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NEST SITE SELECTION IN RAPTOR COMMUNITIES OF THE EASTERN GREAT BASIN DESERT

Dwight G. Smith[1] and Joseph R. Murphy[2]

ABSTRACT.— Measures of niche breadth and overlap were used to compare nest site selection in a community of 10 raptor species and the Raven nesting in the eastern Great Basin Desert. Three variables were examined: nest site type, elevation, and exposure. Results suggest a division of component raptor species into relatively abundant core species that show wide niche breadths and uncommon fringe species with narrow niche breadths. Differences in use of each resource are most pronounced along elevation gradient in which three guilds are evident that correspond to raptor species groupings that nest at higher, middle, and lower elevations. Each guild is comprised of a mix of core and fringe species. Raptor species with highest overlap along one or more nest site variables examined are separated by differences in activity patterns.

In this study we compare nest site selection in a community of 10 raptor species and the Raven (*Corvus corax*) nesting in the eastern Great Basin desert of Utah.

Nest site selection is a function of many variables, including proximity of foraging habitat, protection of nest and young, thermal environment of nest, and spatial interactions within the community. Nest sites of several raptor species in the eastern Great Basin have some common characteristics and appear similar, suggesting the occurrence of interspecific competition for available nest sites. Observations of occasional appropriation of Ferruginous Hawk (*Buteo regalis*) and Red-tailed Hawk (*Buteo jamaicensis*) nests by Great Horned Owls (*Bubo virginianus*); Raven nests by Great Horned Owls; and Great Horned Owl nests by Golden Eagles (*Aquila chrysaetos*) and Prairie Falcons (*Falco mexicanus*) indicate that nest site availability may be a limiting resource operating during periods of high raptor density (Smith and Murphy 1973). Conversely, partitioning of nest site resources may reduce competition among raptor species and facilitate coexistence.

We compared raptor nest site selection and extent of interspecific overlap using three nest site variables: type of placement, exposure, and elevation. The Raven is included in the comparison because it is a functional raptor, constructs nests that may be appropriated by raptor species, and competes for nesting sites with several raptor species.

STUDY AREA

Long-term raptor studies began on a 7700 km² portion of the eastern Great Basin desert in winter 1966–1967. In previous papers we have presented observations on raptor population dynamics on a smaller 207-km² intensive study area (Smith and Murphy 1973) and described the response of large raptor species to fluctuations of their prey (Smith and Murphy 1979, 1981). Data for this study are from a 1170 km² segment of our original study area, which includes portions of Utah and Tooele counties in central Utah.

Topographically, the area is characterized by broad, flat, alkaline valleys separated by high, north-south oriented hills and ranges. Valley elevations range from 1460 to 1620 m and maximum elevations range from 1830 to 2440 m.

Climatically, the area is a northern cold desert (Shelford 1963). Annual precipitation averages 38 cm and monthly temperatures average from –5 C in January to 24 C in July, with wide daily and seasonal variations.

Two distinct vegetative associations are present. The desert shrub community occurs over the lower elevations and covers the valley floors. It consists of shrubs, herbs, and grasses, several of which form large, homo-

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TABLE 1. Yearly raptor populations nesting in the central Utah study area, 1967–1970.

Raptor species	1967	1968	1969	1970	Total nests
Golden Eagle	7	13	13	11	44
Ferruginous Hawk	15	28	34	13	90
Red-tailed Hawk	5	10	12	11	38
Swainson's Hawk	2	2	3	1	8
Prairie Falcon	1	1	1	2	5
Kestrel	3	3	2	2	10
Marsh Hawk	0	2	2	3	7
Great Horned Owl	6	14	16	10	46
Short-eared Owl	0	1	1	1	3
Burrowing Owl	1	2	4	3	10
Raven	4	5	5	3	17

geneous stands under certain edaphic soil conditions. Predominant desert shrub species include big sagebrush (*Artemisia tridentata*) on the better drained soils and greasewood (*Sarcobatus vermiculatus*) on the poorly drained valley floors. The well-drained slopes and hills support a dwarf conifer community of Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus monophylla*), which occur in stands of widely varying density.

A number of abandoned quarries, some of considerable size, are located in the foothills. Many have sheer cliffs ranging from 5–80 m in height. A few structures, all in various states of disrepair, were associated with some quarry sites. These and an abandoned gunnery tower at the U.S. Army Deseret Depot located in Rush Valley provided artificial nesting sites for some raptor species.

