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AVIAN RESPONSE TO NEST BOX ADDITION IN TWO FORESTS OF THE COLORADO FRONT RANGE

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Abstract.—Numbers of birds on 54 circular plots (50-m radius) were counted in two Colorado forest sites for 2 yr, then four artificial nest boxes were added to each of 27 of the plots, and counts continued for 2 more yr. Combined abundances of eight box-using species increased more than threefold on experimental plots compared to unmanipulated control plots, apparently as a result of the box additions. Common cavity-nesting species that responded most strongly to nest box additions included the Mountain Chickadee (*Parus gambeli*), Pygmy Nuthatch (*Sitta pygmaea*) and House Wren (*Troglodytes aedon*). Combined abundances of open-nesting species did not change on experimental versus control plots during the experiment. Results of this study suggest that secondary cavity-nesters were limited by the quantity or quality of available nest sites, but that increased numbers of cavity-nesting species had no affect on abundances of open-nesting species.

RESPUESTAS DE LAS AVES A LA ADICIÓN DE CAJAS PARA ANIDAR EN DOS BOSQUES EN EL ESTE DE LAS ROCOSAS EN COLORADO

Sinopsis.—Se contaron los números de aves en 54 parcelas circulares (50 m radio) en dos áreas boscosas de Colorado por dos años, y luego se anadieron cuatro cajas para anidar en cada una de 27 de las parcelas y se siguió monitoreandolas por dos años más. Las abundancias combinadas de ocho especies que utilizan cajas para anidar aumentaron más de tres veces en las parcelas experimentales al compararlas con las parcelas de control, aparentemente debido a la adición de las cajas. Las especies comunes que anidan en cavidades que respondieron más intensamente a la adición de cajas son *Parus gambeli, Sitta pygmaea* y *Troglodytes aedon*. Las abundancias combinadas de especies que anidan de forma abierta no mostraron cambios entre las parcelas controles y experimentales durante el experimento. Los resultados de este estudio sugieren que aves que anidan en cavidades secundarias estaban limitadas por la cantidad o calidad de lugares de anidar accesibles, pero que un número mayor de aves que anidan en cavidades no tuvieron efecto en la abundancia de aves que anidan de forma abierta.

A central and long-standing debate in avian ecology concerns the importance of interspecific competition in determining the distribution and abundance of birds (Grinnell 1917, MacArthur 1972, Wiens 1989). Although there is widespread agreement that field experiments are the most powerful means of testing hypotheses about competition (Schoener 1983), such experiments have been uncommon in avian ecology, because of difficulties inherent in manipulating bird populations in the field (Brawn et al. 1987, Wiens 1989).

Experimental additions of nest boxes can determine if secondary cavity-nesting birds are limited by competition for suitable nest sites (Brawn and Balda 1988, East and Perrins 1988, Waters et al. 1990). Nest box experiments potentially also permit tests of hypotheses about the role of interspecific competition between cavity and open-nesting species. Specifically, if entire avian assemblages are limited by competition for shared resources, such as insect foods, then open-nesting species might avoid areas where local densities of cavity-nesters have increased following nest box addition.

Hogstad (1975) and Bock et al. (1992) found evidence for reciprocal density changes among birds following nest box additions in a coniferous forest in Norway and in riparian woodlands in southeastern Arizona. By contrast, nest box experiments in pine forests of northern Arizona (Brawn et al. 1987), in British woodlands (East and Perrins 1988), and in forests of central Finland (Mönkkönen et al. 1990), although resulting in increased densities of cavity-nesters, did not result in any evidence of compensatory declines in abundances of open-nesting species.

