

AN ABSTRACT OF THE THESIS OF

Donald E. Youkey for the degree of Master of Science
in Wildlife Science presented on October 15, 1990.
Title: Bird and Rodent Nesting in Excavated Cavities in Piñon-
juniper Woodland, Southeastern Colorado

Abstract approved:

Redacted for Privacy

E. Charles Meslow

I studied bird and rodent nesting in woodpecker-excavated cavities in piñon-juniper (Pinus edulis-Juniperus monosperma) (P-J) woodland in southeastern Colorado during the spring and summer of 1987 and 1988. Two related investigations were conducted: one described characteristics of habitat used by birds and rodents nesting in woodpecker-excavated cavities and the other evaluated whether or not birds and rodents were competing for the nest-cavity resource. Seven species of birds and 4 species of rodents were included in the study: American kestrel (Falco sparverius), western screech-owl (Otus kennicottii), northern flicker (Colaptes auratus), ash-throated flycatcher (Myiarchus cinerascens), plain titmouse (Parus inornatus), Bewick's wren (Thryothorus bewickii), mountain bluebird (Sialia currucoides), white-footed mouse (Peromyscus leucopus), deer mouse (P. maniculatus), piñon mouse (P. truei), and woodrat (Neotoma spp.). 1987 was a preliminary year.

In 1988, 248 nests were located in 433 cavities monitored, and cavity density averaged 1.5/ha. Western screech-owls nested earlier

than all other species ($P < 0.001$), plain titmice nested earlier than ash-throated flycatchers ($P = 0.033$), and other species of birds and rodents nested at the same time ($P < 0.05$). Seven of 19 characteristics associated with nests differed ($P < 0.05$) among species: 4 of 5 at the cavity-level, 2 of 5 at the cavity-tree level, and 1 of 9 at the cavity-site level. Generally, larger species (kestrels, screech-owls, and flickers) nested in larger cavities and smaller species (white-footed, deer, and piñon mice, and Bewick's wren) nested in smaller cavities. Characteristics of cavities used for nesting by secondary cavity-nesting species also differed from characteristics of all cavities monitored most frequently on characteristics associated with cavity size. Differences were demonstrated using univariate analysis (Kruskal-Wallis ANOVA) because with the considerable overlap among species, multivariate analysis (discriminant function analysis [DFA]) could not discriminate among species. Management implications include the need to evaluate impacts to the P-J woodland cavity-nesting community before converting the woodland to rangeland, evaluate impacts of logging in higher elevation forests where many of the cavity-excavating woodpeckers breed, and evaluate the influence of the nest-parasitic brown-headed cowbird (Molothrus ater) and the highly competitive European starling (Sturnus vulgaris).

In 1988, 95 cavities were manipulated to yield 47 rodent exclusions and 48 bird exclusions. Proportions of these manipulated cavities used for nesting by birds and rodents were compared to the proportions of 83 control cavities used for nesting by the appropriate group of species. Cavities were revisited at 10-day intervals 4 May -

6 August 1988 and evidence of use recorded. The proportions of cavities used as nests by rodents was significantly greater in manipulated cavities than in control cavities ($P = 0.0083$). Thus, interspecific competition was experimentally demonstrated between birds and rodents for nest-sites in woodpecker-excavated cavities.

Bird and Rodent Nesting in Excavated Cavities
in Piñon-juniper Woodland, Southeastern Colorado

by

Donald E. Youkey

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed October 15, 1990

Commencement June 1991

APPROVED:

Redacted for Privacy

Professor of Wildlife Ecology in charge of major

Redacted for Privacy

Head of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

Date thesis is presented October 15, 1990

Presented by Donald E. Youkey

ACKNOWLEDGEMENTS

This study was funded by the Environment, Energy, and Natural Resources Division, U.S. Army, Ft. Carson, Colorado through the U.S. Fish and Wildlife Service (USFWS), Colorado Fish and Wildlife Assistance Office, Golden, Colorado and the USFWS Oregon Cooperative Wildlife Research Unit, and the Department of Fisheries and Wildlife, Oregon State University, Corvallis.

I extend special thanks to my major professor, Dr. E. Charles Meslow, for his advice and encouragement from proposal to final draft of this thesis. I thank members of my committee, Dr. Bob Jarvis, Dr. Cliff Pereira, and Dr. Fred Ramsey, for their advice and helpful comments. I also thank fellow graduate student and friend, Ellen Hammond, for many useful suggestions on a previous draft.

Fieldwork conducted by Ellen Weintraub and Melinda Bradford was gratefully appreciated. Support of other researchers at PCMS, especially David Andersen and Eric Gese, aided in collection of data. I am also grateful to the many other people who have helped me in numerous ways on this project over the years.

I thank my parents, John and Linda, for their support and encouragement during this endeavor. And finally, a heartfelt thanks to my partner-in-life, Ellen, for her constant love, encouragement, and patience.

TABLE OF CONTENTS

PART I BIRD AND RODENT NESTING IN WOODPECKER-EXCAVATED CAVITIES IN PIÑON-JUNIPER WOODLAND, SOUTHEASTERN COLORADO

INTRODUCTION	1
STUDY AREA	3
METHODS	5
Cavity Searching	5
Cavity Monitoring	5
Characteristics Associated with Cavities	6
Data Analysis	8
RESULTS	11
Cavities Monitored	11
Cavity Use Through Time	11
Cavity Use - Differences and Similarities Among Species	13
Cavity Use vs. Availability	24
DISCUSSION	26
Cavity Density	26
Cavity Use Through Time	26
Cavity Use - Differences and Similarities Among Species	27
Cavity Use vs. Availability	30
Primary vs. Secondary Cavity-nesters	32
MANAGEMENT IMPLICATIONS	35

PART II COMPETITION BETWEEN CAVITY-NESTING BIRDS AND RODENTS IN PIÑON-JUNIPER WOODLAND, SOUTHEASTERN COLORADO

INTRODUCTION	37
STUDY AREA	41
METHODS	42
RESULTS	46
DISCUSSION	51
CONCLUSION	56
LITERATURE CITED	57

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Location of study site: piñon-juniper woodland on Piñon Canyon Maneuver Site, Las Animas County, southeastern Colorado.	4
2. Cavity dimensions measured include vertical diameter of the entrance (VDE), horizontal diameter of the entrance (HDE), inner-vertical height (IVHT), horizontal depth (HD), and vertical depth (VD).	7
3. Percent of cavities used as nest sites through time by bird and rodent species in piñon-juniper woodland, southeastern Colorado, 1988.	12
4. Circular distributions (in percent) of cavity entrance orientations and ground aspects at base of cavity trees in piñon-juniper woodland, southeastern Colorado, 1987-1988.	20
5. Proportions of cavities used for nesting by birds and rodents during a reciprocal-exclusion experiment in a piñon-juniper woodland, southeastern Colorado, 1988.	48
6. Percent of control cavities used as nest sites through time by birds and cricetine rodents in piñon-juniper woodland, southeastern Colorado, 1988.	49

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Comparisons of mean dimensions of woodpecker-excavated cavities among bird and rodent nests and between nests and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.	14
2. Comparisons of means of tree characteristics associated with bird and rodent nests in woodpecker-excavated cavities, and between nest-cavities and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.	15
3. Comparisons of means of site characteristics associated with bird and rodent nests in woodpecker-excavated cavities and between nest-cavities and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.	16
4. Relative frequency of entrance orientation for cavity-nests and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.	21
5. Relative frequency of ground aspect at base of tree for cavity-nests and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.	22
6. Use and availability (%) of tree species and condition to birds and rodents in piñon-juniper woodland, southeastern Colorado, 1988.	23
7. Comparisons of numbers (and percentages) of cavities used by birds and rodents for nesting between control and other unmanipulated cavities located using different methods in piñon-juniper woodland, southeastern Colorado 1988.	43
8. Numbers (and percentages) of cavities used by birds and rodents for nesting in each treatment during a reciprocal-exclusion experiment in piñon-juniper woodland, southeastern Colorado, 1988.	47

PREFACE

This thesis is written in the optional manuscript format. Two papers are presented as Parts I and II. Part I describes bird and rodent habitat-use while nesting in woodpecker-excavated cavities in piñon-juniper woodland. Part II evaluates competition between birds and rodents for the nest-cavity resource in a piñon-juniper woodland. Both parts are presented in the same format and they share a common Literature Cited section at the end of Part II.

BIRD AND RODENT NESTING IN EXCAVATED CAVITIES
IN PIÑON-JUNIPER WOODLAND, SOUTHEASTERN COLORADO

PART I

BIRD AND RODENT NESTING IN WOODPECKER-EXCAVATED CAVITIES
IN PIÑON-JUNIPER WOODLAND, SOUTHEASTERN COLORADO

INTRODUCTION

Habitat selection by an organism is influenced by its ecological context in space and time and can be viewed at different ecological scales. Nest-site selection is a component of habitat selection that has been extensively studied. Though it is influenced by a complex web of interacting factors, nest-site selection must be adequate to ensure successful reproduction. Cavity-nesting birds have more specific requirements than open-nesting birds and these requirements are less likely to be met ubiquitously (Cody 1985). Characteristics of cavities are important determinants of occupancy by secondary cavity-nesting species; populations of many secondary cavity-nesting species are thought to be limited by the abundance of suitable nest sites for breeding (von Haartman 1957, Rendell and Robertson 1989).

While many researchers have studied cavity-nesting birds or rodents, few studies have been conducted in P-J woodland. P-J woodland is the most extensive forest type in several states of the western U.S., occupying over 19 million ha (West et al. 1975, Buckman

and Wolters 1987). Much of the attention focused on this ecosystem has been on how to convert it to grassland. There is much debate over whether or not this forest type is expanding its historical geographic range and if so, why? (Lanner 1981; West 1984a, 1984b; Gifford 1987; Jameson 1987; Neilson 1987). "The vegetation type is poorly understood, inadequately defined, and often misused." (Everett 1987:forward). Two studies have examined bird communities (Balda and Masters 1980, Sedgwick 1981, 1987) and 4 studies have examined rodent communities (Geluso 1971; Holbrook 1978; Llewellyn 1978, 1980; Ribble 1985; Ribble and Samson 1987) in P-J woodland; none focused on the cavity-nesting aspect of the birds or rodents in P-J woodland.

I studied birds and rodents nesting in woodpecker-excavated cavities in P-J woodland. My objectives were to: (1) describe the phenology of cavity-nesting by birds and rodents, and (2) describe characteristics of woodpecker-excavated cavities in P-J woodland in relation to nesting by birds and rodents.

STUDY AREA

The study was conducted in P-J woodlands on the Piñon Canyon Maneuver Site, Las Animas County, southeastern Colorado (Figure 1). P-J woodlands in this study occurred on limestone breaks, 1640 to 1770 m in elevation, bordered by short-grass prairie (U.S. Dep. Army 1980). In this semi-arid climate, annual precipitation varied widely and averaged 34.1 cm 1940-1980 (Colo. Climate Center 1989). The area was grazed by cattle during the past century until it was acquired by the U.S. Army in 1983 as a remote site for mechanized-military training. Most of the study was conducted in areas off-limits to military vehicles.

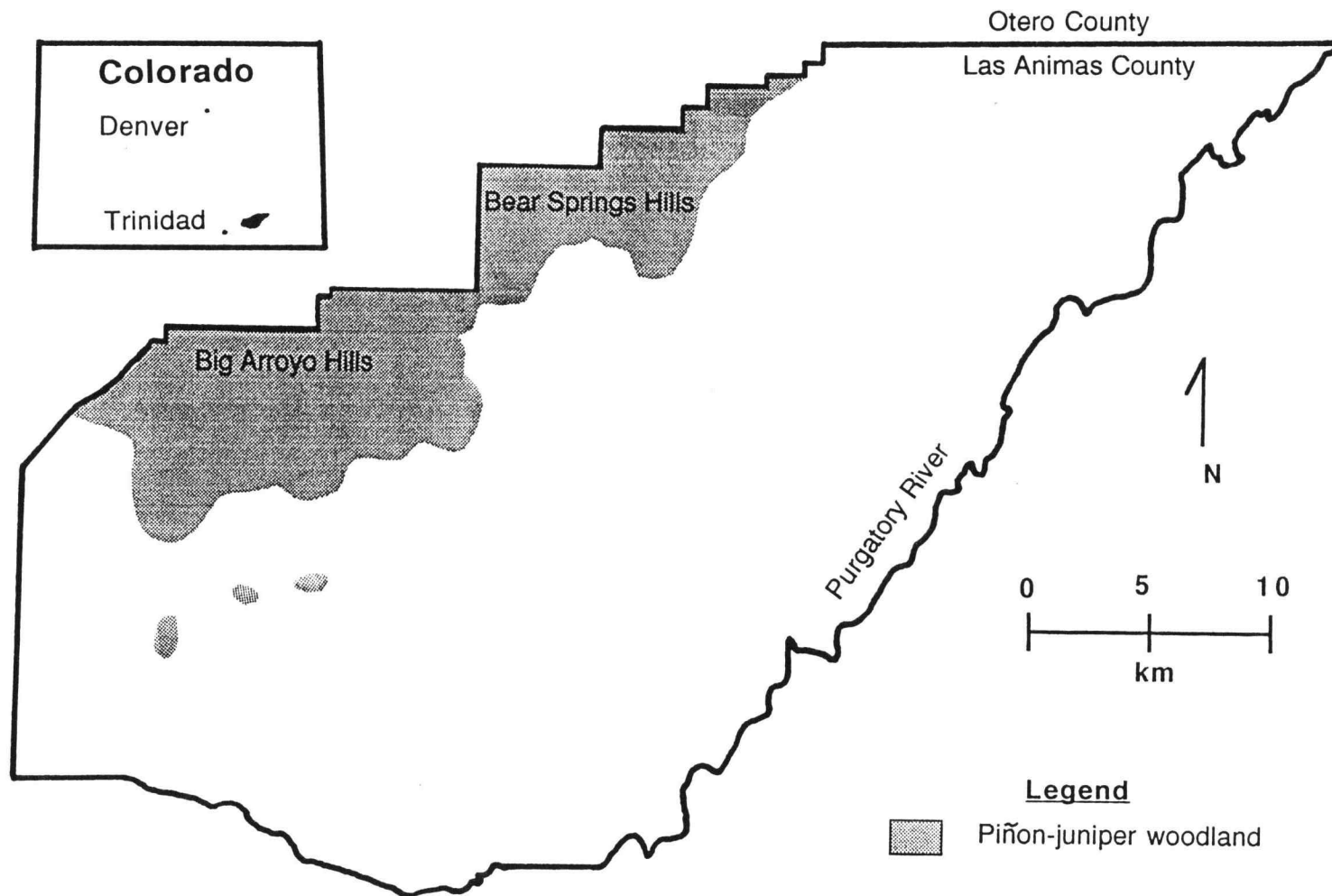


Figure 1. Location of study site: piñon-juniper woodland on Piñon Canyon Maneuver Site, Las Animas County, southeastern Colorado.