METHODS

The study was conducted from November 1966 through July 1971. To locate nests, we subdivided the study area into 2.56-km² units, which were systematically searched in a rotating sequence at biweekly intervals throughout the nesting season. Foot searches of cliffs, rock outcrops, and juniper stands were supplemented by vehicle searches through desert shrub. Fixed-wing aircraft surveys were used two years to find nests but were of limited use due to minimum speed and altitude requirements. Fieldwork each year was from December through August. During this time a minimum of two days per week were spent on the study area, and total fieldwork per year averaged 1640 hours. Rotation of search areas throughout the nesting season ensured that all areas were checked several times, and we believe that we successfully located all raptor nests each year.

For each active nest located we recorded (1) elevation above sea level, (2) direction of exposure, and (3) type of placement. Nest site elevation was measured with a portable altimeter preset at USGS markers located on the study area. Recorded data were grouped in 50 m intervals. The nest site elevation variable permits comparison of how raptor species place their nests above the valley floors over which they hunted. Direction of nest site exposure was determined by orientation of a line projected at 90 degrees from a cliff wall or tree cavity through a nest center and grouped in one of eight equal subdivisions of the compass. Hillside tree and ground nests were classed by direction of slope. Nests on level ground were not included in exposure calculations except where nest site entrance orientation was obvious. We recognized 18 nest-site types including 5 cliff, 7 tree, 5 ground, and burrows (Table 2).

To compare raptor and Raven nest site selection, we used determinations of nest site niche breadth, overlap, and an average community overlap with respect to each of the three nest site variables.

Niche breadth of nest site selection was calculated using the standard information theoretic measure presented by Culver (1972):

$$\beta i = \frac{\sum_j^N {}_{ij} \log N_{ij}}{\Sigma N_{ij} \Sigma N_{ij}} \log r$$

where N_{ij} is the abundance of species in category j and r is the number of categories. The value of β_i may range from 0 to 1.

To compare overlap of raptor and Raven nest site selection we used Horn's (1966) overlap index:

$$ih = \frac{[\sum_j (N_{ij} + N_{hj}) \log (N_{ij} + N_{hj}) - \sum_j N_{ij} \log {}_{ij} - {}_j N_{hj} \log N_{hj}]}{[(N_i + N_h) \log (N_i + N_h) - N_i \log N_i - N_h \log N_h]}$$

where N_{ij} is the value for species in category j, N_{hj} the value of species h in category j, N_i is the total of values for species in all categories and N_h is the total of values for species h in all categories. Overlap values may range from 0 to 1.

Average community overlap of each raptor species within the raptor community was calculated using the formula provided by Cody (1974):

$$\alpha\bar{x} \div \sum_{j}^{n-1} a_{ij}\, n-1$$

where $\bar{x}$ represents average community overlap of a species and all overlap values exclusive of a_{ii} are summed.

Dendrograms were constructed using both unweighted (UPGMA) and weighted (WPGMA) pair group cluster analyses (Sokal and Sneath 1963). Resultant dendrograms were similar and we have presented UPGMA in this paper.

RESULTS

Populations of raptors and ravens nesting on the study area from 1967 to 1970 are presented in Table 1. The Ferruginous Hawk was the most common raptor each year, varying from 13 nesting pairs in 1970 to 34 in 1969. Nesting populations of Great Horned Owls, Golden Eagles, and Red-tailed Hawks were approximately 50 percent smaller: Golden Eagles varied from 7 pairs in 1967 to 13 in 1968 and 1969, Great Horned Owls from 6 in 1967 to 16 in 1969, and Red-tailed Hawks from 5 pairs in 1967 to 12 in 1969. One other large raptor, the Swainson's Hawk (*Buteo swainsoni*) averaged two nesting pairs per year (range 1–3 pairs). Nesting populations of medium- and small-sized raptors were consistently low throughout the study period. Only one or two pairs of Prairie Falcons nested on the study area each year, and the only slightly more abundant Marsh Hawks (*Circus cyaneus*) nested in three of four study years (1968–70). Short-eared Owls (*Asio flammaeus*) were the least common raptor and only one nesting pair was found from 1968 to 1970. Raven nesting populations varied from 3 pairs in 1970 to 5 in 1968 and 1969. Although 6 of 11 species considered in this study were uncommon, they are characteristic components of nesting raptor populations in this portion of the eastern Great Basin.