Additional nest box experiments should reveal more about the circumstances in which cavities are or are not limiting to hole-nesting birds, and, potentially, whether interspecific competition between cavity and open-nesting species is important in determining the composition of avian communities as a whole. We are aware of only one other controlled experiment involving addition of nest boxes to coniferous forests in western North America (Brawn and Balda 1988, Brawn et al. 1987). In the present study, we counted birds for 2 yr on 54 small (50-m radius) plots in two forests of the Colorado Front Range, then added four nest boxes to each of 27 of the plots, and continued the counts for two additional years. Objectives of the study were to determine if nest box addition resulted in increased local abundances of cavity-nesting birds, and if declines of open-nesting species occurred on experimental plots following nest box addition, compared to the patterns on unmanipulated control plots.

METHODS

The two study areas were Betasso Preserve and Walker Ranch, both managed as natural areas by the Boulder County, Colorado, Open Space Department. Betasso Preserve (40°01′20″, 105°21′00″) is at about 1900 m elevation, and includes a mosaic of ponderosa pine (*Pinus ponderosa*) forest and montane meadow. Scattered small drainages are lined with shrubs, including willow (*Salix* spp.), alder (*Alnus* spp.), and skunkbush (*Rhus trilobata*). Walker Ranch (39°58′00″, 105°21′15″) is at about 2300 m elevation, and is a similar landscape except that the forest includes a mixture of ponderosa pine, Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*).

In April 1990, we established 30 circular plots at Betasso Preserve and 24 plots at Walker Ranch, each 50-m radius. The edge of each plot was $>$ 200 m from its nearest neighbor. It is not clear how far apart such small circular plots should be to be considered independent (Verner 1985), but DeSante (1981) suggested 180 m as an appropriate inter-plot distance for wooded habitats. All of our plots included substantial forest, but about half also included some forest/meadow edge.

Our census method was the fixed-distance point count (Verner 1985), in which we stood at a plot center and recorded all birds seen or heard within 50 m, over a 7-min period. Bird detectability doubtless varied among species and plots, but because detectability was essentially constant

TABLE 1. Numbers of birds per plot (means, with SE in parentheses) counted before (1990–1991) and after (1992–1993) addition of artificial nest boxes to experimental plots, compared with numbers counted over the same period on unmanipulated control plots, in two Colorado forest sites.

		Betasso Preserve		Walker Ranch	
Species	Plot type	Before	After	Before	After
Cavity-nesters					
Violet-green Swallow	experimental	0.33 (0.21)	5.60 (1.78)	0.50 (0.23)	5.08 (1.96)
(*Tachycineta thalassina*)	control	0.73 (0.37)	1.40 (0.49)	0.58 (0.29)	0.67 (0.33)
Mountain Chickadee	experimental	3.67 (0.58)	8.73 (1.05)	4.17 (0.80)	7.25 (1.14)
(*Parus gambeli*)	control	3.07 (0.57)	3.80 (0.93)	3.67 (0.71)	3.75 (0.46)
White-breasted Nuthatch	experimental	0.27 (0.12)	4.13 (0.83)	0.42 (0.23)	1.33 (0.51)
(*Sitta carolinensis*)	control	0.40 (0.27)	0.80 (0.30)	0.58 (0.29)	0.92 (0.19)
Red-breasted Nuthatch	experimental	0.40 (0.24)	1.47 (0.56)	0.25 (0.13)	1.67 (0.70)
(*S. canadensis*)	control	0.13 (0.09)	0.33 (0.21)	0.42 (0.23)	1.25 (0.54)
Pygmy Nuthatch	experimental	1.93 (0.56)	13.60 (1.55)	0.67 (0.23)	3.33 (1.12)
(*S. pygmaea*)	control	1.67 (0.64)	5.33 (0.72)	1.67 (0.72)	2.82 (0.83)
House Wren	experimental	0.13 (0.09)	1.93 (0.92)	2.50 (0.60)	27.58 (2.69)
(*Troglodytes aedon*)	control	0.20 (0.15)	0.33 (0.16)	5.00 (1.48)	8.17 (1.55)
Western Bluebird	experimental	0.07 (0.06)	5.20 (1.27)	0	0
(*Sialia mexicana*)	control	1.33 (0.63)	0.87 (0.34)	0.08 (0.08)	0
Mountain Bluebird	experimental	0.13 (0.13)	0	0.75 (0.35)	4.75 (1.12)
(*S. currucoides*)	control	0.40 (0.24)	0	1.83 (1.07)	1.17 (0.52)
Open-nesters					
Broad-tailed Hummingbird	experimental	2.60 (0.69)	1.67 (0.70)	2.75 (0.58)	4.83 (0.92)
(*Selasphorus platycerus*)	control	1.13 (0.26)	0.67 (0.21)	3.33 (0.69)	2.83 (0.61)
Western Wood-Pewee	experimental	1.20 (0.45)	2.33 (0.70)	1.50 (0.63)	3.08 (0.95)
(*Contopus sordidulus*)	control	1.80 (0.46)	1.67 (0.48)	2.17 (0.56)	2.75 (0.81)
Steller's Jay	experimental	1.00 (0.34)	1.33 (0.27)	0.25 (0.18)	0.50 (0.29)
(*Cyanocitta stelleri*)	control	0.80 (0.22)	1.53 (0.55)	0.58 (0.19)	1.08 (0.34)
Townsend Solitaire	experimental	0.80 (0.31)	0.60 (0.27)	0.08 (0.08)	0.75 (0.25)
(*Myadestes townsendi*)	control	0.13 (0.09)	0.27 (0.15)	1.25 (0.59)	1.42 (0.43)