METHODS

Cavity Searching

In 1987 a preliminary study commenced during the summer; 5 ha of P-J woodland were searched for woodpecker-excavated cavities, then occasional revisits were made to the cavities. In 1988, 433 woodpecker-excavated cavities were located, monitored, and their characteristics described. Cavities were located in P-J woodland by searching plots and by walking transects 22 March to 12 May. Twelve 200 x 500 m (10 ha) randomly chosen plots were completely searched. Eighty-six parallel transect lines were searched approximately 10 to 20 m on either side. Transects were spaced 200 m apart. Double-faced tape was placed on the vertical walls of cavity entrances to collect rodent hair. Some cavities were used in a concurrent manipulative study (see Part II) so sample sizes vary depending on requirements of the particular analysis.

Cavity Monitoring

Cavities were revisited at 10-day intervals 4 May - 6 August, 1988 (9 revisits). Presence of nesting material, adult birds, eggs, nestlings, or rodent sign was recorded after inspecting the cavity with a flashlight and mirror. The double-faced tape was collected and replaced if rodent hair was present, or replaced if no longer adhesive. I defined a nest as a cavity containing: (1) a bird or rodent and nesting material; (2) eggs or young; or (3) for rodents, nesting material and rodent hair on the double-faced tape for 3

consecutive visits. Nest cavities were included in the analyses for each nesting bout by the same or different species. Species were identified by observing adults at cavities, eggs in nests, and/or hair on tape (Hall and Kelson 1959, Armstrong 1972, Harrison 1979, National Geographic Society 1983); rodents were not identified to species by hair (Short 1978).

Characteristics Associated with Cavities

Characteristics of cavities and the surrounding area were described at 3 levels: the cavity, the cavity-tree, and the cavity-site (area surrounding the cavity tree). At the cavity level horizontal and vertical depths, inner-vertical height, horizontal and vertical entrance diameters, orientation of entrance, and height above ground were measured (Figure 3). At the cavity-tree level, slope and diameter of trunk/branch at cavity entrance, diameter at breast height (dbh) of trunk/branch with cavity, tree height, number of branches at breast height ≥ 15 cm in diameter, decay status, and tree species were recorded. At the cavity-site level, density of piñons and junipers in 2 size classes ($<$ and ≥ 15 cm dbh), slope and aspect of the ground at the base of the cavity-tree, and distance to water and distance to woodland/grassland edge were measured. Entrance area was assumed to be an ellipse and calculated from its formula: $\pi \times (\text{horizontal entrance diameter} \div 2) \times (\text{vertical entrance diameter} \div 2)$. Aspect of the cavity entrance and of the ground at the base of the cavity tree was measured with a compass. Slope of the branch at the cavity entrance and the slope of the ground at the base of the cavity tree

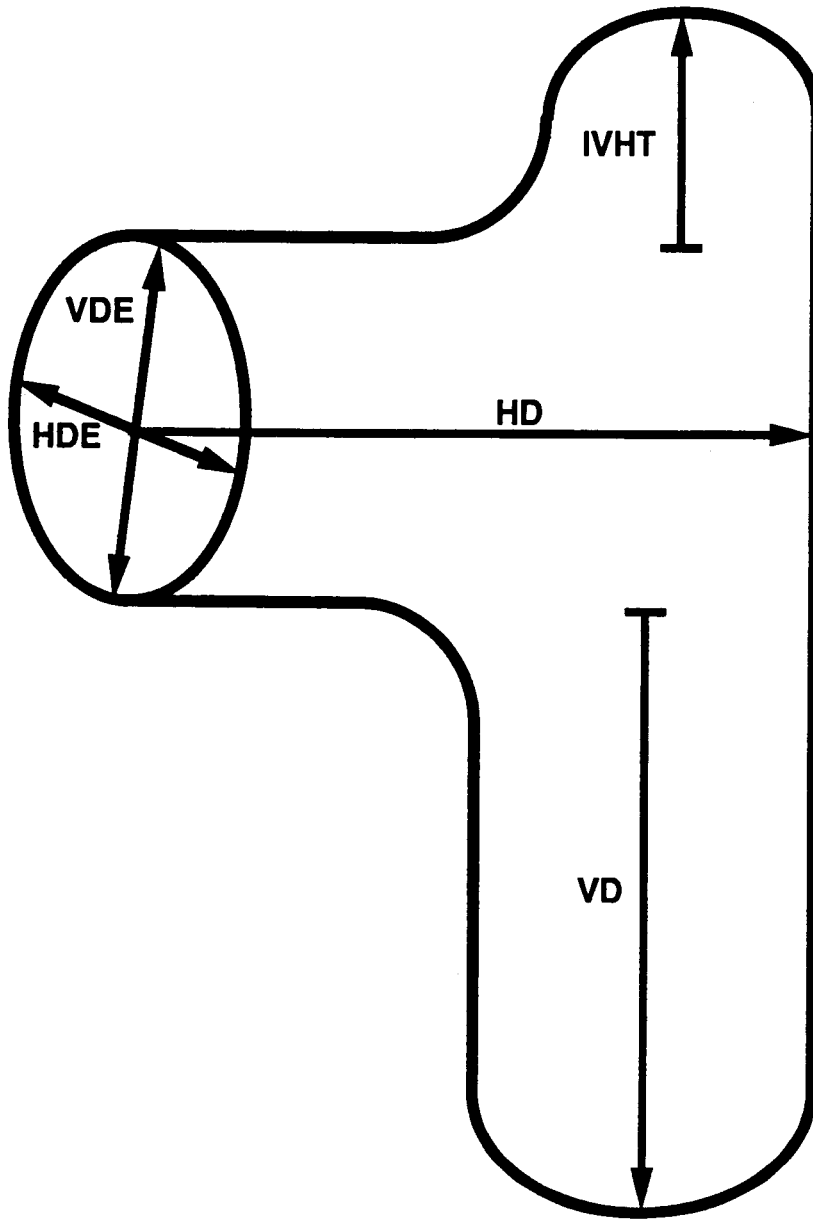


Figure 2. Cavity dimensions measured include vertical diameter of the entrance (VDE), horizontal diameter of the entrance (HDE), inner-vertical height (IVHT), horizontal depth (HD), and vertical depth (VD).

was measured with a clinometer. Total tree height was measured using an Abney level. Tree density was measured by centering a 15m-radius circular plot (0.07 ha) on the cavity. Distance to the edge of the woodland was measured from vegetation-type overlays (prepared by U.S. Fish and Wildlife Service - Western Energy Land Use Team) on 1:24,000 U.S. Geological Survey topographical maps; distance to water was measured on these maps without the overlays.

Data Analysis

Histograms of percent cavity occupancy for each 10-day visit interval were constructed. Nesting chronology was compared among birds and rodents using pooled t-tests (Devore and Peck 1986:370).

Means and standard errors were calculated for continuous variables of cavity, cavity-tree, and cavity-site characteristics for each cavity-nesting species. Data were tested for normality using Shapiro and Wilk's W-statistic (Zar 1984:95, SAS Inst., Inc. 1985a:350), then transformations (square-root or logarithmic) were made on non-normal variables. Because 6 variables still did not approximate normality ($P < 0.01$), nonparametric Kruskal-Wallis ANOVA's (Zar 1984:176-179, SAS Inst., Inc. 1988:717) were employed to determine if habitat use differed among species. Mann-Whitney tests (Zar 1984:138-141, SAS Inst., Inc. 1988:717) were run between each pair of species when the Kruskal-Wallis H-statistic was significant ($P < 0.05$). For discrete variables, comparisons of frequencies of cavity characteristics were made between all cavities monitored and a uniform distribution with chi-square goodness-of-fit tests (Zar 1984:440-442).

Comparisons of used vs. available frequencies of cavity characteristics were made with G log-likelihood tests (Zar 1984:52, SAS Inst., Inc. 1985b).

Stepwise DFA (SAS Inst., Inc. 1988) was used to identify habitat characteristics that separated nesting species (Stauffer and Best 1982; Raphael and White 1984; Sedgwick and Knopf 1986, 1990). A DFA was run with all species included, then pairwise tests were made between species; species with low numbers of observations [American kestrel ($n = 5$), western screech-owl ($n = 7$), and northern flicker ($n = 11$)] were not included in the analyses. Variables that did not approximate univariate normality ($P \geq 0.05$, Shapiro and Wilk's test) were transformed using square root or logarithmic transformations. Transformed variables retained for the DFA were normally distributed. A Pearson correlation matrix (SAS Inst., Inc. 1985a) was calculated and one variable from each pair with an $r \geq 0.7$ was dropped to meet the DFA assumption that variables are not auto-correlated. Variables were dropped based on F -values and ease of ecological interpretation. Cohen's kappa statistic was calculated to assess the utility of each DFA by removing the effects of chance (Titus et al. 1984).

Characteristics associated with cavity nests were compared between each species and all cavities monitored. Pairwise comparisons between each species and all cavities were made on each continuous variable with Mann-Whitney tests (Zar 1984:138-141, SAS Inst., Inc. 1988:717). Transformations were carried out on variables as described previously. Stepwise DFA was used to compare species use of cavities to available nest-sites in multivariate space. For discrete

variables, comparisons of used vs. available frequencies of cavity characteristics were made with G log-likelihood tests (Zar 1984:52, SAS Inst., Inc. 1985b).

RESULTS

Cavities Monitored

In 1987, 13 nests in woodpecker-excavated cavities were located representing 6 species of birds and one mouse (Peromyscus sp.). In 1988, 248 nests were located in 225 of the 433 cavities monitored, representing 8 species of birds and 4 species of rodents. Combining both years, 5 American kestrel, 7 western screech-owl, 11 northern flicker, 21 ash-throated flycatcher, 16 plain titmouse, 25 Bewick's wren, 41 mountain bluebird, 46 piñon mouse, and 89 Peromyscus spp. nests were located and their associated habitat characteristics described. Peromyscus spp. includes white-footed mice, deer mice, and piñon mice. Six brown-headed cowbird (Molothrus ater) "nests," 5 woodrat nests, a wasp (Vespidae) nest, and 2 bullsnakes (Drymarchom corias) were also located in cavities but not included in the analyses. Cavity density averaged 1.5/ha (SD = 0.56).

Cavity Use Through Time

A western screech-owl initiated nesting before I began cavity searching in 1988 and was found incubating on 8 April (Figure 3). A mountain bluebird was the next cavity-nesting bird found initiating nesting on 19 April. However, a piñon mouse was observed nesting on 11 April. Generally, extensive overlap of cavity use among species occurred temporally. Western screech-owls nested significantly earlier than any other species ($P < 0.001$) in 1988; 2 of the 5 cavities used by early nesting screech-owls were used later in the

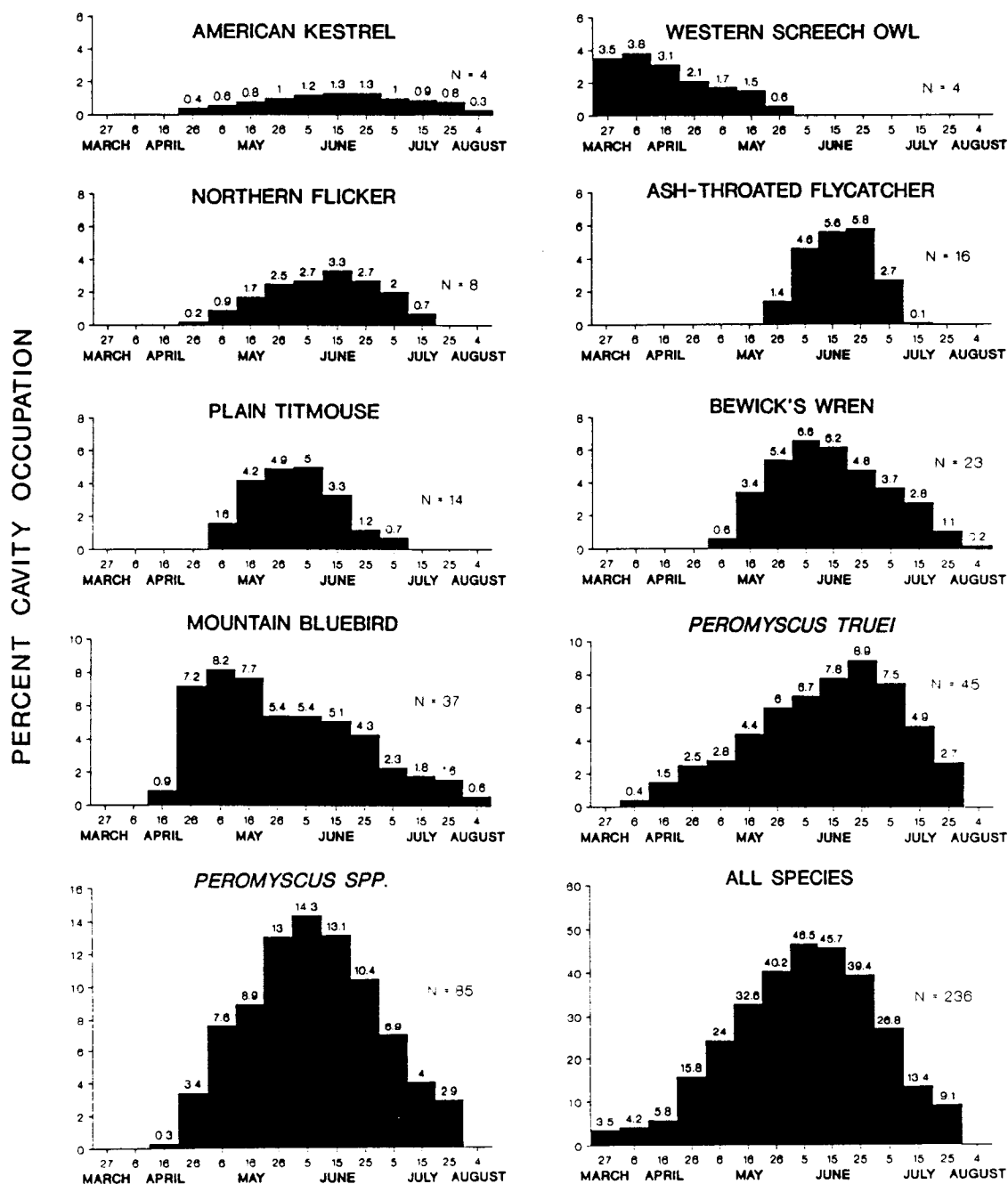


Figure 3. Percent of cavities used as nest sites through time by bird and rodent species in piñon-juniper woodland, southeastern Colorado, 1988. The y-axes on all graphs are the same scale except "ALL SPECIES." Rodent nests were not revisited during the last monitoring period, 4 August, so percent cavity occupation is not presented for these species or "ALL SPECIES" for that interval.

season by northern flickers. Ash-throated flycatchers nested later than plain titmice ($P = 0.033$) but flycatchers did not use any of the cavities vacated by titmice. There was no difference ($P > 0.05$) in temporal use of cavities between any other pair of species.

