

HABITAT AND NEST-SITE USE BY RED-TAILED HAWKS IN NORTHWESTERN WYOMING

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ABSTRACT.—We described Red-tailed Hawk (*Buteo jamaicensis*) habitat in the valley portion of Grand Teton National Park during 1992–94 at three spatial scales: (1) nest tree, (2) microhabitat centered around nest trees, and (3) within the home range. Nests were found in six tree species, 22 (36%) were in coniferous and 38 (64%) were in deciduous trees. Nest-tree height, nest height, nest-tree diameter-at-breast-height (DBH), and percentage height of nest in the tree means were 22 m, 16 m, 50 cm, and 72.7%, respectively. Nests were located predominantly on northwestern aspects and on moderately-steep slopes. Microhabitat selection was determined by comparing nest sites with randomly-located, non-nest sites. We measured nest-site microhabitat characteristics in 0.04-ha circles centered on nest trees and two paired non-nest sites at 60 independent locations. Compared to non-nest sites, nest-sites had a higher number of trees, taller trees, larger DBH and basal area of trees, and greater canopy cover. Among nest sites, 50 of 60 nest trees were the tallest trees in the plot, and 48 of 60 had the largest diameter. Discriminant function analysis indicated that canopy cover, basal area of trees, and distance to forest edge were the most important variables in distinguishing nest sites from non-nest sites. We calculated cover of six vegetation classes within 100% minimum convex polygon home ranges of seven breeding Red-tailed Hawk pairs, and within a 10 640 ha core study area. The proportion of habitat cover types in home ranges varied considerably among individual pairs. Among all home ranges, 75% were non-forested open grassland or shrub and 25% were forested. Habitat characteristics important to Red-tailed Hawks on our study area were mature forests of mixed conifer and deciduous trees on moderately-steep hillsides adjacent to expansive openings consisting of either sagebrush (*Artemisia* spp.)-grassland flats or remnant agricultural sites. Landscape-scale factors other than vegetation cover-type proportions may be more important in determining home range size and location within our study area.

KEY WORDS: *Red-tailed Hawk*; *Buteo jamaicensis*; *nesting habitat*; *habitat use*; *home range*; *Grand Teton National Park*; *Wyoming*.

HABITAT Y USO DEL SITIO DEL NIDO DEL GAVILAN DE COLA ROJA EN EL NOROESTE DE WYOMING

RESUMEN.—Describimos el hábitat del gavilán de Cola Roja (*Buteo jamaicensis*) en el valle del Grand Teton National Park durante 1992–94, en tres escalas espaciales: (1) árbol con nido, (2) microhábitat

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centrado alrededor de árboles con nidos y (3) dentro del rango ocupación. Se encontraron nidos en seis especies de árboles, 22 (36%) fueron en coníferas y 38 (64%) fueron en árboles deciduos. La altura del árbol con nido, la altura del nido, el diámetro a la altura del pecho (DAP) del árbol con nido y el porcentaje de la altura del nido de las medias de los árboles fueron 22 m, 16 m, 50 cm, y 72.7%, respectivamente. Los nidos se localizaron predominantemente en vertientes del noroeste y en pendientes moderadamente empinadas. La selección de micro hábitats se determinó comparando los sitios que tenían nidos, con sitios sin nidos localizados al azar. Se midieron características de los micro hábitats, de los sitios con nido, en círculos de 0.04 ha con centro en los árboles con nido y dos sitios pareados sin nidos en 60 lugares independientes. Al comparar los sitios sin nidos, con los sitios con nido, estos últimos tuvieron un número más alto de árboles, árboles más altos, DAP y área basal de árboles más grandes, y mayor cobertura del dosel. Entre los sitios con nidos, 50 de 60 árboles con nido fueron los árboles más altos en el cuadrante y 48 de 60 tuvieron el diámetro más grande. El análisis de la función de discriminación indicó que la cobertura del dosel, el área basal de los árboles y la distancia al borde del bosque fueron las variables más importantes para distinguir los sitios con nido de los sitios sin nido. Se calculó la cobertura de seis clases de vegetación dentro del 100% del polígono convexo mínimo del rango de ocupación de 7 parejas del gavián de cola roja en reproducción dentro de un área de estudio de 10 640 ha. La proporción de los tipos de cobertura de hábitat en los rangos de ocupación, variaron considerablemente entre parejas. Entre todos los rangos de ocupación, el 75% fueron praderas abiertas sin árboles o arbustos y 25% fueron praderas sin árboles. Las características de los hábitat importantes para los gaviánes de cola roja en el área del estudio, fueron bosques maduros con coníferas y árboles deciduos en laderas moderadamente empinadas, adyacentes a regiones ampliamente pobladas con *Artemisia* spp., pastizales o remanentes de regiones agrícolas. Otros factores de la escala del paisaje además de las proporciones del tipo de cobertura de la vegetación podrían ser más importantes para determinar el tamaño del rango de ocupación y la ubicación dentro del área del estudio.