TABLE 1. Continued.

Species	Plot type	Betasso Preserve		Walker Ranch	
		Before	After	Before	After
American Robin	experimental	4.33 (0.77)	5.80 (0.86)	5.58 (0.92)	6.83 (0.90)
(*Turdus migratorius*)	control	3.33 (0.55)	5.67 (0.70)	4.83 (1.19)	7.25 (0.95)
Solitary Vireo	experimental	2.00 (0.53)	2.13 (0.57)	0.42 (0.15)	0.58 (0.26)
(*Vireo solitarius*)	control	1.60 (0.41)	0.80 (0.28)	0.25 (0.18)	0.33 (0.19)
Virginia's Warbler	experimental	1.47 (0.52)	0.67 (0.23)	1.58 (0.56)	1.08 (0.34)
(*Vermivora virginiae*)	control	1.13 (0.48)	0.67 (0.29)	1.17 (0.47)	1.83 (0.55)
Yellow-rumped Warbler	experimental	1.27 (0.47)	0.73 (0.37)	1.83 (0.38)	2.83 (0.77)
(*Dendroica coronata*)	control	1.13 (0.31)	0.47 (0.19)	1.17 (0.32)	1.42 (0.34)
Western Tanager	experimental	1.20 (0.43)	3.80 (0.53)	2.08 (0.86)	3.08 (0.47)
(*Piranga ludoviciana*)	control	0.87 (0.27)	1.93 (0.56)	0.83 (0.21)	2.33 (0.91)
Green-tailed Towhee	experimental	0.27 (0.18)	1.20 (0.37)	0.42 (0.19)	4.50 (1.33)
(*Pipilo chlorurus*)	control	0	0.47 (0.22)	0.58 (0.23)	6.17 (0.90)
Rufous-sided Towhee	experimental	0.87 (0.50)	2.47 (0.81)	0.17 (0.11)	0.16 (0.11)
(*P. erythrophthalmus*)	control	0.87 (0.39)	2.87 (0.70)	0.25 (0.13)	0.67 (0.28)
Vesper Sparrow	experimental	0.47 (0.29)	0.40 (0.27)	1.08 (0.65)	1.25 (0.69)
(*Pooecetes gramineus*)	control	1.00 (0.35)	0.47 (0.22)	0.42 (0.19)	0.58 (0.36)
Chipping Sparrow	experimental	6.53 (1.16)	9.13 (1.30)	5.25 (1.16)	5.17 (1.07)
(*Spizella passerina*)	control	7.40 (1.08)	9.40 (1.34)	3.75 (0.80)	5.08 (1.25)
Dark-eyed Junco	experimental	2.40 (0.41)	4.40 (0.98)	3.75 (1.01)	3.42 (0.66)
(*Junco hyemalis*)	control	3.33 (1.05)	3.20 (0.68)	3.08 (0.79)	5.50 (1.03)
Brown-headed Cowbird	experimental	0.33 (0.19)	1.20 (0.67)	0.33 (0.33)	1.25 (0.58)
(*Molothrus ater*)	control	0.20 (0.20)	0.53 (0.24)	0.25 (0.13)	0.75 (0.28)
Pine Siskin	experimental	0	0.40 (0.24)	1.00 (0.30)	2.17 (0.82)
(*Carduelis pinus*)	control	0.13 (0.09)	0.40 (0.34)	0.75 (0.33)	2.17 (0.42)
Red Crossbill	experimental	0.53 (0.32)	0.47 (0.32)	0	0
(*Loxia curvirostra*)	control	1.13 (0.56)	0.53 (0.36)	1.16 (0.59)	0.50 (0.42)
Cassin's Finch	experimental	0.53 (0.19)	0.40 (0.19)	2.42 (0.68)	1.58 (0.79)
(*Carpodacus cassinii*)	control	0.80 (0.33)	1.67 (0.60)	1.08 (0.53)	2.25 (0.79)