TABLE 2. Percent distribution of raptor species in 18 nest site type categories.[a]

Nest Site Type	GE	GHO	FH	RtH	SwH	PF	MH	SpH	SeO	BuO	Ra
CLIFF SITES											
Quarry	26.3	19.5	—	7.9	—	30.0	—	40.0	—	—	11.5
20+ m	22.7	6.5	—	7.9	—	10.0	—	—	—	—	23.6
5–19 m	47.5	43.4	—	36.8	—	60.0	—	30.0	—	—	5.9
5 m	—	2.2	3.2	5.3	—	—	—	—	—	—	59.0
Rock outcrop	4.5	—	24.6	—	—	—	—	—	—	—	—
TREE SITES											
Juniper (platform)	—	26.0	53.1	21.2	87.5	—	—	—	—	—	—
Juniper (cavity)	—	—	—	—	—	—	—	20.0	—	—	—
Pinyon Pine	—	2.2	2.1	7.9	—	—	—	—	—	—	—
Cliffrose	—	—	2.1	2.6	—	—	—	—	—	—	—
Cottonwood (platform)	—	—	1.0	5.3	12.5	—	—	—	—	—	—
Cottonwood (cavity)	—	—	—	—	—	—	—	10.0	—	—	—
Lombardy Poplar	—	—	—	5.3	—	—	—	—	—	—	—
GROUND SITES											
Sagebrush	—	—	7.5	—	—	—	74.4	—	33.3	—	—
Ricegrass	—	—	4.3	—	—	—	12.8	—	33.3	—	—
Horsebrush	—	—	2.1	—	—	—	—	—	—	—	—
Winter Wheat	—	—	—	—	—	—	12.8	—	33.3	—	—
Dry Wash	—	—	—	—	—	—	—	—	—	20.0	—
BURROW	—	—	—	—	—	—	—	—	—	80.0	—
Sample size (N)	44	46	90	38	8	5	7	10	3	10	17

[a]GE = Golden Eagle, GHO = Great Horned Owl, FH = Ferruginous Hawk, RtH = Red-tailed Hawk, SwH = Swainson's Hawk, PF = Prairie Falcon, MH = Marsh Hawk, SpH = Sparrow Hawk (American Kestrel), SeO = Short-eared Owl, BuO = Burrowing Owl, Ra = Raven.

Golden Eagles nested in 4 of 18 (23.5 percent) categories, all on cliff sites or rock outcrop (Table 2). Of the large raptors on the study area, Golden Eagles selected the narrowest range of nest sites. Comparatively, Ferruginous Hawks and Red-tailed Hawks selected the widest variety of nest sites, each using 9 of 18 (47.4 percent) types. Although both species used cliff and tree sites, major differences in type and frequency of use are evident. Over twice as many Red-tailed Hawk nests were located in cliffs (57.9 percent vs. 25.6 percent; $d = 6.5$; $P<0.05$). Over 55 percent of Red-tail nests were in cliffs greater than 5 m in height, whereas all Ferruginous Hawk nests were located in low cliffs (<5 m) and rock outcrops. Ferruginous Hawks chose tree sites more frequently (58.3 percent compared to 43.3 percent for Red-tailed Hawks), although both species most commonly constructed nests in junipers. Ferruginous Hawks but not Red-tailed Hawks also constructed nests on the ground (13.9 percent located in three of the four Great Basin Desert shrub communities available).

Great Horned Owls were found in 6 of 18 (13.5 percent) nest-site types, all of which were in cliffs and junipers. Golden Eagles, Prairie Falcons, and Ravens nested exclusively in cliff nest site types, and Swainson's Hawks were restricted to juniper and cottonwood sites. The two smallest raptors on the study area, the American Kestrel (*Falco sparverius*) and Burrowing Owl (*Athene cunicularia*) nested only in cavities, the former in cliffs (70 percent) and trees (30 percent) and the latter in burrows.

Two other species that used a narrow range of nest site types were the Marsh Hawk and Short-eared Owl. Both selected nest sites in desert shrub communities.

Raptor nest site locations in nine elevation categories are presented in Table 3. Although Golden Eagle nest sites were found in eight of nine elevation categories, ranging from 1460 to 1910 m, 78.5 percent were located at elevations greater than 1680 m. On the average, Golden Eagle nests were located at higher elevations than those of any other raptor in the study area. Great Horned Owls and Red-tailed Hawks were most similar to the Golden Eagle in nest site placement.