[Traducción de César Márquez]

Red-tailed Hawks (*Buteo jamaicensis*) are widely distributed in North America and breed and winter in a wide variety of habitats (Bent 1937, Palmer 1988, Preston and Beane 1993). Previous studies have quantified Red-tailed Hawk habitat use at multiple scales, including perch sites (Preston 1980), nest-tree sites (Mader 1978, Titus and Moser 1981, Bednarz and Dinsmore 1982, Speiser and Bosakowski 1988), on a landscape level (Stout et al. 1998), and within nesting (Janes 1984), and over wintering (Preston 1990) territories. Little is known, however, about Red-tailed Hawk habitat use in the intermountain region of the western United States. During 1990 and 1991 we monitored raptor and Common Raven (*Corvus corax*) productivity along the floodplain forests of the Snake River and its tributaries in Grand Teton National Park (GTNP). During those two years, we recorded zero fledglings from 12 Red-tailed Hawk nests. We also documented a high density of breeding Common Ravens, whose breeding populations had increased dramatically since the 1940s (Dunk et al. 1994). In addition, during 1990–91, we periodically found dead hawk chicks below nests. We thus began a broad-based ecological study of Red-tailed Hawks in northwestern Wyoming designed to investigate the causes of low productivity. In par-

ticular we evaluated the effects of parasites on Red-tailed Hawk reproduction (Smith et al. 1998) as well as evaluating breeding habitat use patterns of both Common Ravens (Dunk et al. 1997) and Red-tailed Hawks. Herein, we describe our findings of the associations of Red-tailed Hawks to vegetation at three spatial scales: (1) the nest tree, (2) micro-habitat within 0.04 ha vegetation plots centered around nest trees, and (3) within the home range.

STUDY AREA

The study area was located in northwestern Wyoming within the valley portion of GTNP (43°40'N, 110°43'W), a high mountain valley that is surrounded by the Teton Mountain Range to the west, the Gros Ventre Mountains to the east, the Yellowstone Plateau to the north, and the town of Jackson to the south. We conducted home range analyses within a 10 640 ha core study area that included Moose, Blacktail Butte, and east to the foothills of Shadow Mountain. Vegetation, climate, and landscape features within the study area have been described by Craighead and Craighead (1956), Dunk et al. (1997), and Smith et al. (1998). Elevation of nests within the study area ranged from 1934–2164 m ($N = 74$).

METHODS

The study was conducted from March 1992 to August 1994. Nests were located in April and May by systematic annual searches of the core study area and surrounding areas. Terminology used in this study follow recommendations by Postupalsky (1974) and Steenhof and Kochert

Table 1. Structural habitat variables measured in 0.04 ha vegetation plots centered on nest trees and at randomly-located non-nest plots.

HABITAT VARIABLE	DESCRIPTION
Nest tree spp	Species of nest tree
Nest height	Height of nest tree (m), measured with a clinometer
Nest DBH	Diameter at breast height of nest tree (cm)
Percent nest height	Height of nest in tree divided by nest-tree height \times 100
Number trees	Total number of trees in plot, measured with a clinometer
Tree height	Height of trees in plot, including nest trees, measured with a clinometer
Canopy cover ^a	Percent canopy closure in the plot
Ground cover ^a	Percent ground cover in the plot
Shrub cover ^a	Percent shrub cover in the plot
Distance to edge	Distance from plot center to nearest forest opening
Foliage ht 0–0.3 m ^b	Understory foliage density height 1 (0–0.3 m)
Foliage ht 0.3–3 m ^c	Understory foliage density heights 2–4 combined (0.3–3 m)
Basal area	Basal area of all trees in plot
Slope	Slope of plot, measured with clinometer (degrees)
Aspect	Direction of slope, measured with compass

^a Eight transects 45° apart were walked, stopping every 2 m. At each stop we sighted directly above and below through an ocular sighting tube with cross hairs at one end and recorded presence or absence of vegetation.

^b Modified understory foliage density estimated at four levels with a drop cloth (Noon 1981) placed at the edge of the plot in each of four cardinal directions.

^c Density heights 2–4 did not differ significantly; thus, we used the mean of layer 2–4 combined.

(1982). An occupied nest refers to a nest where: (1) eggs were laid, or young were raised; (2) we saw fresh green boughs on the nest rim or in the nest with adult hawks present; (3) two adults observed in the nest, either perched or actively maintaining the nest; (4) an adult in incubation posture in the nest. All habitat data were collected from occupied nests and the territories they were within.