during the study, we believe the raw counts were accurate indices of changing relative abundances of birds before versus after nest box additions.

We counted birds on the 54 plots on six mornings between late May and early July in both 1990 and 1991. The plots were then divided randomly into control and experimental groups of 15 plots of each type at Betasso Preserve, and 12 plots of each type at Walker Ranch. In October 1991, four Schwegler brand "forest-type" birdhouses were added to each of the 27 experimental plots. The boxes were hung in an east-facing direction on the trunks of trees within 50 m of plot centers. Box height was about 5 m, and diameters of box entrance holes were an equal mix of 32 and 38 mm. We then repeated the counting procedure during the summers of 1992 and 1993.

We made no systematic effort to determine occupancy by opening nest boxes during the breeding season, because such intrusions could have caused cavity-nesting birds to avoid or abandon the box plots, thereby reducing the magnitude of the experimental manipulation. We did record all birds seen entering or leaving the boxes during our visits to the plots.

As repeated counts on individual plots clearly were not independent, the appropriate statistical comparisons between control and experimental plots was repeated measures analysis of variance. We used a multivariate approach, with count date as a within subjects (repeated measures) factor, and plot type as a between subjects (treatment) factor. Repeated measure statistics were calculated comparing numbers of open and cavity-nesting birds counted on experimental versus control plots, both before and after box additions, for both study areas (n = 12 repeated counts of each plot both before and after box addition to experimental plots; n = 15 plots of each type at Betasso Preserve; n = 12 plots of each type at Walker Ranch). No statistical comparisons were made for individual species, because of problems inherent in making multiple comparisons of variables (the species) that could not be assumed to be independent.

RESULTS

Nest box usage.—At Betasso Preserve, we observed birds using 33 of 60 boxes (55%) in 1992, and 30 of 60 boxes (50%) in 1993. In decreasing order of abundance, known box uses by species over both years were Pygmy Nuthatch (21), White-breasted Nuthatch (12), Western Bluebird (12), Mountain Chickadee (11), Violet-green Swallow (4) and House Wren (3). (See Table 1 for scientific names of species.)

Box use was somewhat lower at Walker Ranch: 16 of 48 (33%) in 1992, and 22 of 48 (46%) in 1993. Known box uses by species at Walker Ranch were House Wren (18), Mountain Chickadee (7), Pygmy Nuthatch (4), Mountain Bluebird (4), Violet-green Swallow (3) and White-breasted Nuthatch (2).