A Bewick's wren renested in the same cavity after a nest failure as did 7 mountain bluebirds after 1 failure, 4 successes, and 2 of unknown fate. After a northern flicker nest failed, a mountain bluebird used the cavity. After 2 failures and a successful nesting by 3 mountain bluebirds, 3 ash-throated flycatchers nested in these "bluebird" cavities. After a mountain bluebird nesting bout of unknown fate, mountain bluebirds, ash-throated flycatchers, and a brown-headed cowbird concurrently used this cavity to lay a clutch of 3 bluebird, 3 flycatcher, and 2 cowbird eggs; only the cowbird eggs hatched. Four cavities used for nesting by P. spp. were later used by an ash-throated flycatcher, 2 Bewick's wrens, and a mountain bluebird. Conversely, after a Bewick's wren nested in a cavity it was used by a P. sp. Brown-headed cowbird eggs were found in 6 cavity nests: 2 Bewick's wrens, 2 mountain bluebirds, the combination mountain bluebird/ash-throated flycatcher, and an "unused" cavity.

Cavity Use - Differences and Similarities Among Species

Seven of 19 characteristics associated with nests differed ($P < 0.05$, Kruskal-Wallis tests) among nesting species: 4 of 5 characteristics of the cavity, 2 of 5 characteristics of the cavity-tree, and 1 of 9 characteristics of the cavity-site (Tables 1-3). Measurements at nests of horizontal and vertical depth from the

Table 1. Comparisons of mean dimensions of woodpecker-excavated cavities among bird and rodent nests and between nests and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.

Species	N	Horizontal depth (cm)		Vertical depth (cm)		Entrance area (cm ²)		Inner-Vertical height (cm)		Cavity height (cm)	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
		(range)		(range)		(range)		(range)		(range)	
American kestrel	5	15.2 [*]	1.8 A ^a	33.4 [*]	5.4 A	45.76 [*]	16.75 A	23.1	16.4 A	241	21
		(10.9-20.0)		(22.9-43.1)		(24.60-112.09)		(0.0-87.6)		(174-288)	
Western screech-owl	7	14.9 [*]	1.4 A	49.7 [*]	15.6 A	41.01 [*]	5.31 A	20.6	4.0 A	252	21
		(8.1-19.4)		(23.2-141.6)		(27.36-64.40)		(12.0-39.8)		(155-328)	
Northern flicker	11	16.1	2.6 A	34.9	2.7 A	38.53	3.74 A	17.7	3.4 A	228	15
		(10.6-40.5)		(22.9-51.8)		(27.31-64.17)		(8.8-45.8)		(185-328)	
Ash-throated flycatcher	19	10.9	0.6 ABC	18.0 [*]	1.4 B	22.00	2.36 B	22.9	3.4 A	248	12
		(6.4-14.0)		(8.5-34.7)		(11.22-54.54)		(0.0-57.3)		(158-366)	
Plain titmouse	16	11.3	0.9 AB	15.3	1.0 BC	21.57	2.87 BC	14.3	2.9 A	213	25
		(6.7-17.8)		(9.8-25.4)		(8.55-49.10)		(0.0-40.3)		(106-424)	
Bewick's wren	24	9.4	0.4 C	13.8	1.1 C	17.92	1.43 BC	15.1	3.9 A	222	17
		(6.6-14.2)		(8.4-35.9)		(6.57-37.67)		(0.3-93.1)		(87-388)	
Mountain bluebird	41	11.4	0.4 BC	15.4 [*]	0.7 BC	18.79 [*]	1.02 BC	12.9 [*]	2.0 A	247	15
		(7.7-19.0)		(8.9-23.2)		(8.55-38.92)		(0.3-41.5)		(59-407)	
Piñon mouse	46	9.6	0.4 BC	13.7	1.2 CD	17.30	1.02 BC	25.0	4.1 A	227	12
		(3.5-17.3)		(0.6-30.1)		(5.94-36.72)		(0.0-99.9)		(101-469)	
<i>Peromyscus</i> spp.	88	9.2 [*]	0.3 C	13.6	2.3 D	17.65 [*]	1.27 C	25.8	2.8 A	213	8
		(1.7-18.2)		(0.2-201.2)		(2.89-85.33)		(0.0-99.9)		(106-365)	
P^b		< 0.0001		< 0.0001		< 0.0001		0.0148		0.2555	
All cavities	382	10.2	0.2	15.0	0.9	21.40	0.99	21.4	1.2	226	4
		(1.7-40.5)		(0.2-201.2)		(2.89-308.90)		(0.0-99.9)		(53-481)	

^aMeans within columns followed by the same letter do not differ significantly ($P > 0.05$, Mann-Whitney paired comparisons).

^bAmong species ANOVA (Kruskal-Wallis H-test).

* Characteristics of cavities used for nesting by secondary cavity-nesting species different from characteristics of all cavities monitored ($P < 0.05$, Mann-Whitney tests).

Table 2. Comparisons of means of tree characteristics associated with bird and rodent nests in woodpecker-excavated cavities, and between nest-cavities and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.

Species	N	Cavity Slope (°)		Branch or trunk diameter (cm)		Diameter at breast height (cm)		Tree height (cm)		No. branches at breast height	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
		(range)		(range)		(range)		(range)		(range)	
American kestrel	5	66	5.5	27.8	5.1 A ^a	35.9	6.4	628	65	3.8	0.9 A
		(51-85)		(16.2-46.0)		(17.6-53.9)		(473-778)		(1-4)	
Western screech-owl	7	70	4.2	28.7 [*]	2.1 A	32.1	1.9	562	34	4.6 [*]	0.8 A
		(54-80)		(22.9-40.9)		(26.0-40.0)		(448-715)		(3-9)	
Northern flicker	11	73	2.9	31.2	2.7 A	33.6	1.8	547	61	2.8	0.4 A
		(51-86)		(22.3-49.8)		(22.9-40.7)		(316-715)		(1-5)	
Ash-throated flycatcher	20	71	1.9	23.7	1.1 A	30.7	1.6	542	17	2.3	0.2 A
		(51-89)		(15.4-34.2)		(21.6-47.5)		(367-674)		(1-4)	
Plain titmouse	16	67	4.4	23.5	1.8 A	32.9	3.7	538	38	2.3 [*]	0.5 A
		(22-87)		(13.1-39.0)		(18.4-64.0)		(289-794)		(1-8)	
Bewick's wren	24	63	3.2	20.3	1.1 A	27.3	1.7	521	23	3.5	0.4 A
		(33-83)		(12.2-35.4)		(13.6-43.9)		(280-704)		(1-7)	
Mountain bluebird	41	66	2.4	24.7	1.0 A	30.9	1.3	553	22	3.3	0.3 A
		(22-93)		(15.7-41.2)		(12.8-50.9)		(221-758)		(1-8)	
Piñon mouse	46	64	2.2	21.5	0.7 A	32.0	1.7	507	20	2.7	0.2 A
		(27-91)		(11.7-30.4)		(16.2-59.1)		(156-869)		(1-6)	
<i>Peromyscus</i> spp.	87	68	1.9	21.7	0.6 A	28.5	1.0	499	13	3.0	0.2 A
		(19-115)		(10.5-38.5)		(13.6-77.3)		(156-754)		(1-8)	
p^b		0.4851		< 0.0001		0.1497		0.1774		0.0391	
All cavities	297	68	0.8	22.9	0.4	30.4	0.5	523	7	3.0	0.1
		(19-115)		(10.5-80.8)		(12.8-77.3)		(156-869)		(1-18)	

^aMeans within columns followed by the same letter do not differ significantly ($P > 0.05$, Mann-Whitney paired comparisons).

^bAmong species ANOVA (Kruskal-Wallis H-test).

*Characteristics of cavities used for nesting by secondary cavity-nesting species different from characteristics of all cavities monitored ($P < 0.05$, Mann-Whitney tests).

Table 3. Comparisons of means of site characteristics associated with bird and rodent nests in woodpecker-excavated cavities and between nest-cavities and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.

Species	N	Juniper density ^a		Large juniper density ^a		Piñon density ^a		Large piñon density ^a		Tree density ^a	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
		(range)		(range)		(range)		(range)		(range)	
American kestrel	5	19.0	2.5	6.4	1.7	21.8	6.1	2.2	0.9	40.8	8.2
		(13-28)		(2-11)		(4-37)		(0-5)		(20-65)	
Western screech-owl	7	13.9	1.8	8.9	0.6	4.0*	1.5	0.3	0.2	17.9*	2.8
		(9-24)		(7-11)		(0-11)		(0-1)		(9-30)	
Northern flicker	11	16.1	1.6	8.2	1.9	17.0	4.1	1.8	0.7	33.1	4.5
		(7-28)		(2-22)		(1-44)		(0-7)		(9-61)	
Ash-throated flycatcher	21	16.8	1.6	8.7	0.8	16.0	3.2	1.8	0.5	32.7	4.4
		(3-32)		(2-16)		(0-52)		(0-8)		(3-72)	
Plain titmouse	16	13.8	2.0	7.5	1.2	9.7	2.9	0.6	0.2	23.5	4.2
		(2-32)		(2-17)		(0-38)		(0-2)		(2-62)	
Bewick's wren	24	14.8	1.4	7.6	0.9	13.0	2.8	1.5	0.5	27.8	3.6
		(4-29)		(2-19)		(0-50)		(0-9)		(5-75)	
Mountain bluebird	41	14.1	1.4	6.6*	0.7	12.7	1.9	1.5	0.3	26.8	3.0
		(2-32)		(1-16)		(0-40)		(0-6)		(2-71)	
Piñon mouse	41	16.3	1.2	7.6	0.8	13.6	1.9	1.1	0.3	29.9	2.7
		(5-33)		(1-20)		(0-42)		(0-7)		(5-65)	
<u>Peromyscus</u> spp.	67	16.0	0.8	8.2	0.5	14.3	1.6	1.1	0.2	30.6	1.9
		(4-34)		(2-17)		(0-57)		(0-7)		(4-66)	
\bar{p}^b		0.3427		0.4142		0.1903		0.3022		0.1955	
All cavities	303	15.6	0.4	8.1	0.3	14.1	0.7	1.4	0.1	29.7	0.9
		(2-41)		(0-23)		(0-57)		(0-12)		(2-75)	

Table 3. (cont.)

Species	N	Large tree density ^a		Slope of ground (°)		Distance to edge (m)		Distance to water (m)	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
		(range)		(range)		(range)		(range)	
American kestrel	5	8.6	2.5	8.8	2.2	70 [*]	9 A ^C	965	169
		(3-16)		(4-15)		(40-96)		(550-1488)	
Western screech-owl	7	9.1	0.5	9.7	2.0	16	6 CD	771	117
		(8-11)		(3-19)		(0-40)		(350-1200)	
Northern flicker	11	10.0	2.2	10.9	1.3	50	12 ABC	788	79
		(2-25)		(5-17)		(5-125)		(350-1250)	
Ash-throated flycatcher	21	10.4	1.2	8.2	1.5	39	11 BCD	804	79
		(2-22)		(2-25)		(0-150)		(288-1656)	
Plain titmouse	16	8.1	1.3	5.4	0.8	26 [*]	13 CD	767	88
		(2-19)		(1-13)		(0-216)		(108-1260)	
Bewick's wren	24	9.1	1.1	8.0	1.3	53	12 ABCD	693	65
		(2-20)		(1-25)		(0-192)		(216-1272)	
Mountain bluebird	41	8.1	0.9	7.5	0.8	31	5 BCD	767	71
		(1-22)		(1-18)		(0-115)		(108-1752)	
Piñon mouse	41	8.7	0.9	8.4	1.0	34	8 CD	783	47
		(1-21)		(2-32)		(0-250)		(360-2040)	
<i>Peromyscus</i> spp.	67	9.4	0.6	8.4	0.8	45	4 ABC	731	38
		(2-20)		(0-32)		(0-300)		(168-1710)	
P^b		0.7379		0.3199		0.0121		0.7816	
All cavities	297	9.4	0.3	8.2	0.4	42	3	771	19
		(1-25)		(0-32)		(0-300)		(71-2040)	

^aNumber per 0.07 ha circular plot (15 m radius), centered on the cavity.^bAmong species ANOVA (Kruskal-Wallis H-test).^cMeans within columns followed by the same letter do not differ significantly ($P > 0.05$, Mann-Whitney paired comparisons).*Characteristics of cavities used for nesting by secondary cavity-nesting species different from characteristics of all cavities monitored ($P < 0.05$, Mann-Whitney tests).

entrance, entrance area, and inner-vertical height above entrance differed among species at the cavity-level. The diameter of the trunk/branch at the cavity entrance and the number of branches at breast height ≥ 15 cm differed among species at the cavity-tree level. The distance from nests to the edge of the woodland differed among species at the cavity-site level.