Nest Tree and Microhabitat Characteristics. We measured five nest-tree variables and 12 structural-habitat variables (Table 1) at nest sites at least two weeks after fledging and before drying of understory vegetation. We defined the nest site as the 11.3-m radius (0.04 ha) circle centered on the nest tree (Noon 1981). For each nest site, we located two non-nest sites in a random compass direction and distance 25–200 m from the nest and measured the same 12 structural habitat variables (Table 1). We maintained that a non-nest site located within 200 m from the nest was within a Red-tailed Hawk territory and thus was available to a nesting pair. We calculated means for each pair of non-nest site variables and compared them to nest site variables to investigate nest-site affinities. Non-nest sites were rejected if they did not contain at least one tree with structure suitable to support a nest. Sampling techniques followed those presented by James and Shugart (1970) and Dunk et al. (1997).

Home Range Delineation. Within the 10 640 ha core study area, we delineated Red-tailed Hawk home ranges by direct observation of unmarked male birds at seven breeding territories. Males and females of each breeding pair were distinguished by differences in molting patterns, plumage characteristics or size. We used a spotting scope and binoculars to observe movement patterns and continuously recorded time and activity data. Observa-

tion periods ranged from 2–5 hr, and were equally distributed between 0500 and 2000 H MST. Observations began in early April and continued through the fledging period or until the nesting attempt failed. We plotted the birds' position every 10 min and recorded locations on 1:24 000 topographic maps assisted by aerial photographs. The 10-min time interval was chosen to minimize dependency between successive locations (White and Garrott 1990). We used the ArcView extension ANIMAL MOVEMENT (Hooge and Eichenlaub 1997), to calculate 100% minimum convex polygon (MCP) home range estimates. We determined that home ranges defined by 100% MCPs best suited our needs because our primary goal was to define the outer-most boundary of use and describe general vegetation patterns therein.

We realized that several potential biases could have affected our home range delineations. First, by relying on direct observations of unmarked individual birds, territories could be: (1) underestimated in size as a result of birds sometimes being out of view (Village 1982, Baekken et al. 1987), (2) erroneously described due to failure to identify correctly the focal individual (Altmann 1974), or (3) to record accurately the location on a map of a bird that was greater than 300–400 lateral m from the observer. Our study area was conducive to direct observations, however, because it contained relatively open habitat and little topographic relief. We further mitigated potential biasing effects by careful selection of two or more observation points within each home range, and found that on average, birds were out of view during only 7.2% (SE = 1.39, range = 0–66 min) of each observation session. Further, males in each territory were easily identifiable from a combination of individual morphological characteristics and because of rigorous territorial behavior,

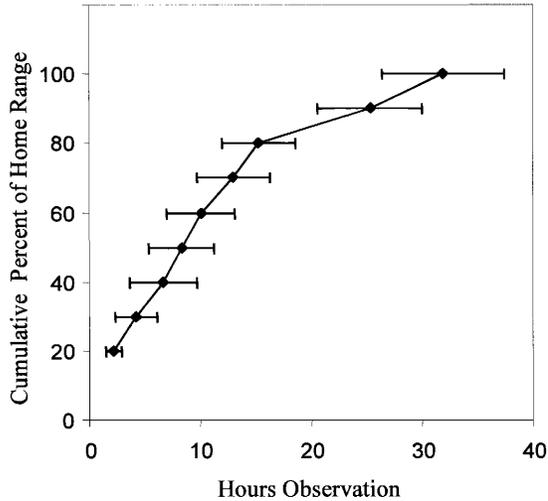


Figure 1. Mean cumulative percentage of home range size determined by hours of observation on seven Red-tailed Hawk territories in Grand Teton National Park, 1993-94. Horizontal bars indicate \pm one SD of error.

thus, erroneous identification of individuals was probably rare. Territory size could also be underestimated by focusing observations on only one sex of the territorial pair. For example, during courtship, incubation, and early brood-rearing, female Red-tailed Hawk's movements were largely restricted to the nest site, while the male foraged for both sexes and defended their territory (Bent 1937, Newton 1979, Preston and Beane 1993). Delineation of home ranges is dependent upon obtaining a sample of locations large enough to accurately represent the area used (e.g., Bekoff and Mech 1984). Therefore, we addressed this by ensuring that for each territory observed, an asymptote in home range size plotted against observation time was obtained (Fig. 1).

Home Range Characteristics. Within each home range and the core study area, we used a ground-truthed digital vegetation cover-type database (Despain 1990) to categorize habitat into six classes: (1) coniferous forest, (2) deciduous forest, (3) mixture of deciduous and coniferous forest, (4) mixture of timber and shrub, (5) sage/shrub, and (6) grass/meadow. A digital elevation model was used to categorize aspect into eight classes and slope in four classes: 1-10%, 11-20%, 21-30%, and 31-40%.