Great Horned Owl nests were found at all elevations, although most (82.5 percent) were located in elevations greater than 1600 m. Red-tailed Hawk nests were found in 8 of 9 (88.9 percent) elevation categories and also were primarily located at higher elevations. Comparatively, nests of two other large raptor species, the Swainson's Hawk and Ferruginous Hawk, were restricted to middle and lower elevations. A total of 85.1 percent of all Ferruginous Hawk nests were found between 1511 and 1660 m and none were placed at elevations higher than 1710 m. All Swainson's Hawk nests were found at elevations between 1460–1610 m. Nest sites of Ravens had the highest average elevation. All were above 1711 m and 94.1 percent were at elevations greater than 1761 m. Nest sites of Prairie Falcons were limited to middle elevations from 1611 to 1760 m, but three species, the Marsh Hawk, Short-eared Owl and Burrowing Owl nested exclusively in lower ele-

TABLE 3. Percent distribution of raptor species nests in nine elevation categories. Elevation in meters.

Species[a]	1460–1510	1511–1560	1561–1610	1611–1660	1661–1710	1711–1760	1761–1810	1811–1860	1861–1910	Number of nests
GE	4.5	0.0	2.3	4.5	22.7	29.5	15.9	6.8	13.6	44
GHO	4.3	4.3	8.7	13.0	21.7	26.1	10.9	4.3	6.5	46
FH	5.3	21.3	45.7	18.1	9.6	0.0	0.0	0.0	0.0	90
RtH	2.6	5.3	5.3	31.6	23.7	13.2	15.8	2.6	0.0	38
SwH	12.5	25.0	62.5	0.0	0.0	0.0	0.0	0.0	0.0	8
PF	0.0	0.0	0.0	20.0	40.0	40.0	0.0	0.0	0.0	5
MH	57.1	28.6	14.3	0.0	0.0	0.0	0.0	0.0	0.0	7
SpH	0.0	0.0	0.0	10.0	50.0	0.0	30.0	10.0	0.0	10
SeO	33.3	66.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3
BuO	30.0	70.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10
Ra	0.0	0.0	0.0	0.0	0.0	5.9	29.4	47.1	17.6	17

[a]GE = Golden Eagle, GHO = Great Horned Owl, FH = Ferruginous Hawk, RtH = Red-tailed Hawk, SwH = Swainson's Hawk, PF = Prairie Falcon, MH = Marsh Hawk, SpH = Sparrow Hawk (American Kestrel), SeO = Short-eared Owl, BuO = Burrowing Owl, Ra = Raven.

vations, below 1610 m for the Marsh Hawk and below 1560 m for the latter two species.

A summary of distribution of raptor nests in eight exposure categories is presented in Table 4. Golden Eagles, Great Horned Owls, Ferruginous Hawks and Red-tailed Hawks had exposures in all eight categories, although each exhibited higher frequencies for certain exposures. Thus, 57.5 percent of all Golden Eagle nests had exposures from WNW-NNE but 52.5 percent of Great Horned Owl nests had WSW-WNW exposures. Exposure preferences of Ferruginous Hawks and Red-tailed Hawks were slightly less definitive, with the former showing highest ESE nest site exposure and the latter WSW. The two raptor species that nest exclusively in cliff and quarry cavities, the Raven and Prairie Falcon, both had maximum WNW nest site exposures. Short-eared Owls exhibited the narrowest range of nest site exposure, with all nests at ENE and ESE, but this may reflect the small sample size for this species.

NEST SITE NICHE BREADTH.— Niche breadth represents the range or diversity of a species along a resource gradient. Niche breadth values of raptor species along each variable are presented in Table 5.

A significant positive correlation between relative abundance of raptor species and niche breadth (β) was found for each of the nest site variables examined, i.e., type (T), elevation (E), and exposure (X), ($r = 0.62$, $t = 2.36$, $P < 0.05$ for β_T; $r = 0.63$, $t = 2.44$, $P < 0.05$ for β_E; and $r = 0.72$, $t = 3.12$, $P < 0.05$, for β_X), suggesting that the most common raptor species select the widest range of nesting sites. The Golden Eagle ranked eighth in range of nest site type (β_T) selection and tenth in nest site elevation (β_E) and had the widest breadth of nest site exposure selection (β_X). The three other most abundant raptors, the Great Horned Owl, Ferruginous Hawk, and Red-tailed Hawk, consistently ranked highest along each variable. If we assume that abundance of the large raptor species reflects their dominance, this is consistent with the predictions of Levins (1968) and McNaughton and Wolf (1970) that dominant community species occupy broader niches. The American Kestrel ranked sixth or seventh along each variable and showed broader values of nest site type and exposure but not elevation than the average β values of all species. Another middle-ranked species, the Raven, had a broad β_X but narrow β_T and β_E. It is widely distributed in this part of the Great Basin desert.

Five less common raptor species, the Prairie Falcon, Swainson's Hawk, Marsh Hawk, Short-eared Owl, and Burrowing Owl, showed β values well below the average in each variable. All showed narrow ranges in one or more of the nest site variables examined.