For the Kruskal-Wallis tests that showed significant differences, Mann-Whitney tests showed differences ($P < 0.05$) among individual species for 4 of 7 variables. The Mann-Whitney tests on inner-vertical height of the cavity, diameter of branch or trunk at the cavity, and number of branches at breast height did not show differences among the species (Tables 1 and 2). Of the 3 characteristics that measure cavity size (horizontal and vertical depth, and entrance area), generally the larger species (American kestrel, western screech-owl, and northern flicker) used larger cavities and the smaller species (plain titmouse, Bewick's wren, piñon mouse, and *P. spp.*) used smaller cavities. However, there was much overlap in cavity size used by smaller and mid-sized species.

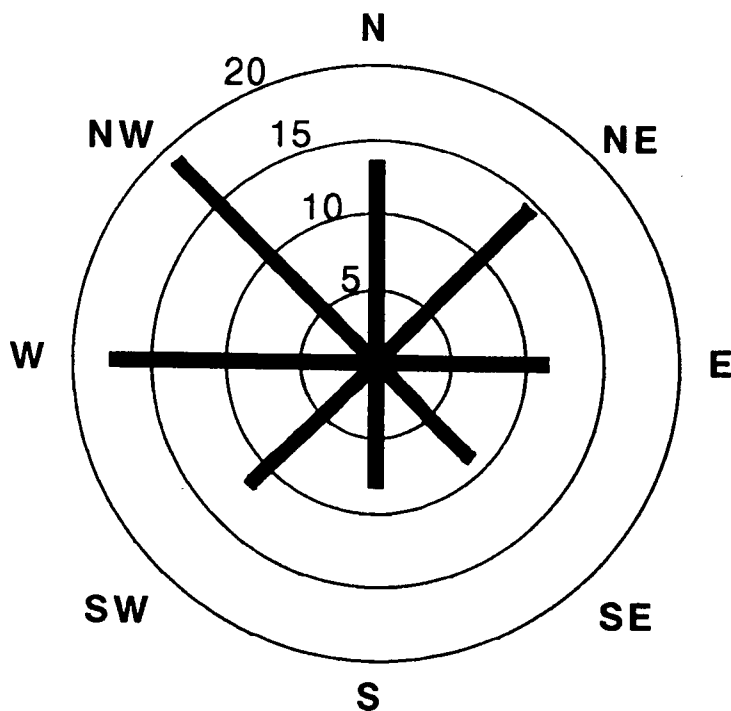
At the level of cavity-tree and cavity-site, the Mann-Whitney tests showed complex patterns of differences among species (Tables 2 and 3). Northern flickers used branches/trunks with the largest diameters ($\bar{x} = 31.2$ cm), Bewick's wren used the smallest ($\bar{x} = 20.3$ cm), while use by the other species overlapped considerably. American kestrels used trees farthest into the woodland from the woodland/grassland edge ($\bar{x} = 70$ m), western screech-owls used trees closest to the edge ($\bar{x} = 16$ m), while the distance from the edge of

woodlands to cavity trees used by each species overlapped considerably.

Orientations of cavity entrances and aspects of the ground at the base of cavity trees differed from a uniform circular distribution for all cavities monitored ($P < 0.001$, $\chi^2 = 34.74$ and $P < 0.001$, $\chi^2 = 32.38$, respectively); northerly and westerly orientations of cavity entrances were most common and northerly and easterly aspects of the ground at the base of cavity trees were most common (Figure 4, Tables 4 and 5). Cavities were located in juniper snags (4.2%), dead portions of live junipers (19.3%), live portions of junipers (71.5%), piñon snags (4.7%), and live piñon trees (0.3%) (Table 6).

Six (diameter of branch/trunk at cavity entrance, number of branches at breast height ≥ 15 cm, inner-vertical height above cavity entrance, cavity height above ground, horizontal depth from cavity entrance, and distance to edge of woodland) of the 16 habitat variables tested contributed to the separation of the 6 species (ash-throated flycatcher, plain titmouse, Bewick's wren, mountain bluebird, piñon mouse, and *P. spp.*) in multivariate space using stepwise DFA (Wilk's lambda = 0.651, $P \leq 0.0001$). However, considerable overlap in cavity characteristics among species led to a percent-classified-better-than-chance of only 11% (Cohen's kappa = 0.11) for the DFA, even though Wilk's lambda was significant. (DFA provides no improvement over chance when kappa = 0 and 100% correct classification when kappa = 1 [Titus et al. 1984]). The 15 pairwise species comparisons yielded similar results in each case: Wilk's lambda ≥ 0.558 , $P \leq 0.0001$, Cohen's kappa < 0.50 .

(a) CAVITY ENTRANCE ORIENTATION



(b) ASPECT OF GROUND AT CAVITY TREE

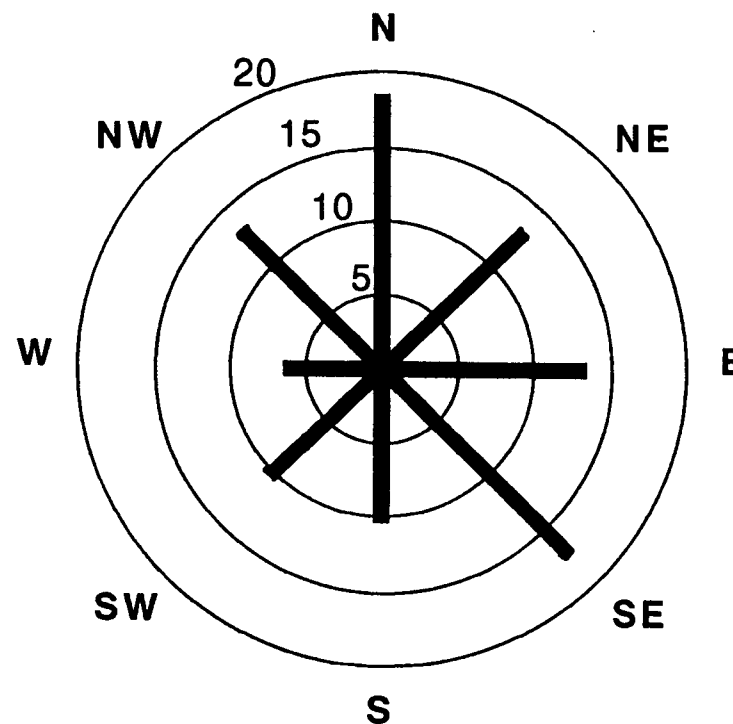


Figure 4. Circular distributions (in percent) of cavity entrance orientations and ground aspects at base of cavity trees in piñon-juniper woodland, southeastern Colorado, 1987-1988. Eight categories were used: N (>337-22), NE (23-67), E (68-112), SE (113-157), S (158-202), SW (203-247), W (248-292), NW (293-337). (a) The null hypothesis of a symmetrical distribution of entrance orientations around a circle was rejected ($P < 0.001$, $\chi^2 = 34.74$, 7 df, $N = 432$). (b) The null hypothesis of a symmetrical distribution around a circle of ground aspects at the base of cavity trees was rejected ($P < 0.001$, $\chi^2 = 32.38$, 7 df, $N = 336$).

Table 4. Relative frequency of entrance orientation for cavity-nests and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.

Cavity entrance orientation (range - °)	American kestrel (<u>N</u> = 5)	Western screech-owl (<u>N</u> = 7)	Northern flicker (<u>N</u> = 11)	Ash-throated flycatcher (<u>N</u> = 21)	Plain titmouse (<u>N</u> = 16)	Bewick's wren (<u>N</u> = 25)	Mountain bluebird (<u>N</u> = 41)	Piñon mouse (<u>N</u> = 46)	<u>Peromyscus</u> <u>spp.</u> (<u>N</u> = 89)	All cavities ^{***} (<u>N</u> = 384)
N (>337-22)	0.20	0.43	0.18	0.10	0.25	0.08	0.07	0.07	0.13	0.13
NE (23-67)	0.00	0.14	0.45	0.10	0.06	0.08	0.15	0.09	0.16	0.14
E (68-112)	0.00	0.00	0.18	0.05	0.06	0.12	0.07	0.09	0.12	0.11
SE (113-157)	0.20	0.00	0.09	0.24	0.06	0.16	0.07	0.07	0.11	0.09
S (158-202)	0.40	0.14	0.09	0.10	0.00	0.08	0.07	0.07	0.06	0.08
SW (203-247)	0.00	0.00	0.00	0.14	0.19	0.12	0.20	0.13	0.06	0.11
W (248-292)	0.00	0.29	0.00	0.14	0.19	0.08	0.22	0.30	0.13	0.17
NW (293-337)	0.20	0.00	0.00	0.14	0.19	0.28	0.15	0.20	0.22	0.19
<u>P</u> ^a	0.252	0.164		0.576	0.529	0.196	0.611	0.387	0.771	

^{***} Observed frequency of cavity orientations not distributed uniformly around the circle ($P < 0.001$, $\chi^2 = 34.74$, $df = 7$).

^aProportions of orientations of cavities used by secondary cavity-nesting species different than proportions of entrance orientations of all cavities monitored (log-likelihood G-test, $df = 7$).

Table 5. Relative frequency of ground aspect at base of tree for cavity-nests and all cavities monitored in piñon-juniper woodland, southeastern Colorado, 1987-1988.

Ground aspect (range - °)	American kestrel (<u>N</u> = 5)	Western screech-owl (<u>N</u> = 7)	Northern flicker (<u>N</u> = 10)	Ash-throated flycatcher (<u>N</u> = 21)	Plain titmouse (<u>N</u> = 16)	Bewick's wren (<u>N</u> = 23)	Mountain bluebird (<u>N</u> = 41)	Piñon mouse (<u>N</u> = 37)	Peromyscus <u>spp.</u> (<u>N</u> = 69)	All cavities ^{***} (<u>N</u> = 297)
N (>337-22)	0.20	0.00	0.00	0.19	0.25	0.17	0.22	0.16	0.23	0.19
NE (23-67)	0.00	0.00	0.10	0.05	0.13	0.13	0.12	0.11	0.06	0.13
E (68-112)	0.00	0.14	0.30	0.10	0.00	0.13	0.12	0.11	0.16	0.13
SE (113-157)	0.20	0.29	0.30	0.10	0.19	0.17	0.24	0.14	0.17	0.17
S (158-202)	0.00	0.29	0.20	0.10	0.00	0.04	0.10	0.19	0.12	0.10
SW (203-247)	0.00	0.14	0.00	0.14	0.25	0.09	0.07	0.08	0.09	0.10
W (248-292)	0.00	0.14	0.00	0.10	0.13	0.04	0.10	0.11	0.06	0.06
NW (293-337)	0.60	0.00	0.10	0.24	0.06	0.22	0.02	0.11	0.12	0.13
<u>p</u> ^a	0.223	0.258		0.654	0.124	0.926	0.504	0.778	0.635	

*** Observed frequency of the ground aspect at the base of trees not distributed uniformly around the circle ($P < 0.001$, $\chi^2 = 32.38$, $df = 7$).

^aProportions of ground aspects at the base of cavity trees used for nesting by secondary cavity-nesting species different than proportions of ground aspects at the base of trees for all cavities monitored (log-likelihood G-test, $df = 7$).

Table 6. Use and availability (%) of tree species and condition to birds and rodents in piñon-juniper woodland, southeastern Colorado, 1988.

Species	N	Juniper			Piñon	
		Dead part of			Snag	Live tree
		Snag	live tree	Live tree		
American kestrel	5	1 (20.0)	0 (0.0)	4 (80.0)	0 (0.0)	0 (0.0)
Western screech-owl	7	2 (28.6)	0 (0.0)	5 (71.4)	0 (0.0)	0 (0.0)
Northern flicker	11	1 (9.1)	2 (18.2)	8 (72.7)	0 (0.0)	0 (0.0)
Ash-throated flycatcher	21	2 (9.5)	5 (23.8)	13 (61.9)	1 (4.8)	0 (0.0)
Plain titmouse	16	1 (6.3)	3 (18.8)	12 (75.0)	1 (6.3)	0 (0.0)
Bewick's wren	25	0 (0.0)	5 (20.0)	19 (76.0)	1 (4.0)	0 (0.0)
Mountain bluebird*	41	2 (4.9)	1 (2.4)	36 (87.8)	2 (4.9)	0 (0.0)
Piñon mouse	46	2 (4.3)	2 (8.7)	39 (84.8)	1 (2.2)	0 (0.0)
<u>Peromyscus</u> spp.	89	4 (4.5)	17 (19.1)	64 (71.9)	4 (4.5)	0 (0.0)
All available	383	16 (4.2)	74 (19.3)	274 (71.5)	18 (4.7)	1 (0.3)

* Cavity-nests of secondary cavity-nesting species in trees with a different proportion of tree species/condition than expected, based on measures of all cavities available ($P < 0.05$, log-likelihood ratio, G -statistic).

Cavity Use vs. Availability

At least 1 of the 10 secondary cavity-nesting species differed significantly in their use of 10 of 19 characteristics associated with nests and the sample of all cavities monitored ($P < 0.05$, Mann-Whitney tests): 12 of 40 comparisons of the cavity, 3 of 40 comparisons of the cavity-tree, and 5 of 72 comparisons of the cavity-site (Tables 1-3). Cavities used for nesting by birds and rodents differed from all cavities monitored for the same variables that separated species in ANOVA at the cavity level: measurements at nests of horizontal and vertical depth from the entrance, entrance area, and inner-vertical height above entrance. A similar pattern was observed at the cavity-tree level: measurements at nests of the diameter of the trunk/branch at the cavity entrance, and the number of branches at breast height ≥ 15 cm. At the cavity-site level the densities of juniper ≥ 15 cm at breast height, the density of piñon, the density of all trees, and the distance from nests to the woodland/grassland edge differed between a few species and all cavities monitored.

