Co-occurrence patterns of cavity-nesting birds in cottonwood-willow communities

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Summary. We studied the covariation of six species of cavity-nesting birds to determine the extent to which species' co-occurrence patterns were attributable to interspecific relations. We tested two null hypotheses: (1) inverse relations did not exist among potential competitors for nest trees or nest cavities, and (2) there were no positive relations among potential commensals for nest cavities. Statistical power analyses, and simple, partial, and multiple partial correlation and regression analyses provided little evidence of species-specific or higher-order inverse or positive relations. Most of the variation in co-occurrence patterns was associated with stand characteristics. Collectively, an abundance of nest trees and nest cavities, differences among species in acceptable nest-tree and nest-cavity dimensions, and different periods of peak nesting activity appear to be responsible for the lack of negative relations among potential competitors. Positive relations among potential commensals were weak presumably because (1) secondary cavity nesters (SCNs) frequently used cavities that originated from wind-, lightning-, and/or disease-damaged limbs and were thus not dependent completely on primary cavity nesters for cavities, and (2) the lag time for cavity use by SCNs is often two or more seasons. Interspecific relations were apparently not major determinants of community structure during our investigation; assemblages of cavity nesters appeared instead to be influenced more by independent species-specific habitat responses.

Key words: Cavity-nesting birds – Co-occurrence patterns – Independent autecological responses – Cottonwood-willow communities

The structure of breeding bird communities is influenced by numerous factors, including competition, predation, brood parasitism, regional population changes, and autecological habitat responses (e.g., Terborgh and Weske 1975; Ambuel and Temple 1983; Gilpin and Diamond 1984; Järvinen and Haila 1984; Sherry and Holmes 1985). For hole-nesting birds, exploitative or interference competition for nest trees or cavities (e.g., von Haartman 1957; Brown 1981; van Balen et al. 1982; Nilsson 1984; Belles-Isles and Picman 1986) could be particularly significant. Delayed commensalism may also strongly influence the structure of cavity-nester communities because nest holes excavated by primary cavity nesters (PCNs) are used later during the same or subsequent breeding seasons by secondary cavity nesters (SCNs) (nonexcavators) (e.g., Gutzwiller and Anderson 1986). Thus, SCNs benefit from the excavating activities of PCNs, but there are neither direct benefits nor direct costs to PCNs in terms of nest cavities. An alternative to the hypothesis that cavity-nester communities are structured by interspecific interaction is that these assemblages arise solely from species-specific habitat responses that are independent, but similar in time and space (cf. Haila et al. 1980; Holmes and Robinson 1981; Wiens 1983:377).

Habitat features do influence assemblages of cavity-nesting birds (Conner and Adkisson 1977; Stauffer and Best 1982; Raphael and White 1984), but to what extent is the variation in species' co-occurrence patterns also attributable to interspecific relations? We addressed this question by first controlling (statistically) for the influence of similar and dissimilar habitat associations among species (cf. Wiens 1983:378; Mountainspring and Scott 1985). Our data are observed patterns of co-occurrence; they are the results of processes, not a characterization of the processes themselves. We therefore emphasize inferences about the extent and nature of relations among species, not the causal mechanisms underlying these patterns. Ideally, process inferences should be based on experimentation. But, like manipulative experiments, analytical control of confounding sources of variation improves inferences about process from pattern by reducing the number of plausible explanations for observed relations (cf. James and McCulloch 1985:23, 25, 44).

Our statistical approach has strengthened the validity of our inferences about process, but we regard them, nevertheless, as tentative and in need of experimental verification. Our interests included species-species, diffuse, and distributed relations. Diffuse inverse relations, in which occupation of an area by one species is precluded by collective negative effects from similar sympatric species (see diffuse competition, MacArthur 1972), has not been studied explicitly as a structuring force in cavity-nester communities. Distributed inverse relations, defined here as relations in which a group of two or more species is excluded from an area because of intense negative interaction originating from one other species, has not been examined for these species either. We tested for patterns (but not process) consistent with diffuse and distributed competition among PCNs and SCNs separately and collectively. We also tested...
for relations in accord with simple and multiple commensalism among PCNs and SCNs. Without an analysis of such patterns the contribution of these types of association in the assembly of cavity-nesting bird communities is unclear. This is unacceptable because avian ecologists are often asked to formulate conservation strategies for entire suites of species. Effective advice can stem only from a lucid understanding of the many forces influencing community structure. We tested two general null hypotheses: (1) inverse relations did not exist among potential competitors for nest trees or nest cavities, and (2) there were no positive relations among potential commensals for nest cavities.