NICHE OVERLAP.— Niche overlap was calculated for all species pairs for each variable. Overlap values provide a measure of the potential impact one species may have on another. Patterns of overlap and community structure are best illustrated by dendrograms (Cody 1974), which show how species combinations that closely overlap along a

TABLE 4. Percent distribution of raptor nests in eight exposure categories.

Species[a]	WSW	WNW	NNW	NNE	ENE	ESE	SSE	SSW	Number of nests
GE	15.0	17.5	22.5	17.5	7.5	5.0	7.5	7.5	40
GHO	29.5	22.7	6.8	2.3	2.3	11.4	6.8	18.2	44
FH	21.6	2.7	8.1	2.7	6.8	27.0	16.2	14.9	74
RtH	23.7	10.5	2.6	7.9	5.3	18.4	18.4	13.2	38
SwH	12.5	0.0	0.0	25.0	25.0	37.5	0.0	0.0	8
PF	40.0	40.0	20.0	0.0	0.0	0.0	0.0	0.0	5
MH	0.0	42.9	0.0	28.6	28.6	0.0	0.0	0.0	7
SpH	10.0	10.0	40.0	0.0	10.0	20.0	10.0	0.0	10
SeO	0.0	0.0	0.0	0.0	66.6	33.3	0.0	0.0	3
BuO	0.0	0.0	14.3	0.0	0.0	57.1	14.3	14.3	7
Ra	23.5	41.2	11.8	0.0	11.8	5.9	0.0	5.9	17

[a]GE = Golden Eagle, GHO = Great Horned Owl, FH = Ferruginous Hawk, RtH = Red-tailed Hawk, SwH = Swainson's Hawk, PF = Prairie Falcon, MH = Marsh Hawk, SpH = Sparrow Hawk (American Kestrel), SeO = Short-eared Owl, BuO = Burrowing Owl, Ra = Raven.

resource dimension will form clusters or guilds. Community dendrograms for each nesting site dimension are presented in Figure 1. Each guild represents a group of species that exploit a specific nest site dimension in a similar manner.

Inspection of the nest site type (NST) dendrogram reveals four guilds, the largest (Guild A) containing six species and the smallest just one (Guild D). Subdivisions within the Guild A are, however, readily apparent: one shows close similarity of NST selection by the Golden Eagle and three other cliff-nesting raptors, Raven, and Prairie Falcon, and the second subdivision shows a close relationship between Great Horned Owls and Red-tailed Hawks. The frequent appropriation of Golden Eagle and Raven nests by Prairie Falcons and *Buteo* nests by Great Horned Owls contribute a significant percentage of the overlap and resulting structure of Guild A. Guild B pairs the Ferruginous and Swainson's hawks and illustrates isolating differences between these and the other large raptor species with respect to selection of nest type. The Marsh Hawk and Short-eared Owl both nest in desert shrub and occupy a separate NST guild. The Burrowing Owl is the only raptor species utilizing burrows for nest sites and is the sole member of its guild.

Both UPGMA and WPGMA dendrograms show the Ferruginous and Swainson's hawk combination closer to the Marsh Hawk and Short-eared Owl guild than Guild A containing the other large raptors. This is inconsistent with observational data: although 14 percent of Ferruginous Hawk nests were ground sites located in desert shrub, another 53 percent were in Juniper and the remainder on either rock outcrops or artificial structures. All Swainson's Hawk nests were located in trees. On the basis of overlap values, Ferruginous Hawks actually were closer to the Great Horned Owl–Red-tailed Hawk guild than the Marsh Hawk–Short-eared Owl guild (average pooled θ values of 0.6994 and 0.3823, respectively).

Clustering is maximal in the nest site elevation (NSF) dendrogram in which two guilds are evident. Golden Eagles are placed in Guild A, along with Great Horned Owls, Red-tailed Hawks, Prairie Falcons, American Kestrels, and Ravens. Raptor species composition of Guild A is identical to Guild A of NST dendrogram and species composition of Guild B corresponds to NST Guilds B, C, D. The two NSE guilds neatly separate raptor species that nest at middle and low elevations from those that select nest sites at comparatively higher elevations. NSE Guild B may be further subdivided into a cluster of two raptor species, the Ferruginous and Swainson's hawks, which nested at middle elevations in the knolls and foothills, and the cluster of three raptor species, the Marsh Hawk, Short-eared Owl, and Burrowing Owl, which nested in the valleys.