American kestrels, western screech-owls, and mountain bluebirds nested in cavities with greater mean horizontal depths and P. spp. nested in cavities with a smaller mean horizontal depth than the mean horizontal depth of all cavities monitored. American kestrels, western screech-owls, ash-throated flycatchers, and mountain bluebirds nested in cavities with greater mean vertical depths than the mean vertical depth of all cavities monitored. Similarly, American kestrels and western screech-owls nested in cavities with greater mean

entrance areas while mountain bluebirds and *P. spp.* nested in cavities with smaller mean entrance areas. Mountain bluebirds nested in cavities with a smaller mean inner-vertical height. Western screech-owls nested in cavities with a greater mean branch/trunk diameter at cavity entrances. Western screech-owls nested in trees with more branches and plain titmice nested in trees with fewer branches. Western screech-owls nested in stands with a lower mean density of piñon and a lower mean density of all trees. Plain titmice nested closer and American kestrels nested farther from the woodland/grassland edge than the mean distance to edge for all cavities monitored.

Orientations of cavity entrances and aspects of the ground at the base of cavity-trees showed no differences between those used and those available for any secondary cavity-nesting species ($P \geq 0.196$ and $P \geq 0.124$, respectively) (Tables 4 and 5). Mountain bluebirds nested in cavities in live parts of junipers more frequently and used cavities in dead parts of junipers less frequently than predicted, based on measures of available cavities ($P = 0.026$, log-likelihood ratio, G -test) (Table 6).

Stepwise DFA indicated that cavity characteristics associated with nest-cavities differed from cavity characteristics available for nesting, but the model failed to classify species correctly ($P \geq 0.0318$, Wilk's $\lambda \geq 0.956$, Cohen's $\kappa = 0$).

DISCUSSION

Cavity Density

The woodpecker-excavated cavity density of 1.5/ha found on my study site was lower than that found in many other areas: 6.5 cavities/ha (Balda 1975) and 5.2 cavities/ha (Cunningham et al. 1980) in Ponderosa pine (Pinus ponderosa) forests in Arizona, 12.9 cavities/ha in a cottonwood (Populus sargentii) floodplain of Colorado (Sedgwick and Knopf 1990), 2.1 cavity trees/ha in slash pine (Pinus elliotii) plantations in Florida (Land et al. 1989), and 4.1 cavities/ha in an oak-pine woodland in northern California (Waters et al. 1990). Cavity density is difficult to measure in many vegetation types and few studies have reported it.

Cavity Use Through Time

Little temporal partitioning of the nest-cavity resource among species occurred during the breeding season (Figure 3). In 1988, western screech-owls nested earlier than any other species ($P < 0.001$) and 40% (2) of the cavities used by screech-owls were later used by northern flickers. Ash-throated flycatchers began nesting latest in the season and took advantage of vacated cavities for 29% (5 of 17) of their nests in 1988. Four cavities used by early nesting P. spp. were later used by birds. Ribble (1985, pers. commun.) sampled rodent reproductive status in P-J woodland on the Piñon Canyon Maneuver Site during June through December, 1983. He found almost 70% of the piñon mice in reproductive condition in early June, declining to <10% by

mid-August. Conversely, approximately 50% of the deer mice and 40% of the white-footed mice were in breeding condition in early June, increasing to approximately 70% and 100%, respectively, by mid-August. Since piñon mice are more arboreal than deer mice or white-footed mice, they seem more likely to use woodpecker-excavated cavities for nesting. In addition, they reproduce concurrently with most of the birds. Though the rodent species may have partitioned the reproductive season through time, piñon mice were the species most likely to interact with cavity-nesting birds and they reproduced at the same time.

Cavity Use - Differences and Similarities Among Species

After accounting for chance, DFA failed to discriminate well among species based on characteristics associated with their nest-sites, classifying only 11% of them correctly. Generally, DFA is used in place of a series of univariate comparisons among all species because it accounts for correlations of the variables and better controls experiment-wise (Type I) error rates (Raphael 1981). The poor classification rate of the discriminant model indicates considerable overlap among species in the nest and site characteristics measured. However, even at the low classification rate, the same pattern was observed with multivariate and univariate methods: most of the significant differences among species occurred at the cavity-level. But because the classification rate by DFA was so poor, I relied primarily on univariate statistics to describe differences of habitat characteristics used among species.

Cavity-level.--The 10 cavity-nesting species fell into 2 general groups based on body size: the large species (American kestrel, western screech-owl, and northern flicker) used larger cavities (based on horizontal cavity depth, vertical cavity depth, and entrance area), and the smaller species used smaller cavities (Table 1). The larger species probably would not physically fit into smaller cavities. Explanations put forth for small secondary cavity-nesting species using small cavities include aiding in thermoregulation (Moore 1945) and lessening predation, and/or competition risks (von Haartman 1957).

Species use of cavities differed for the inner-vertical height measurements in the Kruskal-Wallis ANOVA ($P = 0.0148$) but the Mann-Whitney tests failed to discriminate among species. However, both groups of rodents (piñon mice and *P. spp.*) nested in cavities with the greatest inner-vertical cavity heights. Trees with the largest inner-vertical cavity heights are probably more prone to be decayed throughout the bole, allowing rodents to burrow. Rodents have been observed using trees with extensive bole decay by other researchers (Wolff and Hurlbutt 1982). I observed 2 bullsnakes in woodpecker-excavated cavities and it seems the risk of predation would be lower in trees with extensive bole decay where the likelihood of an alternative entrance is greater.

Differences among species were greatest for characteristics measured at the cavity-level in other studies as well. All 7 variables described by Sedgwick and Knopf (1990) at the cavity-level differed significantly among the 6 species of cavity-nesting birds they studied. Similarly, those characteristics used by cavity-nesting

birds described by Peterson and Gauthier (1985) at the cavity-level differed more frequently among species than did tree- or site-level characteristics.

Cavity-tree Level.--Characteristics of the cavity trees used by the 10 cavity-nesting species overlapped considerably (Table 2). Only the diameter of the branch/trunk at the cavity entrance and the number of branches at breast height differed among species ($P \leq 0.0391$), but pairwise comparisons between species indicated considerable overlap. Similar to the cavity-level, the 3 largest species of birds used the trunks/branches with the largest diameters at the cavity entrance; this characteristic did not separate American kestrels from the smaller species, probably because of large variance associated with a small sample sizes ($N = 5$). Larger physical size of the cavity will require a larger branch/trunk diameter to hold it. Mountain bluebirds used branch/trunks with larger diameters than Bewick's wrens, piñon mice and P. spp. Western screech-owls used cavity trees with significantly more branches than 6 of the other species; again this is likely a function of tree size. There was considerable overlap in the use of branch/trunk size by the other species.

Cavity-site Level.--Characteristics of cavity-sites used by the 10 cavity-nesting species overlapped considerably (Table 3). Only distance into the woodland from the woodland/grassland edge differed among species ($P = 0.0121$). Among the larger species the western screech-owl nested significantly closer to the woodland edge. The American kestrel nested farthest from the edge, however its measured distances overlapped several other species.

Cavity Use vs. Availability

Similar to the DFA model discriminating among habitat characteristics associated with nesting species, the DFA model of use vs. availability failed to discriminate between cavities used and those available to secondary cavity-nesters, classifying 0% of them correctly better than chance (Cohen's kappa = 0). This classification indicates considerable overlap in the characteristics of cavities used for nesting and the characteristics of all cavities monitored. Another explanation for this result could be that many suitable cavity nest-sites were available but not used because of low densities of the breeding species present. It seems unlikely that all 9 secondary cavity-nesting species would simultaneously be at low densities relative to the number of suitable cavities available to them. Nonetheless, because the classification rate by DFA was so poor, I used univariate statistics to describe differences of habitat characteristics used between each species and all cavities monitored.

Cavity-level.--Of the 9 cavity-nesting species tested (northern flickers were not tested because they are cavity excavators), 8 selected cavities whose means of measured characteristics differed ($P < 0.05$) from means of measured characteristics of all cavities monitored (Tables 1 and 4). American kestrels and western screech-owls nested in larger cavities based on measurements of horizontal and vertical cavity depths and entrance area; these species simply require larger cavities to accommodate their body size and thus are constrained to larger cavities and cannot exhibit selection. Mountain

bluebirds selected cavities with greater mean vertical depth and mean entrance area but also selected cavities with a smaller mean inner-vertical height. Mountain bluebirds have been shown to lay larger clutches in larger nest-boxes (Zeleny 1977); perhaps mountain bluebirds were maximizing their clutch size by choosing cavities with these characteristics. Or, I may be creating a statistical artifact: numerically, the means of characteristics of cavities used by mountain bluebirds were only slightly greater than those of all cavities monitored and many other species in this study. The P. spp. group selected cavities with smaller horizontal depths and entrance areas. These smaller cavities provide more protection from predators and competitors and allow for increased thermoregulation. Cavity aspect was nonrandom for all cavities but no selection was made by secondary cavity-nesters; Pinkowski (1976) and Stauffer and Best (1982) reported similar results for secondary cavity-nesting species.

Cavity-tree Level.--Three species nested in cavities with tree characteristics different from the average available ($P < 0.05$) (Tables 2, 5, and 6). Western screech-owls selected cavities in trees with larger branch/trunks diameters; this corresponds to the larger cavities they selected. Western screech-owls also selected trees with more branches at breast height. Conversely, plain titmice selected trees with fewer branches at breast height; their behavior or foraging requirements do not seem to explain this selection. Mountain bluebirds used more cavities in live juniper and fewer cavities in dead portions of live juniper; they seemed to be choosing newly excavated cavities based on my observations of the color of cavity

entrances, but I did not quantify this characteristic.

Cavity-site Level.--Three species nested in cavities with average site characteristics different from the average available ($P < 0.05$) (Table 3). Western screech-owls nested in areas with a lower density of piñon trees and lower density of all trees. This may help in their nocturnal hunting because most piñon trees on the study site were small, producing dense stands that may inhibit flight at night and detection of prey. Plain titmice used nest-sites closer to the woodland/grassland edge (within the woodland) and American kestrels used nest-sites farther from the woodland/grassland edge; yet an 8 m and a 28 m difference from the mean distance for all cavities monitored for 2 bird species does not seem ecologically significant. Similar to differences among species, most differences between use and availability occurred at the cavity-level.

Primary vs. Secondary Cavity-nesters

Secondary cavity-nesters are restricted by choices made by cavity excavators. In this cavity-nesting bird community during the breeding season only the northern flicker was a primary cavity nester and composed 8.8% of the cavity-nesting bird community in 1988. Selection of nest-sites by the rest of the species was constrained to available cavities, and the associated cavity-tree and cavity-site characteristics, that were selected by the excavating species. Natural cavities (non-woodpecker excavated) were rare relative to the number of woodpecker-excavated cavities and only 1 pair of birds (Bewick's wrens) was observed nesting in them, though natural cavities

seemed to be used more frequently by rodents than by birds.

Several species of woodpeckers were seen in P-J woodland on the study site. During approximately 72 hours of bird surveying during May and June 1987 and 1988, 2 Lewis' woodpeckers (Melanerpes lewis), 1 red-bellied woodpecker (M. carolinus), 6 ladder-backed woodpeckers (Picoides scalaris), 1 hairy woodpecker (P. villosus), and 29 northern flickers were detected (Youkey and Meslow 1989). Only northern flickers were found nesting.

Most of the cavities monitored were probably not excavated by northern flickers based on cavity size (entrance area, horizontal and vertical depths). If we assume all cavities used by northern flickers, American kestrels, and western screech-owls were excavated by northern flickers and entrance areas smaller than 24.6 cm², the smallest entrance area used in this group, were excavated by other species, then only 22% of the cavities monitored were excavated by flickers. Based on bird survey work done in southeastern Colorado (Sclater 1912, Bailey and Niedrach 1965, Lane and Holt 1987, Chase et al. 1982, Laurion 1985, Tazik et al. 1988, Youkey and Meslow 1989) and the size of these cavities, hairy, downy, and ladder-backed woodpeckers probably excavated the smaller cavities. None of the above species were detected nesting during the course of this study.

There are 2 explanations for the "mystery cavities": (1) 1 or more woodpecker species may migrate to P-J woodland during the winter and excavate roosting cavities, or (2) populations of the smaller excavating species have declined in recent years. Three subspecies of hairy woodpeckers possibly occur in P-J woodland on the study site on

an annual basis: P. v. monticola is a common winter resident, breeding at higher elevations in the mountains, P. v. septentrionalis is a rare casual winter migrant, breeding to the north, and P. v. villosus is an uncommon year-round resident (Bailey and Niedrach 1965). Most hairy woodpeckers in eastern Colorado leave the plains in the summer to breed in the mountains (Sclater 1912, Bent 1939, Bailey and Niedrach 1965, Lane and Holt 1987, Chase et al. 1982). Three subspecies of downy woodpecker possibly occur in P-J woodland on the study site on an annual basis: P. p. leucurus is a fairly common winter resident, breeding at higher elevations in the mountains, P. p. medianus is an uncommon year-round resident, and P. p. nelsoni is an irregular winter migrant (Bailey and Niedrach 1965). Most downy woodpeckers in eastern Colorado leave the plains in the summer to breed in the mountains (Sclater 1912, Bent 1939, Bailey and Niedrach 1965, Lane and Holt 1987, Chase et al. 1982). Ladder-backed woodpeckers are uncommon year-round residents in southeastern Colorado (Bailey and Niedrach 1965, Lane and Holt 1987, Chase et al. 1982). Hairy and downy woodpeckers excavate winter roosting cavities (Bent 1939, Ehrlich et al. 1988). Hairy woodpecker populations have been declining and were listed on the National Audubon Society's "Blue List" from 1975 to 1982 and as a species of special concern in 1986, including the area of the study site (Tate 1986). Thus, both explanations may be true.