Responses of cavity-nesting birds.—Counts of all cavity-nesting birds in-

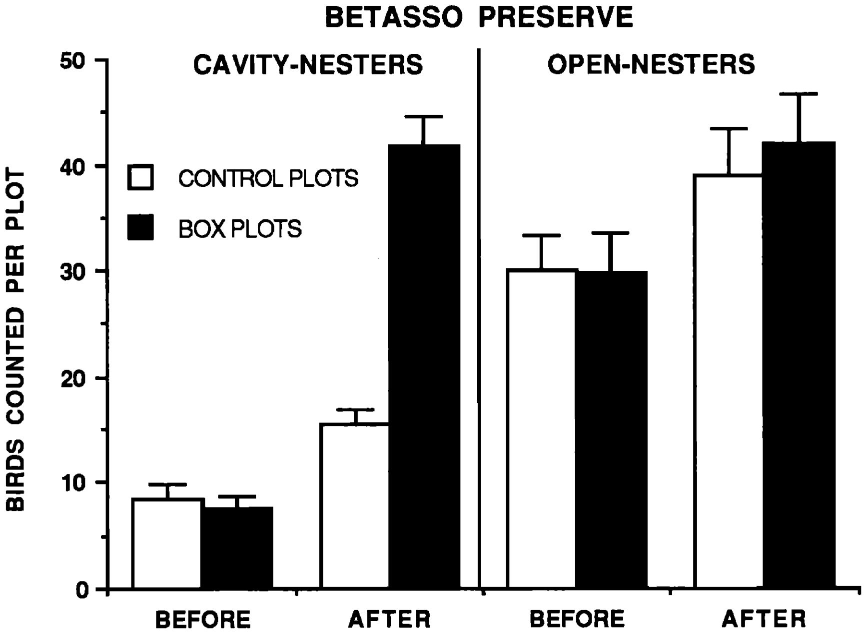

FIGURE 1. Total numbers of cavity-nesting and open-nesting birds (means + SE) counted before (1990–1991) and after (1992–1993) addition of artificial nest boxes to experimental (box) plots at Betasso Preserve, compared with numbers counted over the same period on unmanipulated control plots (n = 15 plots of each type). Data shown are numbers counted cumulatively for each plot during 12 counts of 7 min each, but analysis was by repeated measures ANOVA, with each count treated separately.

creased by a factor of 5.5 at Betasso Preserve, and by 5.0 at Walker Ranch, after nest box addition to the experimental (box) plots (Figs. 1 and 2).

Counts of cavity-nesting birds did not differ between experimental and control plots before nest box additions at either site (repeated measures ANOVA, treatment effect $P > 0.20$). After box additions, counts of cavity-nesting birds were highly significantly different between plot types at both sites. Results of repeated measures ANOVA were as follows. (1) Betasso Preserve, treatment effect ($F = 83.77$, $P < 0.0001$, df = 1, 28), repeated measures effect ($F = 1.20$, $P = 0.29$, df = 11, 308), interaction ($F = 0.69$, $P = 0.75$, df = 11, 308). (2) Walker Ranch, treatment effect ($F = 58.06$, $P < 0.0001$, df = 1, 22), repeated measures effect ($F = 2.33$, $P < 0.01$, df = 11, 242), interaction ($F = 3.16$, $P < 0.001$, df = 11, 242). The somewhat greater response at Betasso Preserve is consistent with the apparently higher rate of nest box use at that site.

Individual species that we observed most frequently using the boxes also were the species that showed the strongest numerical responses to our experiment (Table 1). At Betasso Preserve, these were the Violet-green Swallow, Mountain Chickadee, White-breasted Nuthatch, Western