Statistical Procedures. Univariate comparison of habitat variables at nest and non-nest sites were completed using two-tailed paired Student's *t*-tests. Comparisons between deciduous and coniferous nest tree characteristics were conducted using two-sample *t*-test. We used a stepwise discriminant-function analysis (DFA) with a forward-variable selection and a tolerance value of 0.15 to arrive at the best subset of habitat-related predictor variables most useful in separating nest plots from paired non-nest sites. We used a jackknife classification procedure and variables with canonical structure coefficients greater than 0.30 from the first stepwise discriminant procedure in a final discriminant analysis. To assess the effectiveness

of the DFA, we calculated Cohen's Kappa statistics for the classification matrix. This statistic indicates whether the model classified observations into their respective groups significantly better than by chance (Titus et al. 1984). We tested the randomness of the aspect of sites using Watson-Williams's (1956) multisampling testing of angles and Rayleigh's *z*-test (Zar 1984). Due to the small number of observed home ranges, we opted not to test hypotheses regarding these data, and present descriptive measurements of habitat use, slope, and aspect at the landscape scale. Descriptive statistics are presented as mean \pm SE. Statistical analyses were conducted using Systat software (Wilkinson 1997).

RESULTS

Nest-tree Characteristics. We located 22, 29, and 23 occupied nests in 1992, 1993, and 1994, respectively. Of these 74 occupied nests, 12 were reoccupied twice during the three years of study, and two nests were occupied all three years. Habitat data from nests that were occupied in more than one year were included in our analyses only once. Nests were located in a variety of habitats, including riparian bottoms, timbered hillsides consisting of mixed conifer and deciduous trees, and in trees along irrigation ditches located in remnant agricultural areas. We found Red-tailed Hawk nests in six tree species; 22 (36.6%) were in coniferous and 38 (63.3%) were in deciduous trees (Table 2). One nest was in a snag. Two other tree species found in our study area, but not used by nesting Red-tailed Hawks were limber pine (*Pinus flexilis*) and subalpine fir (*Abies lasiocarpa*). Mean nest-tree height and mean nest height were higher in coniferous than deciduous trees ($t = 6.67, P < 0.001, \bar{x} = 26.98$ m vs. $\bar{x} = 18.15$ m, and $t_{58} = 6.05, P < 0.001, \bar{x} = 20.95$ m vs. $\bar{x} = 13.62$ m), respectively. We found no difference in nest-tree DBH or percent height of the nest in the tree between coniferous and deciduous nest trees. Douglas Fir (*Pseudotsuga menziesii*) nest trees were taller than the other five nest-tree species ($F_{1,54} = 13.2, P < 0.001, \bar{x} = 30.8$ m, SE = 1.32; Tukey HSD multiple comparisons). Mean nest diameter and depth were 81.3 cm (SE = 0.43, range = 75-88 cm) and 39.0 cm (SE = 0.91, range = 29-61 cm) respectively ($N = 50$ nests). There was no difference in nest size (diameter) among the three years ($F_{1,47} = 0.78, P = 0.46$).

Microhabitat Characteristics. Fifty of 60 (83.3%) nest trees were the tallest trees in the nest-site plot. Nest trees had the largest DBH in 48 of 60 (80%) plots. Mean aspect of slope at nest plots and non-nest plots differed from a uniform distribution

Table 2. Mean characteristics of Red-tailed Hawk nests ($N = 60$) in northwest Wyoming, 1992–94 (standard errors in parentheses).

TREE SPECIES	NUMBER OF TREES	PERCENT TOTAL NEST TREES	TREE DIAMETER (cm)		TREE HEIGHT (m)		NEST HEIGHT (m)		PERCENT TREE HEIGHT ^a	
			MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE
Quaking aspen (<i>Populus tremuloides</i>)	22	37.5	33.4	1.8	17.6	0.84	12.7	0.67	72.2	(0.01)
Narrowleaf cottonwood (<i>Populus angustifolia</i>)	16	25.8	63.5	6.3	19.0	1.5	15.0	1.3	78.1	0.02
Douglas-fir (<i>Pseudotsuga menziesii</i>)	10	16.1	70.6	4.8	30.8	1.3	24.8	1.3	80.5	0.02
Lodgepole pine (<i>Pinus contorta</i>)	6	9.6	38.2	5.1	24.3	1.5	18.2	1.3	75.1	0.03
Blue spruce (<i>Picea pungens</i>)	4	6.4	57.6	4.9	23.3	1.9	17.7	1.6	76.0	0.02
Engelman spruce (<i>Picea engelmannii</i>)	2	3.2	46.5	3.5	23.3	0.4	16	1.0	69.0	5.1
All species	60		50.2	2.8	21.4	0.81	16.3	0.73	76.1	0.01

^a Nest height divided by tree height \times 100.