MANAGEMENT IMPLICATIONS

The greatest threat to the species nesting in woodpecker-excavated cavities in P-J woodland is habitat destruction. Much of the P-J woodland in the western U.S. has been and is still being converted to rangeland (Sedgwick 1981, Buckman and Wolters 1987). P-J woodland is of limited economic value so conversion to rangeland to create more forage for livestock and big game is not uncommon (Wasson 1987). Impacts on the P-J ecosystem should be considered before woodland is removed.

In much of the P-J woodland that remains, fuelwood harvesting has potentially devastating effects for cavity-nesting species. Though snags did not account for a large proportion of nest-sites in this study, each species did use them; snag use may be higher in a more "natural" (undisturbed) area. In addition, 51% of nest-sites were in dead portions of live juniper trees. Forty-eight percent of the cavity-trees we monitored had branches removed with a saw or ax, most likely for fuelwood or fenceposts. It is difficult to know if these were dead or alive at the time of their removal, but in either case, nesting habitat was removed. Snags should be left standing and dead portions of live trees should remain intact to preserve cavities that exist and maintain substrate for primary cavity-nesters to create new cavities.

Because most (approx. 78%) of the cavities on the study site seemed to be excavated by woodpeckers that breed at higher elevations, impacts on their breeding habitat will influence secondary cavity-

nesters in P-J woodland. Forest practices on these higher elevation forests are reducing the number of snags there (Winternitz and Crumpacker 1985). Therefore, to manage for secondary cavity-nesters in P-J woodland, nesting habitat in higher elevation forests must also be maintained.

Brown-headed cowbirds and European starlings (Sturnus vulgaris) both occurred on the study site but did not seem to impact cavity-nesting species. Starlings were not found nesting on the study site and cowbirds were nesting only in low numbers (I found 6). This area is within the natural-historic range of the cowbird so other species occurring here have probably coevolved with them. Cowbirds and starlings increase with habitat fragmentation and proximity to farming, ranching, and urban areas. In P-J woodland more influenced by habitat fragmentation and human development, impact of cowbirds and starlings on the cavity-nesting community merits examination.

The secondary cavity-nesting community uses a variety of cavity/habitat characteristics. The variety of cavity sizes available will only be maintained if winter roosting populations of primary cavity-nesters persist. A diverse range of other characteristics used by secondary cavity-nesters will be maintained if several species of primary cavity-nesters excavate them as nesting or roosting sites. Winter surveys will indicate whether or not the smaller species of cavity excavators are present and their populations trends; management decisions can be based on this information.

PART II

COMPETITION BETWEEN CAVITY-NESTING BIRDS AND RODENTS

IN PIÑON-JUNIPER WOODLAND, SOUTHEASTERN COLORADO

INTRODUCTION

"Competition occurs when a number of animals (of the same or different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process" (Birch 1957).

Competition theory helps to explain patterns of species distribution, abundance, and resource use in some systems; yet the theory has been very controversial (Connell 1983, Roughgarden 1983, Simberloff 1983, Strong 1983, and many others). This controversy has been philosophical (is there a best way to do science, and if so, what is it?) and technical (the testability of hypotheses and the relevance of experimental designs). Different perspectives on the importance of hypotheses and experimental designs have been expressed. Nonetheless, our understanding of the world can be advanced through the use of competition theory to help explain patterns observed in nature.

Competition for resources is often measured by changing the density of the organisms, or group of organisms, being tested and observing the response of the hypothesized competitors (Brown and Davidson 1977, Connell 1983, Schoener 1983, Gustaffson 1988). Responses often measured include a change in density, a change that could affect density, or a niche shift.

By employing manipulations, competition has been demonstrated between a variety of species or groups of species in many taxonomic classes (see Schoener 1983 for review). Though there have been many studies of competition in both birds and rodents, there have not been any between these classes. Schoener (1983) reviewed all field experiments on interspecific competition through 1982 and found 7 studies of birds and 19 studies of rodents; 1 of the studies of birds was on competition for nest-cavities. Since 1982 a few more experiments on competition for nest-cavities have been published (Nilsson 1984, Gustaffson 1988, Weitzel 1988, Dooley and Dueser 1990).

von Haartman (1957) hypothesized that nest-cavity availability was the factor limiting the breeding population size of cavity-nesting birds. He manipulated nest-box density and found that as it increased so did breeding bird density. By manipulating nest-box density, Brawn and Balda (1988) demonstrated that cavities limited numbers of secondary cavity-nesters in ponderosa pine forests in northern Arizona. Gustaffson (1988) did a similar experiment, manipulating nest-box density in Sweden, and found competition among species. Van Balen et al. (1982) manipulated a combination of natural-cavity and nest-box entrance diameters to demonstrate competition between European starlings and great tits (Parus major) in The Netherlands. Manipulations involving nest boxes are useful but the natural variability of cavity characteristics may not be taken into account unless natural cavities are utilized in studies.

Several studies of natural cavity use have been conducted. Brush (1983) found that breeding densities of secondary cavity-nesting birds

declined after all cavity entrances were blocked in riparian habitat in Arizona. However, Waters et al. (1990) performed a similar experiment and found the density of secondary cavity-nesting birds did not decline in an oak-pine woodland in California, after 38% and 60% of natural-cavity entrances were blocked in consecutive years.

Though many researchers have documented the use of arboreal cavities by cricetine rodents (Nicholson 1941, Gysel 1961, Smith and Speller 1970, Madison 1977, Mineau and Madison 1977, Wolff and Hurlbutt 1982, Barry et al. 1984), only 1 investigated competition for these sites (Dooley and Dueser 1990). Dooley and Dueser (1990) performed a reciprocal-removal experiment with deer mice and white-footed mice in a Virginia hardwood forest and found "ecologically insignificant" niche shifts when the hypothesized competitor was removed. Their study coincided with low population densities of the 2 species and nest-sites may not have been limiting. No studies have been conducted on competition between birds and rodents for cavity nest-sites.

I investigated competition between birds and cricetine rodents for nest-sites in woodpecker-excavated cavities in P-J woodland of southeastern Colorado during the breeding season. In this habitat, both groups of species nest in cavities. No studies have been conducted specifically on cavity nesting by birds or rodents in P-J woodland. This is a good system in which to study competition because cavities are discrete entities and it is fairly clear whether they have been used for nesting. I evaluated the following null hypotheses: (1) birds nesting in woodpecker-excavated cavities do not influence use of the cavities by rodents for nesting and (2) rodents nesting in

woodpecker-excavated cavities do not influence use of the cavities by birds for nesting.

STUDY AREA

The study was conducted in P-J woodlands on the Piñon Canyon Maneuver Site, Las Animas County, southeastern Colorado (Figure 1). P-J woodlands used in this study occurred on limestone breaks, 1640 to 1770 m in elevation, bordered by short-grass prairie (U.S. Dep. Army 1980). In this semi-arid climate, annual precipitation varied widely and averaged 34.1 cm 1940-1980 (Colo. Climate Center 1989). The area was grazed by cattle during the past century until it was acquired by the U.S. Army in 1983 as a remote site for mechanized-military training. Most of the study was conducted in areas off-limits to military vehicles. Evidence of piñon and juniper harvest prior to acquisition by the Army was observed on the site.

METHODS

To evaluate the null hypotheses I conducted a reciprocal-exclusion experiment on birds and rodents. The proportion of cavities used for nesting by birds in cavities from which rodents were excluded was compared to the proportion of cavities used for nesting by birds in unmanipulated control cavities. And reciprocally, the proportion of cavities used for nesting by rodents in cavities from which birds were excluded was compared to the proportion of cavities used for nesting by rodents in unmanipulated control cavities.

Woodpecker-excavated cavities were located in P-J woodland by walking transects and searching plots 22 March to 12 May, 1988. For the experiment, approximately 10 to 20 m on either side of 86 parallel transect lines were searched and cavity locations mapped. The first cavity located along each transect was randomly assigned to 1 of 3 treatments: a rodent exclusion, a bird exclusion, or a control. Cavity searching continued along each transect but 200 m were walked before the next cavity was randomly assigned to a treatment to minimize the influence of manipulated cavities on each other and control cavities. Transects were spaced 200 m apart. In this way, 47 cavities were manipulated to exclude rodents, 48 cavities were manipulated to exclude birds, and 42 cavities were unmanipulated controls. Two other groups of cavities used in a concurrent descriptive study (see Part I) were tested against the control treatment cavities for possible pooling if no differences existed for bird and rodent use (Table 7): (1) 41 cavities located along transects in the intervening 200 m between treatment cavities and greater than 200 m from manipulations, and

Table 7. Comparison of numbers (and percentages) of cavities used by birds and rodents for nesting between control cavities and other unmanipulated cavities located using different methods in piñon-juniper woodland, southeastern Colorado, 1988.

Species	Control group ^a (<u>n</u> =42)	Transect group ^b (<u>n</u> =41)	Plot group ^c (<u>n</u> =173)
American kestrel	0 (0)	1 (2.4)	1 (0.6)
Western screech-owl	1 (2.4)	1 (2.4)	2 (1.2)
Northern flicker	0 (0)	0 (0)	3 (1.7)
Ash-throated flycatcher	3 (7.1)	1 (2.4)	4 (2.3)
Plain titmouse	2 (4.8)	1 (2.4)	7 (4.0)
Bewick's wren	4 (9.5)	2 (4.9)	9 (5.2)
Mountain bluebird	5 (11.9)	5 (12.2)	7 (4.0)
Subtotal ^d	12 (28.6)	10 (24.4)	29 (16.8)*
Piñon mouse	5 (11.9)	0 (0)	24 (13.9)
<u>Peromyscus</u> spp.	4 (9.5)	13 (31.7)	37 (21.4)
Woodrat	0 (0)	1 (2.4)	4 (2.3)
Subtotal ^d	9 (21.4)	14 (34.1)	58 (33.5)
TOTAL	21 (50.0)	24 (55.8)	87 (50.3)

^aCavities located along transects and randomly assigned to the control treatment using the same method as for manipulated cavities.

^bCavities located along transects between treatment cavities; cavities located less than 200 m from manipulated cavities were not included.

^cCavities located by completely searching 12, 10 ha randomly chosen plots; cavities located less than 200 m from a manipulated cavity were not included.

^dSubtotal is not equal to the sum of cavity use by individual species because some cavities were used more than once for nesting.

*Birds nested in a significantly greater proportion of cavities in the control group than in the plot group ($P < 0.05$, z -test, DeVore and Peck 1986:384).

(2) 173 cavities located on 12, 200 x 500 m (10 ha) randomly chosen plots. Plots were completely searched and cavity locations mapped, allowing a calculation of cavity density. I believe that essentially all cavities on plots were located because of the open nature and low stature of this P-J woodland. There was no difference ($P < 0.05$, z -test, DeVore and Peck 1986:384) in bird and rodent use between control treatment cavities and the other 41 unmanipulated cavities located along transects, so they were pooled to increase sample size.

Rodents were excluded from cavities by attaching metal flashing (28 cm wide) around the base of cavity trees, then placing Sherman live traps in the trees; birds could still access these cavities. Birds were excluded from using cavities by placing hardware cloth, bent to form a tunnel, over the cavity entrance; rodents could still access these cavities. Cavities used as controls were not manipulated. Exclusion devices were in place by 26 April and were removed between 3 and 9 July. Manipulated cavities were at least 200 m from another cavity used in the study. Replicates of treatments were well interspersed. Double-faced tape was placed on the vertical walls of cavity entrances to collect rodent hair.

Cavities were revisited at 10-day intervals 4 May - 6 August, 1988 (9 revisits). The last 2 revisits were made after exclusion devices were removed. Presence of nesting material, adult bird, eggs, nestlings, or rodent sign were recorded after inspecting the cavity with a flashlight and mirror. At rodent-exclusion cavities, traps were rebaited and reset if closed. The double-faced tape was collected and replaced if rodent hair was present or replaced if the

tape was no longer adhesive. A nest was defined as a cavity that contained: (1) bird or rodent and nesting material; (2) eggs or young; or (3) for rodents, nesting material and rodent hair on the double-faced tape for 3 consecutive visits. Species were identified by observing adults at cavities, eggs in nests, and/or hair on tape (Hall and Kelson 1959, Armstrong 1972, Harrison 1979, National Geographic Society 1983); rodents were not identified to species by hair (Short 1978). Rodents were trapped and identified prior to the study to facilitate identification in the field.

Proportions of cavities used for nesting in manipulated and control groups were compared with use of the z -test (DeVore and Peck 1986:384). Results from all visits were pooled for analysis. Histograms of percent cavity occupancy for each 10-day visit interval were constructed. Nesting chronology was compared among birds pooled and rodents pooled using pooled t -tests (DeVore and Peck 1986:370).

RESULTS

Seven species of birds and 4 species of cricetine rodents made up the groups that I tested against one another for the presence of competition (Table 8). Only the northern flicker excavates its own nest-site. Many mice were only identified to the genus Peromyscus.

Exclusion devices were not totally effective. Piñon mice nested in 3 of the 47 (6.4%) rodent-exclusion cavities. Three birds (1 ash-throated flycatcher and 2 Bewick's wrens) nested in 3 of the 48 (6.3%) bird-exclusion cavities. These 6 cavities were excluded from the analyses leaving 44 rodent-exclusion cavities, 45 bird-exclusion cavities, and 83 control cavities. In addition, 4 cavity-nesting birds were captured in the live-traps placed above rodent exclusions; 3 died.

The proportion of cavities used as nests by rodents was significantly greater in manipulated cavities than in control cavities ($P = 0.0083$) (Table 8, Figure 5). Rodents nested in 48.9% of the cavities from which birds were excluded and 27.7% of the control cavities. Birds nested in 29.5% of the cavities from which rodents were excluded and 26.5% of the control cavities. Rodents used 21.2% fewer cavities as nests when birds had access and birds used 3.0% fewer cavities as nests when rodents had access.