Two guilds are also formed in the nest site exposure (NSX) dendrogram. Raptor species composition of these guilds reveals interesting similarities and differences when compared to NST and NSE dendrograms previously examined. Differences in NSX preferences split the Ferruginous Hawk-

TABLE 5. Niche breadth parameters of nest site dimensions.[1]

Species	Number of nests[2]	Nest type β_T	Nest elevation β_E	Nest exposure β_X
Golden Eagle	44	.4581 (8)	.8241 (10)	.9439 (11)
Great Horned Owl	46	.4679 (9)	.9043 (11)	.8625 (8)
Ferruginous Hawk	90	.5033 (10)	.6268 (8)	.8870 (9)
Red-tailed Hawk	38	.6312 (11)	.8030 (9)	.9929 (10)
Swainson's Hawk	8	.1280 (1)	.4097 (3)	.6352 (5)
Prairie Falcon	5	.3050 (4)	.4801 (5)	.5073 (2)
Marsh Hawk	7	.2706 (3)	.4351 (4)	.5189 (3)
American Kestrel	10	.4347 (7)	.5317 (6)	.7740 (7)
Short-eared Owl	3	.3731 (6)	.2897 (2)	.3061 (1)
Burrowing Owl	10	.1699 (2)	.2780 (1)	.5551 (4)
Raven	17	.3637 (5)	.5403 (7)	.7422 (6)
Average (all species)		.3734	.5566	.7023

[1]Figures in parentheses indicate rank within parameter.
[2]Sample sizes used in nest site exposure determinations differ as follows: Golden Eagle, 40; Ferruginous Hawk, 74.