(Rayleigh's $z = 27.3$ and 43.3 , respectively; $P < 0.001$), and the two sample means did not differ from each other ($F_{1,178} = 3.89$, $P > 0.25$; Watson-Williams test for two samples; Zar 1984). The mean slope aspect for the nest and non-nest plots was 347° . Nests were typically situated on 10–20% slopes. Univariate paired t -tests analyses indicated differences between nest plots and non-nest plots

for five variables (Table 3). We found no difference between distances to forest edge at nest sites versus random sites from our univariate t -tests. However, discriminant function analysis included distance to edge along with canopy cover and basal area in a model that best explained the differences between nest and non-nest plots (Wilk's $\Lambda = 0.82$, $P < 0.0001$). Using the reduced model derived by

Table 3. Mean microhabitat characteristics in 0.04 ha plots centered around Red-tailed Hawk nest sites ($N = 60$) and available sites ($N = 118$) in Grand Teton National Park, 1992–94.

VARIABLES	NEST-SITE		NON-NEST SITE		STATISTIC	
	MEAN	SE	MEAN	SE	t	P
Percent Canopy cover ^a	51.7	2.4	34.4	2.4	6.8	<0.01
Basal (m ² /0.04 ha)	0.92	0.09	0.53	0.05	5.3	<0.01
Diam. breast ht ^a	29.8	1.9	24.9	1.0	2.9	0.01
Tree height ^a	14.1	0.67	12.5	0.47	2.7	0.01
Number of trees	13.3	1.2	11.1	0.91	2.1	0.03
Ground cover ^a	72.2	2.6	74.2	2.1	0.50	0.61
Shrub cover ^a	20.4	2.3	21.5	2.1	0.71	0.47
Foliage ht 0–0.3 m	68.8	3.6	70.5	3.1	0.58	0.56
Foliage ht 0.3–1 m	39.6	3.1	36.4	2.7	1.0	0.32
Foliage ht 1–2 m	26.9	2.9	24.9	2.4	0.67	0.50
Foliage ht 2–3 m	26.5	2.9	24.1	2.3	0.86	0.39
Distance to edge	21.7	3.2	22.9	3.4	0.24	0.81
Aspect ^b	NW (347°)	—	NW (347°)	—	—	—
Percentage slope	22.6	3.2	19.1	5.7	0.23	0.81

^a Mean of plot means.

^b Cardinal Direction, (mean azimuth, Watson-Williams 1956).

Table 4. Two-group discriminant function analysis of Red-tailed Hawk nest-site characteristics compared to non-nest (available) sites in northwest Wyoming for years 1992–94 combined.

VARIABLE	GROUP MEANS (SE)		STRUCTURE COEFFICIENTS
	NEST-PLOT	NON-NEST PLOT	
Canopy cover	51.7 (2.4)	34.4 (2.4)	0.83
Basal area	0.92 (0.09)	0.53 (0.05)	0.41
Distance to forest edge	21.7 (3.2)	22.9 (3.4)	0.44
Sample size	60	118	
Wilk's lambda		0.82	
Approx. <i>F</i> -statistic		12.5 ^a	
Cohen's kappa		4.9	
Percent correct classification	43/60 = 71.6	82/118 = 69.5	
Overall % correct classification		70.2	

^a $P < 0.0001$

the stepwise DFA (Table 4), jackknife classification procedures successfully predicted 71% of nest sites and 69% of non-nest sites. The overall correct classification was 70.2%, which differed only slightly from a random classification rate (Titus et al. 1984).

Home Range Characteristics. On average it took 25 hr (range = 11.6–44.3, SE = 4.7, $N = 7$) of observation to delineate 90% of the home range, and 32 hr (range = 13.1–49.2, SE = 5.5, $N = 7$) for 100% delineation (Fig. 1). Total observation time by nest ranged from 24.5–73.5 hr ($\bar{x} = 47.4$, SD = 17.1). Mean MCP home range size was 241 ha (SD = 119 ha, range = 181–480 ha; Table 5). This mean was similar to the mean of 225 ha (SD = 1.0 ha, range = 77–385 ha) obtained for eight nesting pairs of Red-tailed Hawks on the same study area in 1947 (Craighead and Craighead 1956). Among the seven home ranges, the percentage of non-forested cover ranged from 48–95% ($\bar{x} = 76\%$). Also, we observed considerable variation in the percentage cover of shrubland and grass meadow vegetation types (5–83% and 4–63%, respectively), while the total percentage cover of each were relatively equal (Table 5). The core study area was characterized by 76% open vegetation, primarily sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), grasslands, and remnant agriculture, and 24% forested vegetation that included both coniferous and deciduous trees (Table 5). Relative to the core study area, four of seven home ranges contained considerably more grass/meadow cover type, and five of seven contained considerably less sage/shrub cover type. Similarly, two of seven home ranges contained slopes greater

than 11% (range = 0–26%). The core area contained more area of south and southeast aspects than the combined home ranges.