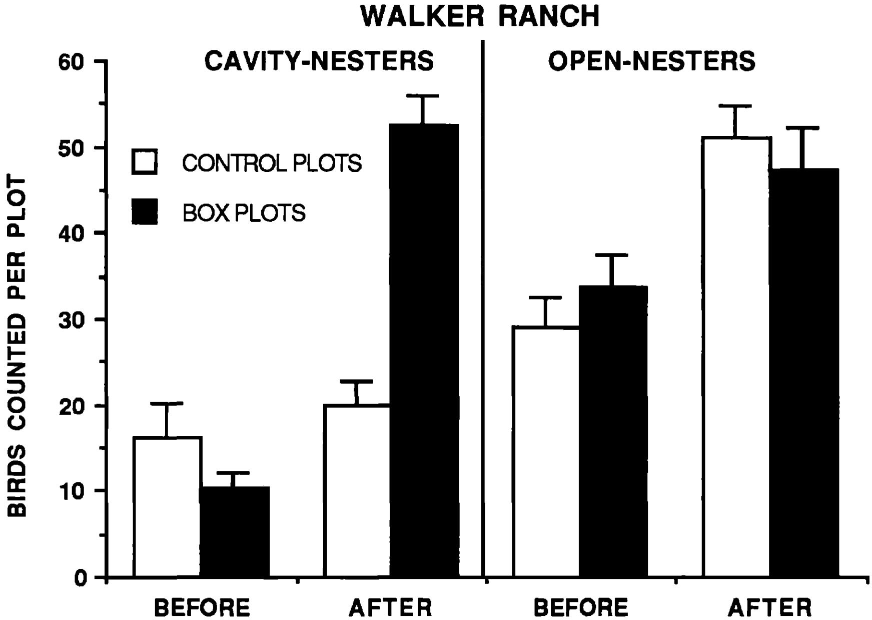

FIGURE 2. Same as Figure. 1, but for Walker Ranch (n = 12 plots of each type).

Bluebird and especially the Pygmy Nuthatch. At Walker Ranch, the cavity-nesters most responsive to our experiment were the Violet-green Swallow, Mountain Chickadee, Mountain Bluebird and especially the House Wren.

Responses of open-nesting birds.—Combined counts of open-nesting birds were higher overall in the 2 yr following nest box additions (Figs. 1 and 2), but results did not differ between control and box plots at either site, either before or after nest box addition (repeated measures ANOVA, treatment effect $P > 0.20$ for all comparisons).

The most common open-nesting species at Betasso Preserve were Western Wood Pewee, American Robin, Solitary Vireo, Western Tanager, Chipping Sparrow and Dark-eyed Junco. At Walker Ranch they were Broad-tailed Hummingbird, Western Wood Pewee, American Robin, Virginia's and Yellow-rumped Warblers, Western Tanager, Chipping Sparrow, Dark-eyed Junco and Cassin's Finch. There was no consistent response to the experiment among these and the remainder of the 18 most common open-nesting species (Table 1). Certain species happened to be more abundant on one set of plots than the other prior to box addition, but for the most part these differences persisted throughout the 4 yr. Examples included the Townsend Solitaire at both sites, the Cassin's Finch at Betasso Preserve, and the Red Crossbill at Walker Ranch. For unknown reasons, both Green-tailed and Rufous-sided Towhees increased dramatically on both experimental and control plots during the study. Overall, our results indicated that open-nesting bird populations were both spatially and temporally variable on our study sites, but that nest box addition had no consistent or appreciable impact on these patterns.

DISCUSSION

Secondary cavity-nesters responded positively and dramatically to nest box additions at both Betasso Preserve and Walker Ranch, providing strong field experimental evidence that breeding densities of these birds, both collectively and as individual species, were limited by the quantity or quality of available natural nesting sites.

Previous nest box experiments frequently have yielded results similar to those of the present study, although the magnitude of the response has varied with habitat condition. For example, in northern Arizona ponderosa pine forests, and in riparian woodlands on the lower Colorado River, responses of secondary cavity-nesters to nest box addition depended in part upon availability of natural cavities (Brawn and Balda 1988, Brush 1983). In our study, the somewhat stronger response of secondary cavity-nesters at Betasso Preserve may have resulted from a relative scarcity of snags. Although we did not quantify this difference between our two study sites, Walker Ranch supported a heterogeneous variety of dead and live aspen, Douglas fir, and ponderosa pine, while Betasso Preserve was almost exclusively living pine.