**Methods**

**Nest detectability and abundance**

We studied cavity-nesting bird communities in 34 disjunct cottonwood-willow (*Populus-Salicis*) stands during 1983 and 1984 along 22.2 km of the North Platte River between Guernsey and Fort Laramie in Platte and Goshen Counties, Wyoming, USA. Stands were groups of trees (≥10.2 cm diameter at breast height) separated from all other such groups or individual trees by at least 30 m (Gutzwiller and Anderson 1987a). Individuals were assumed to be tending one nest in only one stand at any given time. Every 2 wk (four times each nesting season) KJG searched the entire area of each stand for active nests at a rate of 15 min/ha. To avoid daily and seasonal biases arising from bird activity levels, the time of daily searches was randomized and the sequence of searches was reversed between seasons.

Among species, there may have been differences in visibility (due to color and/or size) or audibility (from nestlings and/or feeding or defensive adults) at nests. Differences in time necessary to locate nests would be evident in comparisons of results from 15-min/ha and 30-min/ha searches within and among species. Specifically, species whose nests were difficult to detect would be expected to have a considerably higher average nest abundance based on a 30-min/ha search, relative to a 15-min/ha search in the same stand and at a comparable time, because there would be more time for nest discovery. Further, any increase in the number of nests found between 15- and 30-min/ha searches should be greater for "secretive" versus readily detected species because fewer nests of the former would be found during the shorter searches. Our results of such comparisons indicated almost no difference in nest abundance between regular searches (15 min/ha) and combined searches (results from initial regular searches plus a second regular search 2–3 days later [collectively a 30 min/ha search]) within or among species, suggesting negligible detection bias (Gutzwiller 1985:95–96). Because the results of the regular searches approximate (but are not necessarily equivalent to) true abundance, they are concomitantly reasonable estimates of relative nest abundance.

We believe differential nest detectability among species was minimal for several reasons. First, the stands we studied were primarily open, park-like habitats in which visual and aural detection of all species was excellent. And, because all species nested in boles and dead limbs of mature trees, not their crowns or areas completely concealed by foliage, movements by all species near nests were quite visible. Secondly, every species scolded KJG from perches near nests upon discovering him, thereby revealing even the most obscure nest locations. Finally, adults of every species made frequent trips to their nests with food, and the incessant back-and-forth movement was easily noticed for all species. Vegetative features that could have produced visibility or aural bias (e.g., densities of snags and healthy trees, shrub cover, distance between upper and lower canopies, distance to edge, distance to opening) were indistinguishable among species' nest sites and randomly selected sites (Gutzwiller and Anderson 1987a). With respect to these features, no species nested in habitat that was more or less dense than the stands in general (as represented by random sites). Further, adult and nestling behavior (movement and/or vocalization) probably differed little, if any, within a species across all stands. We believe our estimates of nest abundance are reasonably accurate, but even if there were differences among species in nest detectability, the biases would have been the same for each stand because of similar habitat conditions and avian behavior. Consequently, the actual slopes of positive or negative relations among abundances of species' nests would still be represented well by our results.

Nests were searched for from mid May to early July each year, a period involving nest initiation, incubation, and the feeding of nestlings (and/or fledging) for most pairs of all species. Exceptions include some early nesting European Starlings (*Sturnus vulgaris*) (which fledged young in late May) and late-nesting House Wrens (*Troglodytes aedon*), American Kestrels (*Falco sparverius*), and Red-headed Woodpeckers (*Melanerpes erythrocephalus*) (which fledged young after mid July). Attempts to displace nests, takeover cavities, and destroy nest contents were clearly evident during searches but were very few in number (Gutzwiller and Anderson 1986). If such competitive effects were more common, this would have been reflected in the searches and observations at nests.

We were careful to include in our analysis only those nests that could be verified as such. Some cavities that were excavated were not used as nest cavities, although they may have been used for roosting. Further, nest desertion may arise from many factors other than competition, including wind damage (K. J. Gutzwiller, personal observation), death of initiator(s), lack or disruption of a pair bond, and parasite infestation and pathogen infection of cavities (Clark and Mason 1985). Male House Wrens often prepare more than one cavity to advertise to females (Harrison 1978:230), but not all of these are used as nest cavities. If interpreted incorrectly, these and similar phenomena would lead to less accurate estimates of nest abundance and interspecific relations. Our use of verified nests avoids these problems.

This study involves nest abundances of three PCNs (Northern Flicker [*Colaptes auratus*], Red-headed Woodpecker, Downy Woodpecker [*Picoides pubescens]*) and three SCNs (American Kestrel, *Falco sparverius*). The hypotheses tested required two separate data sets on nest abundances. For the hypothesis about inverse relations, we computed average abundance (mean abundance for 1983 and 1984 combined) for each species and stand. To avoid artifactitious relations derived from single-season analyses (see Wiens 1981), data for the two years were combined to permit inferences about the two-season period as a whole. Such combinations can mask differences in abundance among species and/or between years within species and thus misrepresent reality. But this did not appear to