DISCUSSION

We observed Red-tailed Hawks nesting only in trees. In another Wyoming study area, 40% ($N = 10$) of Red-tailed Hawks nested on cliffs (MacLaren et al. 1988). Most, (83%) of the nests in our study area were situated high in forest canopy, in the top one-fourth of the tree, and in the tallest tree in the immediate area. These findings corroborate other studies that suggest Red-tailed Hawks select nest-sites that afford unobstructed access and a high viewpoint of the surrounding area (e.g., Orians and Kuhlman 1956, Bednarz and Dinsmore 1982, Preston and Beane 1993, Stout et al. 1998). Distance to forest edge and slope may also be important factors. For example, Speiser and Bosakowski (1988) reported Red-tailed Hawk nests significantly closer to forest openings than random plots in both young and mature hardwood forests, reporting a mean distance to forest edge of 155 m. Conversely, Titus and Mosher (1981) detected no difference in distance to edge between Red-tailed Hawk nest plots and random plots in western Maryland, and they reported a mean distance of 235 m to the nearest forest edge. Like Titus and Mosher (1981), we detected no difference between distances to forest edge at nest sites versus random sites. However, on average, nests in our study area were within only 15 m of large patches of sagebrush, grasslands or remnant cultivated fields, suggesting an attraction of open areas.

Several studies have reported nest sites situated

Table 5. Minimum Convex Polygon (MCP) home range sizes (100%) and vegetation cover for seven breeding pairs of Red-tailed Hawks in northwestern Wyoming, 1992–93.

NEST TERRITORY	DAYS OBS.	HOURS OBS.	100% MCP (ha)	VEGETATIVE COVER IN HECTARES (%)							
				NON-FORESTED ^a	FORESTED	CONIF. FOREST	DECID. FOREST	MIXED FOREST	FOREST/SHRUB	SAGE/SHRUB	GRASS/MEADOW
Green 92	7	26.4	180.9	146 (80.7)	34.9 (19.3)	9.3 (5.1)	1.3 (0.7)	17 (9.4)	7.3 (4.0)	51.6 (28.5)	94.4 (52.2)
Hunter 92	7	24.5	162.6	78.1 (48)	84.6 (52)	6.4 (3.9)	33.8 (20.8)	1.5 (0.9)	42.9 (26.4)	37.7 (23.2)	40.4 (24.8)
Lobo 92	10	31.5	480.1	373.3 (77.7)	106.9 (22.3)	32.0 (6.7)	51.7 (10.8)	0	23.2 (4.8)	355.3 (74)	18 (3.7)
Moulton 93	15	73.5	318.1	299.5 (94.5)	18.6 (5.5)	0	18.6 (5.9)	0	0	263.8 (82.9)	35.7 (11.3)
Blacktail 93	10	41.6	145.0	99.8 (68.9)	45.1 (31.1)	34.4 (23.7)	1.3 (0.9)	3.4 (2.3)	6.0 (4.1)	7.9 (5.5)	91.9 (63.4)
S. Green 93	12	57.2	203.8	177 (86.9)	26.7 (13.1)	8.4 (4.1)	0	14.5 (7.1)	3.8 (1.9)	40.6 (19.9)	136.4 (67)
Wilson 93	14	60	196.7	154 (78.3)	42.6 (21.7)	15.4 (7.8)	9.6 (4.9)	10.7 (5.4)	6.9 (3.5)	47.6 (24.2)	106.4 (54.1)
Mean	10.7	47.4	241	192.3 (76.4)	51.3 (23.5)	15.1 (7.3)	16.6 (6.3)	6.7 (3.6)	12.9 (6.4)	117.5 (36.9)	74.7 (39.5)
SE	3.1	17.1	119.3	42.0 (6.1)	12.2 (5.6)	5.0 (2.9)	7.4 (2.8)	2.7 (1.4)	5.7 (3.4)	52.8 (11.1)	16.5 (9.7)
Totals	75	322.1	—	1327.7 (78.7)	359.4 (21.3)	105.9	116.3	47.1	90.1	823.1	523.2
Study area	—	—	—	7750.8 (72.8)	2805.3 (26.4)	1203.1 (11.3)	664.6 (6.2)	211.9 (2.0)	725.7 (6.8)	4970 (46.7)	2651.6 (26.9)

^a Non-forested areas (ha) within the study area also included: barren ground = 25, burned = 15, water = 88, and urban = 86 ha

on sloped hillsides (Titus and Mosher 1981, Bednarz and Dinsmore 1982, Speiser and Bosakowski 1988). Titus and Mosher's (1981) data implied that Red-tailed Hawks select for nest sites on steep hillsides, and Speiser and Bosakowski (1988) suggested that Red-tailed Hawks may gain better soaring capability and an easier, downward departure flight from the nest on steeper hillsides relative to nests on flat terrain. Although we found no difference in slope between nest and non-nest sites, nests were typically situated on moderately-sloped (\bar{x} = 22%) hillsides, which also facilitated nest access and views of the surrounding terrain. We also regularly observed Red-tailed Hawks actively foraging while perched at the nest and tending nestlings (i.e., searching and stooping from nests during prey capture attempts), suggesting that foraging efficiency may be important in nest site selection. We believe that, in addition to tree height, both proximity to edge and slope were important for Red-tailed Hawks in our study area for the reasons discussed above, but that our technique for locating

random plots (within 200 m of nest sites) may have biased our comparisons for these variables. Indeed, it is likely that the site-specific combination of tree height, slope, and distance to edge, as well as nest-tree branch structure, determines nest access.