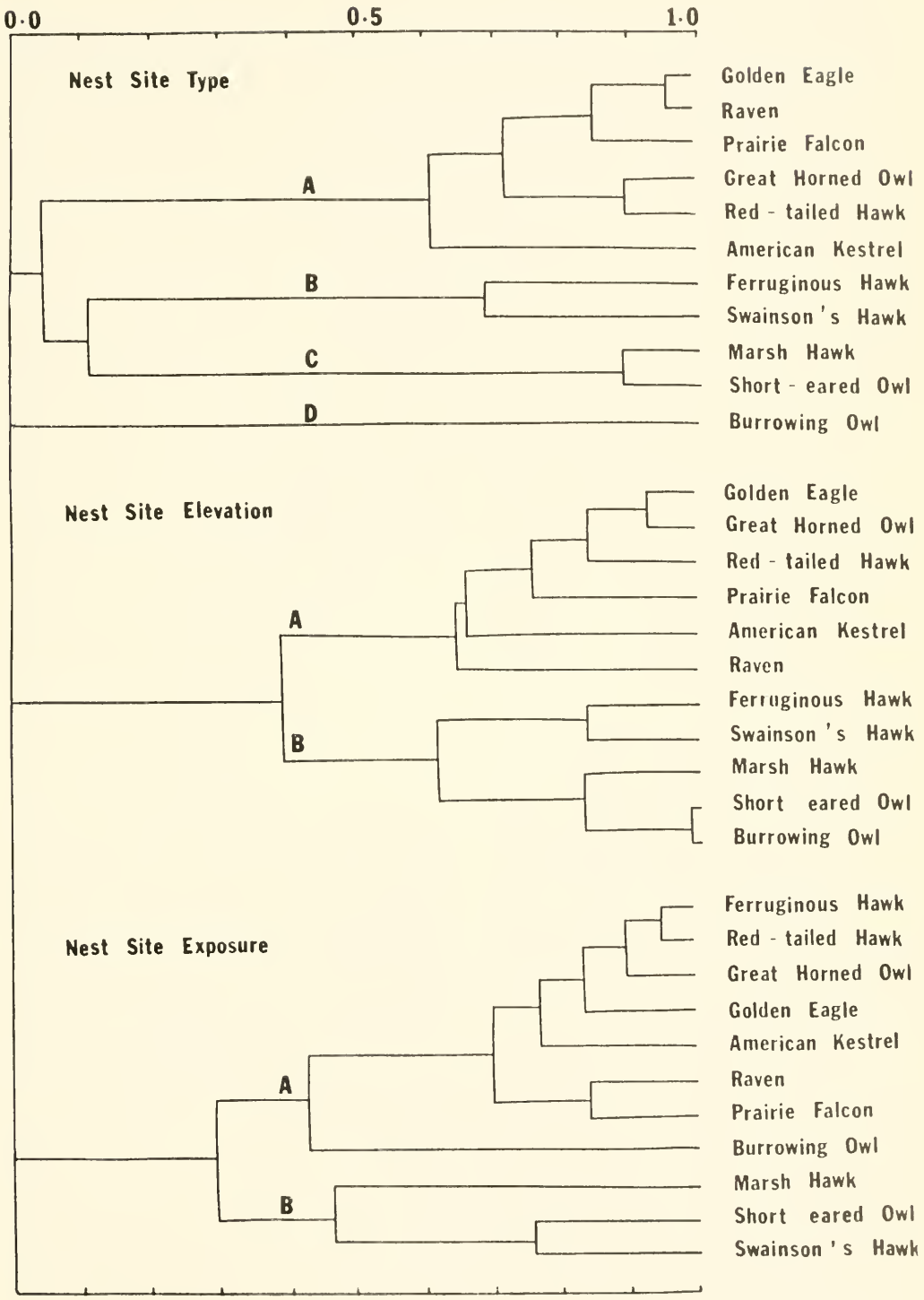

Fig. 1. Dendrograms resulting from UPGMA cluster analysis of niche overlap matrices of nest site selection dimensions among raptor species and the Raven. Separate dendrograms are constructed for each nest site resource dimension.

Swainson's Hawk combination, with the former now included in Guild A containing the other large raptor species and the latter placed in the Marsh Hawk and Short-eared Owl cluster. Two species with very similar NSX requirements are the Raven and Prairie Falcon of Guild A. Both utilize a high proportion of cavity nest sites with WNW and NNW exposure.

AVERAGE COMMUNITY OVERLAP.— Average community overlap (α) within the raptor species community was calculated for each nest site variable (Table 6). Average community overlap provides a method for broadly defining core species that characteristically show high ($\alpha > \alpha\bar{x}$) values and fringe species with low average ($\alpha < \alpha\bar{x}$) values). These α values of core species indicate high average overlap with other community raptors, whereas fringe species are more ecologically isolated.

Average community overlap may also show the degree of competitive interaction along a resource. For the raptor species community, average overlap was greatest in NSX variable ($\alpha\bar{x}$ = .5692) and least in NST ($\alpha\bar{x}$ = .2691). The lower NST and NSE overlap may suggest segregation of raptor species along these resources. The Golden Eagle again ranked high in average community overlap in all three nest site variables. Only Great Horned Owls and Red-tailed Hawks had a higher average community overlap in two nest site variables, NST and NSE, and only the Red-tailed Hawk had a higher community overlap in NSX.

There is a correlation between raptor species abundance and average community overlap, with the most common raptor species showing highest average community overlaps and qualifying as core species. This pattern is consistent with abundance correlations previously discussed. Ferruginous Hawk NST community overlap (α_T = .2213) deviates from this pattern because of its comparatively restricted choice of nest sites. Although this species used 10 of 19 NST categories, 75.5 percent of nests were located in but two categories, junipers and rock outcrops. NST and NSX average overlap (α_T = .3373; α_X = .6474) of the Raven places it among the core species, although its typical selection of nest sites at higher, more remote elevations on the study area resulted in the lowest NSE average niche overlap rank (α_E = .2102). Three raptor species have marginal rankings, the Prairie Falcon, American Kestrel, and Swainson's Hawk. The Prairie Falcon had high NST overlap (α_T = .3988) but low NSE and NSX overlap values (α_E = 3.35; α_X = .2102) and should probably be considered a marginally core member of the raptor community. Overall low average community overlaps of the Marsh Hawk, Short-eared Owl, and Burrowing Owl qualify these raptors as fringe species.

TABLE 6. Average community overlap values.[1]

Species	Nest site type	Nest site elevation	Nest site exposure
Golden Eagle	.3873 (8)	.4600 (8)	.6830 (10)
Great Horned Owl	.4632 (11)	.5453 (11)	.6758 (8)
Ferruginous Hawk	.2213 (5)	.4639 (9)	.6764 (9)
Red-tailed Hawk	.4269 (10)	.5186 (10)	.6857 (11)
Swainson's Hawk	.1604 (4)	.3548 (6)	.5318 (5)
Prairie Falcon	.3988 (9)	.3335 (2)	.4762 (4)
Marsh Hawk	.1144 (3)	.3812 (7)	.4046 (2)
American Kestrel	.2980 (6)	.3504 (5)	.6412 (6)
Short-eared Owl	.1130 (2)	.3410 (4)	.3798 (1)
Burrowing Owl	.0000 (1)	.3391 (3)	.4595 (3)
Raven	.3773 (7)	.2101 (1)	.6474 (7)
Average (all species)	.2691	.3907	.5692

[1]Figures in parentheses indicate rank.

