al. (2004) suggested that Hairy Woodpeckers and Northern Flickers engineered most of the cavities that supported the nest web in that system. In natural fire-maintained southern pine ecosystems, Conner et al. (2001) have proposed that the Red-cockaded Woodpecker (*Picoides borealis*) was essentially the exclusive keystone cavity excavator. In our own studies of nest-web linkages in the western hemlock (*Tsuga heterophylla*)–Douglas-fir forests of the Olympic Peninsula, we have documented that the Hairy Woodpecker is the principal cavity provider in that system (Huss et al. 2002, Ripper 2002). This pattern, that nest webs and the resulting community diversity and myriad ecological interactions among these secondary cavity users in a given forest ecosystem may be founded on one or two principal keystone species, has huge conservation implications. Future studies dissecting the nest webs of additional forest systems are needed to determine if this pattern is universal.

But does a tree simply need to die to become a cavity-ridden snag occupied by a succession of birds, mammals, and other forest creatures? Another important theme emerging from these papers and other recent research is the role of fungal decay in creating wood that is suitable for excavation. Jackson and Jackson (2004) synthesize what is known about the fungal processes involved in the creation of suitable cavity trees. Their work suggests fungi provide the vital catalytic conditions that enable keystone excavators to perform the essential service of transforming decayed (usually) wood into the cavities that support complex nest webs. Jackson and Jackson (2004) relate how fungal invasion facilitates cavity excavation by woodpeckers. Their review reveals that a key question is whether a fungal infection is necessary for primary cavity excavation. The answer to this question appears to be a tentative yes, except possibly for two species, Red-cockaded Woodpecker and Acorn Woodpecker (*Melanerpes formicivorus*), which occasionally excavate cavities in living, undecayed wood (Jackman 1975, Jackson and Jackson 2004). To our knowledge, no non-cooperatively breeding woodpecker has been documented to excavate a cavity in the living part of a tree (Jackman 1975).

Farris et al. (2004) describe the interactions of wood-boring and bark beetles, sapwood fungi, and woodpecker use of trees for foraging. These researchers employed the interesting approach of using a resistograph to measure sapwood density, and then correlated this variable with woodpecker use of foraging trees. Farris et al. (2004) suggested woodpeckers may promote fungal invasion and sapwood decay in ponderosa pine (*Pinus ponderosa*) systems based on two findings: (1) fungi were isolated from woodpecker bills in greater frequencies than in a reference sample of non-bark-foraging birds, and (2) high levels of woodpecker foraging were associated with lower-density (i.e., decayed) wood. On the other hand, insect activity was not related to wood density. Therefore, the data collected by Farris et al. (2004) suggest that woodpeckers could represent important vectors for establishing fungal decay in sapwood, which would in turn provide suitable sites for cavity establishment in ponderosa pine. This suggests the possibility of an intriguing symbiosis, whereby woodpeckers disperse fungi, and the fungi later facilitate cavity excavation. Whether this could represent a coevolved process or just an interesting phenomenon with secondary ecological consequences remains to be explored.

An important point derived from Farris et al. (2004), as well as the other research reported in these papers, is that management strategies to maintain healthy, functioning forests must recognize and retain these complex multispecies processes. A variety of data indicate strongly that not all snags are created equal in terms of suitability for cavity excavation and use by cavity nesters (Jackson and Jackson 2004). Simply maintaining a certain number of snags per area in all likelihood will not result in the retention of natural keystone processes involving primary cavity excavators. Rather, the data presented in the following papers suggest appropriate conservation strategies to protect interdependent forest communities must be designed to maintain the complex biotic interactions among fungi, insects, other microorganisms, and cavity excavators. We hope the presentation of these papers stimulates further inquiry into these topics and leads to more effective conservation strategies to preserve the ecological integrity of our forest systems.

A shift in focus from the single-species approach to the complex community and process-based approach has far-reaching implications for the conservation of forest habitat (Martin et al. 2004). The following papers present new paradigms, develop new methodology for the study of keystone interactions, and define insightful research questions involving cavity-nesting birds. We suggest that future research in forest ecosystems continue to take into account interactions between primary and secondary cavity nesters as well as the natural processes that create suitable habitat for all cavity-nesting animals. Forest management practices intended to conserve a diverse wildlife community, and the processes that shape these communities, must be based on quantitative assessments of these complex ecological interactions.

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