Nest and non-nest sites in our study area were found predominately on north aspects and similar slopes (Table 3), however, this similarity may be a function of the relatively close proximity of a non-nest plot (within 200 m) from a nest tree. Two ecological factors may be relevant here. First, in our study area's temperate and relatively arid environment, moisture regimes associated with slope effect (Knight 1994) favored more well-developed forested areas on north aspects, simply providing the stands with more abundant large trees that were selected by hawks. Second, nests on north aspects may provide some protection from our study area's prevailing southwest winds and associated rain and snow. Similarly, several other studies have noted the importance of aspect in reducing possible negative effects of prevailing weather on nestling rap-

tors (Newton 1979, Titus and Mosher 1981, Bednarz and Dinsmore 1982, Speiser and Bosakowski 1988, Preston and Beane 1993, Stout et al. 1998).

We observed large variation in the proportion of habitat types used among the seven home ranges. The absence of strong vegetation preferences, other than open grass/meadow cover type, at the landscape scale may indicate that: the number of home ranges sampled were inadequate, or upon arrival onto territories, these birds are first selecting habitat from the scale of the nest tree and the microhabitat site second. If the hawks are selecting habitat at a larger scale, it appears to be smaller than that of the entire home range. Bingham and Noon (1997) found "core areas" of ca. 200 ha to be used much greater than other areas within the home ranges of Northern Spotted Owls (*Strix occidentalis*). Perhaps Red-tailed Hawks also select habitat at some intermediate scale between area immediately surrounding the nest and the home range boundary. For Red-tailed Hawks, it appears that the availability of adequate nesting trees and their proximity to foraging areas are important characteristics that influence their selection of breeding areas. Selection of open habitat with trees or forested components is a consistent finding in other studies of Red-tailed Hawk habitat (see Preston and Beane 1993), although Bednarz and Dinsmore (1982) investigated Red-tailed Hawk habitat features within 3.14 km² "home ranges" in Iowa and found home ranges typically contained equal proportions of woodland, pasture and croplands. But consistent with other studies, Bednarz and Dinsmore argue that open areas, particularly pasture land, provided the key foraging habitats for nesting Red-tailed Hawks in Iowa.

The importance of specific nest-site and home range variable comparisons among multiple studies is diminished in the absence of similar comparisons of larger landscape patterns. Other components, including vegetative structure and physiognomy, food availability (Luttich et al. 1970, Marquiss and Newton 1981), and the presence of territorial conspecifics and other competitors (Rothfels and Lein 1983), each undoubtedly influence nest-site and home range selection. For future evaluations of Red-tailed Hawk habitat, it would seem prudent to focus more effort at spatial scales between: (1) the microhabitat scale and the home range, and their influence on Red-tailed Hawk populations, especially where human-caused landscape changes are likely to occur (Craighead and Mindell 1981), and

(2) landscape features surrounding the home range. Nevertheless, when considering this and other Red-tailed Hawk habitat studies, common patterns emerge that underscore the importance of nest access, and open areas associated with forest/non-forest ecotones.

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LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behavior* 49:227-265.
- BAEKKEN, B.T., L.O. NYBO, AND G.A. SONERUD. 1987. Home-range size of Northern Hawk Owls: dependence on calculation method, number of tracking days, and number of plotted perchings. Pages 145-148 in R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre [Eds.], *Biology and conservation of northern forest owls*. United States Forest Service General Technical Report RM-142.
- BENT, A.C. 1937. Life histories of North American birds of prey, Part. 1. U.S. Nat. Mus. Bull. No. 167.
- BEKOFF, M. AND L.D. MECH. 1984. Simulation analyses of space use: home range estimates, variability, and sample size. *Behav. Res. Meth. Instr. Comp.* 15:32-37.
- BEDNARZ, J.C. AND J.J. DINSMORE. 1982. Nest-sites and habitat of Red-shouldered and Red-tailed Hawks in Iowa. *Wilson Bull.* 94:31-45.
- BINGHAM, B.B. AND B.R. NOON. 1997. Mitigation of habitat "take": application to habitat conservation planning. *Conserv. Biol.* 11:127-139.
- CRAIGHEAD, J.J. AND F.C. CRAIGHEAD. 1956. *Hawks, Owls, and Wildlife*. Stackpole Co., Harrisburg, PA and Wildlife Management Inst., Washington, DC U.S.A.
- CRAIGHEAD, F.C. AND D.P. MINDELL. 1981. Nesting raptors in western Wyoming, 1947 and 1975. *J. Wildl. Manage* 45:865-872.
- DESPAIN, D.C. 1990. Cover types of Grand Teton National Park. Electronic ArcInfo grid file. Grand Teton National Park, Moose, WY U.S.A.
- DUNK, J.R., S.L. CAIN, M.E. REID, AND R.N. SMITH. 1994. A high breeding density of common ravens in northwestern Wyoming. *Northwest. Nat.* 75:70-73.
- , R.N. SMITH, AND S.L. CAIN. 1997. Nest-site selection and reproductive success in Common Ravens. *Auk* 114:116-120.