DISCUSSION

Whittaker et al. (1973) reviewed the history and conceptual development of the terms *niche* and *habitat* as methods of describing how a species relates to the physical and biological variables within a community. They proposed that *niche* be used to describe the relationship of a species to intracommunity variables such as food size and feeding behavior, whereas *habitat* should be restricted to such spatial gradients of a community as elevation or exposure.

Nest site selection is an active process in which species respond to stimuli based on complexes of environmental variables (Fretwell 1972), although tradition and previous experience may reduce the importance of certain environmental factors (White 1969). In essence, the selection of a nest site is a behavioral response similar to the stimulus-response behaviors by which a species restricts its foraging within certain environmental constraints such as height above

ground, e.g., foraging height niche of the Blue-gray Gnatcatcher (*Polioptila caerulea*) described by Root (1967). In this context, nest site selection may be considered as one axis of the n-dimensional niche hyperspace of a species.

We believe the three variables considered, type, elevation, and exposure, represent basic habitat characteristics. We assume that raptors will select some portion within each of these dimensions that collectively provide the most suitable nesting site. Raptors may, for example, choose nest site types that potentially provide such benefits as a wide platform base for rearing large broods of young (e.g., Ferruginous Hawk platform nests in tops of junipers); inaccessibility (e.g., Golden Eagle nests on high, sheer cliffs or Burrowing Owl nests in burrows), or shelter (e.g., cavity nests of Ravens and Prairie Falcons).

Nest site elevation may promote nest inaccessibility and therefore offer brood protection, provide a commanding view of the territory, or enhance lift capabilities by local updrafts resulting from uneven heating of valley floors and ridges. In this latter context selection of nesting sites at middle and higher elevations may be especially advantageous to Golden Eagles and larger hawks and owls by enabling them to forage more efficiently and return large prey to the nest.

Mosher and White (1976) elucidated the importance of directional exposure of nest site with special reference to Golden Eagles. They pointed out that exposure of young raptors to extremes of temperature and direct insolation may be a major source of thermoregulatory stress during early stages of development. Thus, raptor species will presumably tend to select nest sites with exposures that offer an optimum microclimate within reasonable variations.

Several factors are immediately evident with respect to nest site partitioning within the raptor community of this study. First, there is a significant correlation between niche breadth, average community overlap, and relative abundance of raptor species that divides the raptor community into groups of core species such as the Golden Eagle with comparatively broad niches and fringe species with narrow niches. This pattern is especially notable within guilds where it may reduce competition between species with very similar nest site requirements by restricting population size of the fringe species. Thus, along each variable we find three basic groups that correspond to raptor species that tend to nest at high, middle, and low elevations within the range of topographic habitats found in the study area. Competition within these clusters is potentially more intense compared with competition between clusters, but is reduced by two isolating mechanisms. First, raptor species of each cluster include core and fringe species. Core species common to Guild A of NST and NSE dendrograms include the Golden Eagle, Great Horned Owl, Red-tailed Hawk, and Raven. The Prairie Falcon is marginally core in this cluster, and the American Kestrel may represent a fringe species. Core and fringe species in the middle cluster are the Ferruginous Hawk and Swainson's Hawk, respectively. The three raptor species in the lower cluster rank as fringe species. Of these the Burrowing Owl is a common component of raptor communities in the eastern Great Basin desert.

Wiens (1977) noted that competition theory predicts that other species may successfully invade communities during periods of high resource availability. In this context the presence and abundance of fringe species may be a function of food supply available to the core species. Core species such as the Golden Eagle increase territory size when their prey base is low and reduce average territory size when their prey base is high (Smith and Murphy 1973, 1979). This reduction may collectively be sufficient to allow invasion by fringe species. Conversely, in low prey years core species compensate by increasing territorial size and may thereby exclude such fringe species.

A second factor that reduces competition within clusters is different time-activity patterns. This mechanism separates the nocturnal Great Horned Owl from two diurnal raptor species with very similar nest site requirements, the Red-tailed Hawk and Golden Eagle. A parallel isolation is also evident within the Marsh Hawk and Short-eared Owl guild. The crepuscular activity of the Ferruginous Hawk at least partially isolates it from the more diurnal Swainson's Hawk.

In summary, raptor species partition nest sites along the three environmental variables examined, although several within cluster species show comparatively broad overlap. At least part of this overlap may be attributed to niche hyperspace differences not examined in this study, such as foraging area, prey selection, and breeding chronology.

The nest site relationships and structure of the raptor community are a measure of intra- and interspecific raptor species populations adapting to habitats of the eastern Great Basin desert and should not be construed as levels of general adaptability or relationships equally applicable in all habitats.

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