Habitat differences also may explain the varying responses of certain secondary cavity-nesters to nest box addition at our two study sites. For example, Western Bluebirds and Pygmy Nuthatches typically are associated with ponderosa pine in Colorado (Andrews and Righter 1992), and they were much more abundant at Betasso Preserve. House Wrens usually nest in relatively open areas with substantial herbaceous ground cover (Finch 1989). This sort of habitat was more prevalent at Walker Ranch, compared to the relatively dense second-growth pine forests of Betasso Preserve. We cannot explain why House Wrens and White-breasted Nuthatches responded positively to nest box addition in our study areas but not in generally similar habitat in northern Arizona (Brawn and Balda 1988).

Walankiewicz (1991) found no evidence that natural cavities were limiting to bird densities in an old growth forest in Poland, and concluded following a literature review that many studies suggesting such a limitation have occurred in second-growth forests lacking abundant snags or large mature trees. We did not measure availability of natural cavities in our study areas. Both, however, were part of a region dominated today by relatively young forests that became established following extensive logging and stand replacement fires prior to 1920 (Veblen and Lorenz 1991).

Future nest box experiments in western North America should include habitats of all sorts, but especially those areas where substantial mature forests remain uncut and intact. Assumptions that secondary cavity-nesting birds are limited by nest site availability are unwarranted without evidence from properly controlled field experiments (Waters et al. 1990). Nest box addition in second-growth forests and woodlands apparently can be an effective means of increasing nesting opportunities for local populations of secondary cavity-nesters, although additional data are required to determine the relative breeding success of birds using natural cavities versus nest boxes.

Will nest box addition and consequent increases of secondary cavity-nesting birds result in local declines in densities of birds with similar foraging ecologies that build open nests? Our results and those of Brawn et al. (1987) for northern Arizona suggest this decline is unlikely to happen in Rocky Mountain forests. Similarly, most Old World nest box experiments have failed to detect declines in open-nesting species following nest box addition (East and Perrins 1988, Enemar and Sjostrand 1972, Mönkkönen et al. 1990; but see Hogstad 1975).

Nest box experiments such as ours have certain limitations as tests of hypotheses about interspecific competition among birds. They provide no clear means of determining the mechanisms by which competitive interactions might be occurring. As individual species populations can vary across time and space due to many causes, it may be difficult to distinguish responses to nest box addition from chance numerical fluctuations related to other, unknown, factors. The lack of response of open-nesting species as a group, however, both in the present study and in most others, supports MacArthur's (1972) contention that avian assemblages in high latitude and high altitude forests are unlikely to be involved in interspecific competition for limited food resources.

In contrast to results of the present field experiment and most others in northern or montane forests, open-nesting birds in riparian habitats in southeastern Arizona avoided experimental relative to control plots following nest box addition (Bock et al. 1992). This avoidance occurred despite the fact that increases in counts of box users were only about half those in our study in Colorado. Additionally, nest box usage averaged only 20% per year in Arizona, in contrast to 33–55% in Colorado.

We do not know why assemblage-wide (diffuse) interspecific competition might be more important among southwestern riparian birds than among species of montane and/or higher latitude forests. It has been argued, however, that secondary consumers such as avian insectivores are more likely to limit their prey (and therefore to be limited by it) in relatively productive ecosystems (Abrams 1993, Fretwell 1987, Oksanen 1988). In contrast to northern and montane forests, southwestern riparian woodlands are highly productive, and support both diverse and abundant avian assemblages (Anderson and Ohmart 1977, Carothers et al. 1974, Stamp 1978, Strong and Bock 1990).

The experimental approach used in the present study and others is an effective means of testing hypotheses about avian interspecific competition, in any community with appreciable numbers of secondary cavity-nesting species. We encourage its replication in other habitats, such as mesic temperate and tropical forests, to elucidate further those circumstances where competition between cavity and open-nesting species may be an important determinant of avian community composition. Nest box addition experiments will be especially valuable if they also include measurement of key variables such as the quantity and quality of available natural cavities, dietary overlap among species, and reproductive success.

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