- HOOG, P.N. AND B. EICHENLAUB. 1997. Animal movement extension to Arcview, Ver. 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK U.S.A.
- JAMES, F.C. AND H.H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- JANES, S.W. 1984. Influences of territory composition and interspecific competition of Red-tailed Hawk reproductive success. *Ecology* 65:862-868.
- KNIGHT, D.H. 1994. Mountains and plains: the ecology of Wyoming landscapes. Yale Univ. Press, New Haven, CT U.S.A.
- LUTTICH, S., D.H. RUSCH, E.C. MESLOW, AND L.B. KEITH. 1970. Ecology of Red-tailed Hawk predation in Alberta. *Ecology* 51:190-203.
- MACLAREN, P.A., S.H. ANDERSON, AND D.E. RUNDE. 1988. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. *Great Basin Nat.* 48: 548-553.
- MADER, W.J. 1978. A comparative nesting study of Red-tailed Hawks and Harris' Hawks in southern Arizona. *Auk* 95:327-337.
- MARQUISS, M. AND I. NEWTON. 1981. A radio-tracking study of the ranging behavior and dispersion of European Sparrowhawks. *J. Anim. Ecol.* 51:111-133.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.
- NOON, B.R. 1981. Techniques for sampling avian habitats. In D.E. Capen [ED.], The use of multivariate statistics in studies of wildlife habitat. USDA, USFS, General Technical Report RM-87. Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO U.S.A.
- ORIAN, G. AND F. KUHLMAN. 1956. Red-tailed Hawk and horned owl populations in Wisconsin. *Condor* 58:371-385.
- PALMER, R.S. 1988. Handbook of North American birds, Diurnal Raptors Part 2. Yale Univ. Press, New Haven, CT U.S.A.
- POSTUPALSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Pages 21-31 in F.N. Hamerstrom, Jr., B.E. Harrell, and R.R. Olendorff [EDS.], Management of raptors. Raptor Research Report No. 2. Raptor Research Foundation, Inc., Vermillion, SD U.S.A.
- PRESTON, C.R. 1980. Differential perch site selection by color morphs of the Red-tailed Hawk (*Buteo jamaicensis*). *Auk* 97:782-789.
- . 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor* 92:107-112.
- AND R.D. BEANE. 1993. Red-tailed Hawk (*Buteo jamaicensis*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 52. The Academy of Natural Sciences Philadelphia, PA and The American Ornithologists' Union, Washington, DC U.S.A.
- ROTHFELS, M. AND M.R. LEIN. 1983. Territoriality in sympatric populations of Red-tailed and Swainson's hawks. *Can. J. Zool.* 61:60-64.
- SMITH, R.S., S.L. CAIN, S.H. ANDERSON, J.R. DUNK, AND E.S. WILLIAMS. 1998. Blackfly-induced mortality of nestling Red-tailed Hawks. *Auk* 115:368-375.
- SPEISER, R. AND T. BOSAKOWSKI. 1988. Nest site preferences of Red-tailed Hawks in the highlands of southeastern New York and northern New Jersey. *J. Field Ornithol.* 59:361-368.
- STEENHOF, K. AND M.N. KOCHERT. 1982. An evaluation of methods used to estimate raptor nesting success. *J. Wildl. Manage.* 46:885-893.
- STOUT, W.E., R.K. ANDERSON, AND J.M. PAPP. 1998. Urban, suburban and rural Red-tailed Hawk nesting habitat and populations in southeast Wisconsin. *J. Raptor Res* 32:221-228.
- TITUS, K. AND J.A. MOSHER. 1981. Nest-site habitat selected by woodland hawks in the central Appalachians. *Auk* 98:270-281.
- , ———, AND B.K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *Am. Midl. Nat.* 111:1-7.
- VILLAGE, A. 1982. The home range and density of kestrels in relation to vole abundance. *J. Anim. Ecol.* 51:413-428.
- WATSON, G.S. AND E.J. WILLIAMS. 1956. On the construction of significance tests on the circle and the sphere. *Biometrika* 38:330-336.
- WHITE, G.C. AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA U.S.A.
- WILKINSON, L. 1997. SYSTAT 8.0: the system for statistics. SYSTAT, Inc., Evanston, IL U.S.A.
- ZAR, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ U.S.A.

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