As determined by inspection of control cavities, the nesting seasons for bird and rodent species did not differ temporally ($P < 0.001$) (Figure 6). A western screech-owl initiated nesting before I began searching for cavities in 1988 and was found incubating on 8

Table 8. Numbers (and percentages) of cavities used by birds and rodents for nesting in each treatment during a reciprocal-exclusion experiment in piñon-juniper woodland, southeastern Colorado, 1988.

Species	Control (n=83)	Rodent exclusions (n=44)	Bird (n=45)
American kestrel	1 (1.2)	0 (0)	
Western screech-owl	2 (2.4)	0 (0)	
Northern flicker	0 (0)	0 (0)	
Ash-throated flycatcher	4 (4.8)	2 (4.5)	
Plain titmouse	3 (3.6)	3 (6.8)	
Bewick's wren	6 (7.2)	4 (9.1)	
Mountain bluebird	10 (12.0)	8 (18.2)	
Subtotal ^a	22 (26.5)	13 (29.5)	
Piñon mouse	5 (6.0)		6 (13.3)
<u>Peromyscus</u> spp.	17 (20.5)		16 (35.6)
Woodrat	1 (1.2)		0 (0)
Subtotal	23 (27.7)		22 (48.9) [*]
TOTAL	45 (54.2)		

^aSubtotal is not equal to the sum of cavity use by individual species of birds because 4 (4.8%) control cavities and 4 (9.1%) rodent-exclusion cavities were used more than once by nesting birds.

^{*}Rodents used significantly more cavities for nesting in the bird-exclusion treatment than the control treatment ($P < 0.05$, χ^2 -test, DeVore and Peck 1986:384).

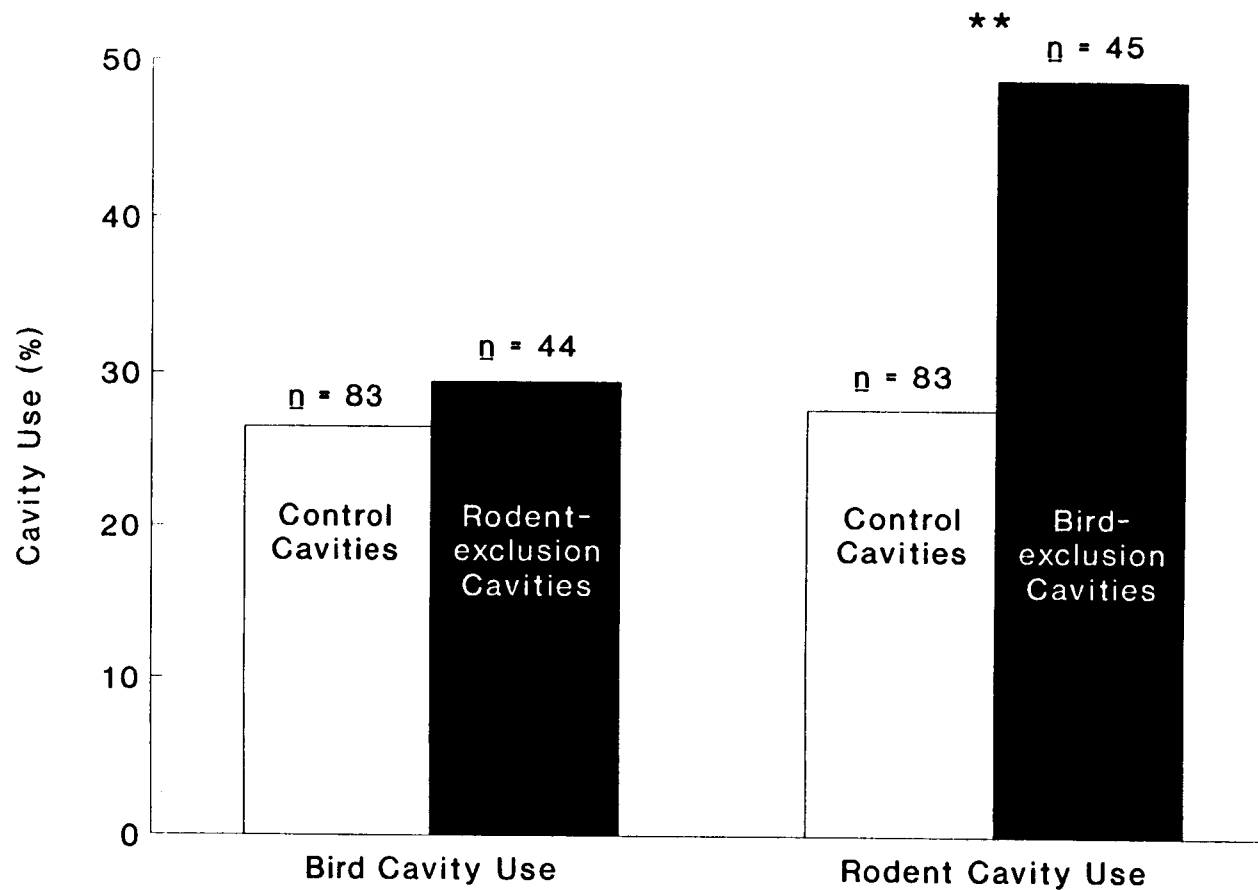


Figure 5. Proportions of cavities used for nesting by birds and rodents during a reciprocal-exclusion experiment in a piñon-juniper woodland, southeastern Colorado, 1988. ** Rodents nested in a significantly greater proportion of manipulated cavities than control cavities ($P < 0.01$, z -test).

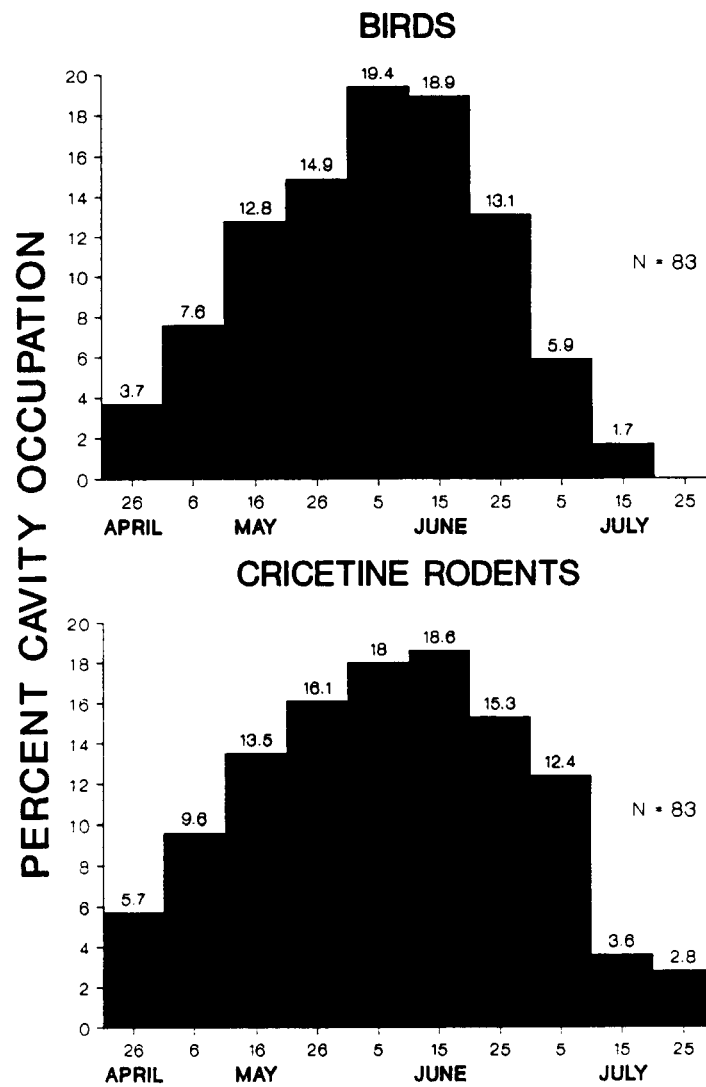


Figure 6. Percent of control cavities used as nest sites through time by birds and cricetine rodents in piñon-juniper woodland, southeastern Colorado, 1988.

April. A piñon mouse was the next species observed nesting on 11 April. Cavity-nesting peaked for birds and rodents in early-mid June, then declined for both taxa into August. Fifty-four percent of control cavities were used for nesting during the season.

DISCUSSION

Though 3 exclusion devices in each manipulated treatment failed to keep out the desired group of species, most were successful. Rodents nested in 27.7% of control cavities but only in 6.4% of rodent-exclusion cavities. Birds nested in 26.5% of control cavities but only in 6.3% of bird-exclusion cavities. So even though all exclusions did not keep out the desired taxon, enough did to experimentally demonstrate competition. In addition, 3 Bewick's wrens died in live-traps placed above rodent exclusions, possibly reducing bird use of rodent-exclusion cavities by up to 6.8%. I do not know why the use of cavities by birds for nesting differed between control cavities and unmanipulated cavities located on plots (Table 6); cavities located on plots were not utilized in the analyses, but if they had been the conclusions drawn from the experiment would have been the same.

Birds limited rodent use of cavities for nesting to a greater extent than rodents limited bird use of cavities for nesting. When birds were excluded, rodents increased their use of cavity nest-sites by 22.2% and when rodents were excluded, birds increased their use of cavity nest-sites by 3.0%. Rodents may be able to take advantage of an increased number of available nest cavities more readily than birds because they typically occur at higher densities in P-J woodland and because they can utilize other resources for nesting such as non-woodpecker-excavated cavities and hollow logs. Schoener's (1983) review of field studies on competition revealed that of 61 studies

that explicitly tested symmetry of competition, 51 (83.6%) demonstrated asymmetrical competition between species or among groups of species. My results may have been different if this system had been studied for more than one breeding season or in more than one locality. Since cavity-nesting birds and rodents have probably coevolved in P-J woodland, their responses to short-term artificial exclusion of competitors was probably limited (Brown and Davidson 1977).

Though the proportion of cavities used as nests by birds was not significantly greater in cavities from which rodents were excluded than in control cavities, several observations seem to indicate that birds were negatively affected by rodent presence. Bird use of manipulated cavities increased relative to control cavities in the direction one would expect if birds were competing with rodents. The less than ideal conditions of this field experiment led to the death of 3 birds at rodent-exclusion cavities, which may have decreased bird use of rodent-exclusion cavities by up to 6.8%. Also, birds used 9.1% of the cavities from which rodents were excluded for a second nesting bout while they only used 4.8% of the control cavities for a second nesting bout.

This study met the criteria set forth by Schoener (1983) for a field experiment of interspecific competition by manipulating the abundances of the hypothetically competitive species. But how can cavities be a limiting resource if only 54.2% of them were used for nesting throughout the breeding season? Individual species may be selecting only a subset of the cavities monitored based on certain

characteristics associated with the cavities such as cavity size (see Part I, Tables 1-6). Smaller cavity entrances can decrease the chance of eviction by a larger species or of predation (Moed and Dawson 1979). Some cavities are undesirable because they contain large parasite populations due to repeated use as nests (Brown and Brown 1986, Nilsson 1986). Some cavities may not be available for nesting because they are also defended by the occupants of a nearby territory.

Some species show nest-site fidelity, with individuals using the same cavity each year; if that cavity is unavailable because a more aggressive individual now occupies it, then competition is occurring for that limited resource even though there may be other vacant cavities. After blocking all cavities (20) on a 20 ha study area, Brush (1983) found the number of cavity-nesting bird territories declined only from 13.5 to 8; most of the cavity-nesting birds remained in the area during the breeding season even though nest cavities were not available. I put a bird-exclusion device over a cavity in which a mountain bluebird had built a nest but had not laid eggs. Upon removing the exclusion 3 months later, a mountain bluebird immediately revamped the nest and laid eggs. So even though the proportion of cavities used for nesting seems low, availability was influencing this cavity-nesting community.

Cavity density also influences whether cavities limit secondary cavity-nesting populations. I found an average of 1.5 cavities/ha (SD = 0.56) whereas other studies reported higher mean densities: 2.5 - 12.9 cavities/ha (Balda 1975, Cunningham et al. 1980, Land et al. 1989, Sedgwick and Knopf 1990, Waters et al. 1990). When Brawn and

Balda (1988) increased the density of cavities available to secondary cavity-nesters by adding nest boxes in northern Arizona ponderosa pine forests the overall breeding density increased on 2 of 3 treatment plots, indicating that cavities limited bird population sizes. At low densities of cavity nest-sites, competition for them seems more likely to influence community structure, assuming cavity-nesters are available to fill vacancies.

Temporal partitioning of the nest-cavity resource between birds and rodents was not apparent (Figure 6). In 1988, 2 (40%) of the cavities used by early-nesting western screech-owls were later used by northern flickers. Ash-throated flycatchers began nesting latest in the season and took advantage of vacated cavities for 29% (5 of 17) of their nests in 1988. Four cavities used by early nesting *P. spp.* were later used by birds. Ribble (1985, pers. commun.) sampled rodent reproductive status on the Piñon Canyon Maneuver Site during June through December, 1983. He found almost 70% of the piñon mice in reproductive condition in early June, declining to <10% by mid-August. Conversely, approximately 50% of the deer mice and 40% of the white-footed mice were in breeding condition in early June, increasing to approximately 70% and 100%, respectively, by mid-August. Since piñon mice are more arboreal than deer mice or white-footed mice (Armstrong 1972), they are more likely to use woodpecker-excavated cavities for nesting. In addition, they reproduce concurrently with most of the birds. Though rodent species may be partitioning the reproductive season through time among themselves, the species most likely to interact with cavity-nesting birds reproduced at the same time as

birds.

To better assess the role of competition between birds and rodents in the P-J community several avenues of research could be pursued. Several more years using the same study design will help indicate whether cavity-nest sites were in short supply in 1988. Larger sample sizes always increase the power of discriminating patterns with statistics, and this study is no exception. Mapping territories of cavity-nesting birds and live-trapping rodents, during this study would have indicated percent of non-breeding pairs present, or breeding in other places (especially for rodents). Adding natural (non-woodpecker-excavated) cavities would complement the study, giving a more complete description of total cavity use. To more directly assess the impact of competition on fitness, a closer monitoring of the number of young produced in each treatment is necessary. But food will probably influence the number of young produced, once a nesting cavity is secured, and it will be difficult to control for (or isolate) the influence of food use on productivity.

CONCLUSION

The null hypothesis was rejected and interspecific competition was experimentally demonstrated between birds and rodents for nest-sites in woodpecker-excavated cavities. Exclusion of potential competitors to cavity-nesting rodents, cavity-nesting birds, resulted in a statistically significant increase in nest-cavity use by rodents. A significant increase in bird use of cavities from which rodents were excluded was not demonstrated but several observations indicate a reciprocal competitive interaction likely existed. The importance of competition between birds and rodents in structuring this cavity-nesting community merits further investigation by repeating this type of experiment temporally and spatially.

LITERATURE CITED

- Armstrong, D. M. 1972. Distribution of mammals in Colorado. Natural History Monograph, University of Kansas 3:1-415.
- Bailey, A. M. and R. J. Niedrach. 1965. Birds of Colorado. Vol. 2. Denver Museum of Natural History, Denver, Colorado. 895pp.
- Balda, R. P. 1975. Vegetation structure and breeding bird diversity. Pages 59-80 in D. R. Smith, technical coordinator. Proceedings of the symposium on management of forest and range habitats for nongame birds. U.S. Forest Service General Technical Report WO-1.
- _____, and N. Masters. 1980. Avian communities in the pinyon-juniper woodland: a descriptive analysis. Pages 146-167 in R. M. DeGraaf, technical coordinator. Workshop proceedings--management of western forests and grasslands for nongame birds. U.S. Forest Service General Technical Report INT-86.
- Barry, R. E., Jr., M. A. Botje, and L. B. Grantham. 1984. Vertical stratification of Peromyscus leucopus and Peromyscus maniculatus in southwestern Virginia. The Journal of Mammalogy 65:145-148.
- Bent, A. C. 1939. Life histories of North American woodpeckers. Smithsonian Institute, U.S. National Museum Bulletin 174. 334pp.
- Birch, L. C. 1957. The meanings of competition. The American Naturalist 91:5-18.
- Brawn, J. D. and R. P. Balda. 1988. Population biology of cavity nesters in northern Arizona: do nest sites limit breeding? The Condor 90:60-71.
- Brown, C. R. and M. B. Brown. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (Hirundo pyrrhonota). Ecology 67:1206-1218.
- Brown, J. H. and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in a desert ecosystem. Science 196:880-882.
- Brush, T. 1983. Cavity use by secondary cavity-nesting birds in response to manipulations. The Condor 85:461-466.
- Buckman, R. E. and G. L. Wolters. 1987. Multi-resource management of pinyon-juniper woodlands. Pages 2-4 in R. L. Everett, compiler. Proceedings - pinyon-juniper conference. U.S. Forest Service General technical Report INT-215.

- Chase, C. A. III, S. J. Bissell, H. E. Kingery, and W. D. Gaul, eds.
1982. Colorado bird distribution latilong study. Colorado Field Ornithologists. Denver, Colo. 78pp.
- Cody, M. L. 1985. An introduction to habitat selection in birds.
Pages 3-56 in M. L. Cody ed. Habitat Selection in Birds.
Academic Press, Inc. Orlando, Flor.
- Colorado Climate Center. 1989. Unpublished data.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist 122:661-696.
- Cunningham, J. B., R. P. Balda, and W. S. Gaud. 1980. Selection and use of snags by secondary cavity-nesting birds of the ponderosa pine forest. U.S. Forest Service Research Paper RM-222. 15pp.
- DeVore, J. L. and R. L. Peck. 1986. Statistics, the exploration and analysis of data. West Publishing Co., St. Paul, Minn. 699pp.
- Dooley, J. L. and R. D. Dueser. 1990. An experimental examination of nest-site segregation by two Peromyscus species. Ecology 71:788-796.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook: a field guide to the natural history of North American Birds. Simon and Schuster, New York, N.Y. 785pp.
- Everett, R. L. 1987. Proceedings--pinyon-juniper conference. U.S. Forest Service General Technical Report INT-215. 581pp.
- Geluso, K. N. 1971. Habitat distribution of Peromyscus in the Black Mesa region of Oklahoma. The Journal of Mammalogy 52:602-607.
- Gifford, G. F. 1987. Myths and fables and the pinyon-juniper type. Pages 34-37 in R. L. Everett, compiler. Proceedings--pinyon-juniper conference. U.S. Forest Service General Technical Report INT-215.
- Gustaffson, L. 1988. Inter- and intraspecific competition for nest holes in a population of the collared flycatcher Ficedula albicollis. Ibis 130:11-16.
- Gysel, L. W. 1961. An ecological study of tree cavities and ground burrows in forest stands. The Journal of Wildlife Management 25:12-20.
- Hall, E. R. and K. R. Kelson. 1959. The mammals of North America. Vol. 2. Ronald Press Co., New York, N.Y. 1183pp.

- Harrison, H. H. 1979. A field guide to western birds' nests. Houghton Mifflin Co., Boston. 279pp.
- Holbrook, S. J. 1978. Habitat relationships and coexistence of four species of Peromyscus in northwestern New Mexico. The Journal of Mammalogy 59:18-26.
- Jameson, D. A. 1987. Climax or alternative steady states in woodland ecology. Pages 9-13 in R. L. Everett, compiler. Proceedings--pinyon-juniper conference. U.S. Forest Service General Technical Report INT-215.
- Land, D., W. R. Marion, and T. E. O'Meara. 1989. Snag availability and cavity nesting birds in slash pine plantations. The Journal of Wildlife Management 53:1165-1171.
- Lane, J. A. and H. R. Holt. 1987. A birder's guide to Colorado. L & P Press, Denver, Colo. 163pp.
- Lanner, R. M. 1981. The piñon pine, a natural and cultural history. Univ. Nev. Press, Reno. 208pp.
- Laurion, T. R. 1985. Avifauna survey of the Piñon Canyon Maneuver Site, Colorado. Unpublished report to U.S. Army, Ft. Carson. 56pp.
- Llewellyn, J. B. 1978. Reproductive patterns in Peromyscus truei truei in a pinyon-juniper woodland of western Nevada. The Journal of Mammalogy 59:449-451.
- . 1980. Seasonal changes in the aggressive behavior of Peromyscus maniculatus inhabiting a pinyon-juniper woodland in western Nevada. The Journal of Mammalogy 61:337-341.
- Madison, D. M. 1977. Movements and habitat use among interacting Peromyscus leucopus as revealed by radiotelemetry. The Canadian Field-naturalist 91:273-281.
- Mineau, P. and D. Madison. 1977. Radio-tracking of Peromyscus leucopus. Canadian Journal of Zoology 55:465-468.
- Moed, A. and D. G. Dawson. 1979. Breeding of starlings in nest-boxes of various types. New Zealand Journal of Zoology 6:613-618.
- Moore, A. D. 1945. Winter habits of birds. The Wilson Bulletin 57:253-261.
- National Geographic Society. 1983. Field guide to the birds of North America. National Geographic Society. 464pp.

- Neilson, R. P. 1987. On the interface between current ecological studies and the paleobotany of pinyon-juniper woodlands. Pages 93-98 in R. L. Everett, compiler. Proceedings--pinyon-juniper conference. U.S. Forest Service General Technical Report INT-215.
- Nicholson, A. J. 1941. The homes and social habits of the wood-mouse (Peromyscus leucopus noveboracensis) in southern Michigan. American Midland Naturalist 25:196-223.
- Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of predation and competition. Ornis Scandinavica 15:167-175.
- _____. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. The Auk 103:432-435.
- Peterson, B. and G. Gauthier. 1985. Nest site use by cavity-nesting birds of the Cariboo Parkland, British Columbia. The Wilson Bulletin 97:319-331.
- Pinkowski, B. C. 1976. Use of tree cavities by nesting eastern bluebirds. The Journal of Wildlife Management. 40:556-563.
- Raphael, M. G. 1981. Interspecific differences in nesting habitat of sympatric woodpeckers and nuthatches. Pages 142-151 in D. E. Capen, ed. The use of multivariate statistics in the studies of wildlife habitat. U.S. Forest Service General Technical Report RM-87.
- _____, and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monograph 86. 66pp.
- Rendell, W. B. and R. J. Robertson. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows in natural cavities. The Condor 91:875-885.
- Ribble, D. O. 1985. Microhabitat associations of small mammals in southeastern Colorado. M.S. Thesis, Colorado State University, Ft. Collins. 89pp.
- _____, and F. B. Samson. 1987. Microhabitat associations of small mammals in southeastern Colorado with special emphasis on Peromyscus (Rodentia). The Southwestern Naturalist 32:291-303.
- Roughgarden, J. 1983. Competition and theory in community ecology. The American Naturalist 122:583-601.
- SAS Institute, Inc. 1985a. SAS procedures guide for personal computers, version 6 edition. SAS Inst. Inc., Cary, N.C. 373pp.

- SAS Institute, Inc. 1985b. SAS/STAT guide for personal computers, version 6 edition. SAS Inst. Inc., Cary, N.C. 378pp.
- SAS Institute, Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Inst., Inc., Cary, N.C. 1028pp.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *The American Naturalist* 122:240-285.
- Sclater, W. L. 1912. A history of the birds of Colorado. Witherby and Co., London. 576pp.
- Sedgwick, J. A. 1981. Breeding bird and small mammal habitat relationships in northwestern Colorado. M.S. Thesis, Colorado State University, Ft. Collins. 139pp.
- _____. 1987. Avian habitat relationships in pinyon-juniper woodland. *The Wilson Bulletin* 99:413-431.
- _____, and F. L. Knopf. 1986. Cavity-nesting birds and the cavity-tree resource in plains cottonwood bottomlands. *The Journal of Wildlife Management* 50:247-252.
- _____, and _____. 1990. Habitat relationships and nest-site characteristics of cavity-nesting birds in cottonwood floodplains. *The Journal of Wildlife Management* 54:112-124.
- Short, H. L. 1978. Analysis of cuticular scales on hairs using the scanning electron microscope. *The Journal of Mammalogy* 59:261-268.
- Simberloff, D. 1983. Competition theory, hypothesis testing, and other ecological buzzwords. *The American Naturalist* 122:626-635.
- Smith, D. A. and S. W. Speller. 1970. The distribution and behavior of Peromyscus maniculatus gracilis and Peromyscus leucopus noveboracensis (Rodentia: Cricetidae) in a southeastern Ontario woodlot. *The Canadian of Zoology* 48:1187-1199.
- Stauffer, D. F. and L. B. Best. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. *The Wilson Bulletin* 94:329-337.
- Strong, D. R. Jr. 1983. Natural variability and the manifold mechanisms of ecological communities. *The American Naturalist* 122:636-660.
- Tate, J., Jr. 1986. The blue list for 1986. *American Birds* 40:227-236.

- Tazik, D. J., M. L. McKnight, and W. D. Severinghaus. 1988. Bird species habitat relationships and effects of Army training activities on bird communities at the Pinon Canyon Maneuver Site, Colorado -- a subinstallation of Ft. Carson. Unpublished report, U.S. Army Corps of Engineers, CERL. 115pp.
- Titus, K., J. A. Mosher, and B. K. Williams. 1984. Chance-corrected classification for use in discriminant analysis. *The American Midland Naturalist* 111:1-7.
- U. S. Department of the Army. 1980. Draft environmental impact statement for acquisition of training land in Huerfano, Las Animas, and Pueblo counties, Colorado. Ft. Carson, Colorado. 284 pp.
- Van Balen, J. H., C. J. H. Booy, J. A. Van Franeker, and E. R. Osieck. 1982. Studies on hole-nesting birds in natural nest sites 1. availability and occupation of natural nest sites. *Ardea* 70:1-24.
- von Haartman, L. 1957. Adaptation in hole-nesting birds. *Evolution* 11:339-347.
- Wasson, G. E. 1987. The American Indian response to the pinyon-juniper conference. Pages 93-98 in R. L. Everett, compiler. Proceedings--pinyon-juniper conference. U.S. Forest Service General Technical Report INT-215.
- Waters, J. R., B. R. Noon, and J. Verner. 1990. Lack of nest site limitation in a cavity-nesting bird community. *The Journal of Wildlife Management* 54:239-245.
- Weitzel, N. H. 1988. Nest-site competition between the European starling and native breeding birds in northwestern Nevada. *The Condor* 90:515-517.
- West, N. E. 1984a. Factors affecting treatment success in the pinyon-juniper type. Proceedings Utah shrub ecology workshop 2:21-33.
- _____. 1984b. Successional patterns and productivity potentials of pinyon-juniper ecosystems. Pages 1301-1332 in Developing strategies for rangeland management. Westveiw Press.
- _____, K. H. Rea, and R. J. Tausch. 1975. Basic synecological relationships in pinyon-juniper woodlands. Pages 41-53 in G. F. Gifford and F. E. Busby, eds. The pinyon-juniper ecosystem: a symposium. Utah State Univ., Logan.

- Winternitz, B. L. and D. W. Crumpacker, eds. 1985. Colorado wildlife workshop: species of special concern. Colorado Division of Wildlife Denver, Colo. 92pp.
- Wolff, J. O. and B. Hurlbutt. 1982. Day refuges of Peromyscus leucopus and Peromyscus maniculatus. The Journal of Mammalogy 63:666-668.
- Youkey, D. E. and E. C. Meslow. 1989. Response of breeding avifauna to Army training, Piñon Canyon Maneuver Site, Colorado. Unpublished report (15 April 1989) to U.S. Army, Ft. Carson, Colo. 40pp.
- Zar, J. H. 1984. Biostatistical analysis. Second ed. Prentice-Hall, Inc., Englewood Cliffs, N.J. 718pp.
- Zeleny, L. 1977. Nesting box programs for bluebird and other passerines. Pages 55-60 in S. A. Temple, editor. Endangered birds: management techniques for preserving threatened species. Univ. of Wisconsin Press, Madison.