RESOURCE PARTITIONING AMONG THREE *BUTEO* SPECIES IN THE CENTENNIAL VALLEY, MONTANA[1]

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Birds most commonly partition resources along habitat dimensions, followed by food, then temporal dimensions (Cody 1974, Schoener 1974). Studies in Alberta (Schmutz et al. 1980), Oregon (Cottrell 1981), and Washington (Bechard et al. 1990) reported partitioning of nesting habitat among Red-tailed (*Buteo jamaicensis*), Ferruginous (*B. regalis*), and Swainson's Hawks (*B. swainsoni*) while broad overlap occurred in prey use and nesting chronology. One species was much less common than the other two in each of those studies. In contrast, these closely related hawks coexist in equal abundance in the Centennial Valley, Montana. Do mechanisms that allowed coexistence in previous studies operate in areas where these hawk species are equally abundant? The objective of this study was to determine if and how these hawks partitioned habitat, food, and temporal resources in the Centennial Valley.

STUDY AREA AND METHODS

The study area, encompassing 319 km^2 in the Centennial Valley of southwestern Montana (44°37'N, 112°15'W), was bordered north by the Snowcrest Range and south by the Centennial Range. Mountains (elevation to 2,544 m) sloped gently to the nearly level valley floor (1,974 m) where vegetation was dominated by grasses (*Agropyron* spp.) with interspersed low growing shrubs (*Artemisia* spp.). Dense stands of tall (3–6 m) shrub willow (*Salix* spp.) grew along mountain streams flowing into the valley. Small (0.1–0.4 ha) stands of aspen (*Populus tremuloides*) occurred around seeps at higher elevations. Land use on the study area was primarily summer livestock grazing.

During the 1987 and 1988 nesting seasons, I systematically searched the study area on foot and plotted hawk nest locations on 7.5-min U.S.G.S. topographic maps. Only active nests (evidence of eggs or young) were considered in analyses because inactive hawk pairs (occupying an area but not laying eggs) often were associated with more than one nest. At active nests I recorded substrate type and height, nest height, long distance exposure (LDE), slope aspect, nest exposure, percent slope, and elevation. LDE was the field of view (in degrees) from the center of the nest unobstructed for at least 200 m (Ensign 1983).

Prey use was determined by recording prey remains in nests and by analyzing regurgitated pellets collected from nests and perch sites. I checked remains in nests against pellets collected during subsequent visits to minimize duplication. Numbers of prey were determined conservatively, based on presence of characteristic bones and feathers.

The nearest neighbor method (Clark and Evans 1954) was used to describe spacing of active hawk nests. The ratio "*R*" of observed to expected mean distance between nests indicated whether observed nest distribution was clumped ($R \leq 1.00$), random ($1.00 < R < 2.15$), or regular ($R = 2.15$). Nest site characteristics of each species were compared using one-way analysis of variance. Nest substrate overlap "O" between two species was calculated using Pianka's (1973) formula: $O = \Sigma\ p_iq_i/(\Sigma\ p_i^2\ \Sigma\ q_i^2)^{\prime\prime}$ where p_i is the proportional use of substrate i by one species and q_i is its proportional use by the second species. Index values range from 0 (no overlap) to 1 (complete overlap). I also used this formula to calculate dietary overlap.

RESULTS AND DISCUSSION

NEST SITE SELECTION

Ninety-eight hawk pairs were located representing 86 active nests: 20 Red-tailed, 24 Ferruginous, and 42 Swainson's Hawks. Where these buteos have been sympatric elsewhere (Schmutz et al. 1980, Cottrell 1981, Bechard et al. 1990) one species was much less common than the other two because ideal habitats for each species were not uniformly distributed. In contrast, habitats and thus buteo species on my study area were evenly distributed.

Most nests (88%) were located in foothill drainages surrounding the valley floor. Distances between nests were less than expected (1987: $R = 0.84$, $P = 0.043$; 1988: $R = 0.73$, $P = 0.001$). Nest spacing was conservatively estimated because inactive pairs occupied areas between active nests. Hawks did not nest significantly closer to or farther from conspecifics, but all three species nested closer to either one of the other two species (1987: Red-tailed, $R = 0.67$, $P = 0.037$; Ferruginous, $R = 0.37$, $P < 0.001$; Swainson's, $R = 0.75$, $P = 0.032$; 1988: Red-tailed, $R = 0.30$, $P < 0.001$; Ferruginous, $R = 0.32$, $P < 0.001$; Swainson's, $R = 0.78$, $P = 0.056$). Aggregation of nests reflected the limited distribution of potential nest substrates. The only elevated nest substrates available were small stands of aspen at drainage heads, willows bordering foothill streams, and scattered Douglas fir (*Pseudotsuga menziesii*). The valley floor was flat and therefore poor ground nesting habitat for Ferruginous Hawks, a spe-

TABLE 1. Characteristics of Red-tailed, Ferruginous, and Swainson's Hawk nests on the Centennial Valley study area, Montana, 1987 and 1988. Samples sizes: Red-tailed (20), Ferruginous (24), and Swainson's Hawks (42).

	Red-tailed		Ferruginous		Swainson's	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Nest substrate height (m)	13.9	5.9	5.2	2.3	5.1	1.2*
Nest height (m)	8.9	3.6	3.9	2.2	3.8	1.1*
Long distance exposure (°)	23	29	68	50	14	22*
Slope (%)	11	8	10	10	7	8
Elevation (m)	2,125	66	2,075	36	2,105	53*

* $P < 0.01$.

cies that prefers to nest on sloped ground (Gilmer and Stewart 1983).

Nest site characteristics differed among species (Table 1). Red-tailed Hawks nested more in trees and less in willows than Ferruginous Hawks ($\chi^2 = 16.94$, df = 1, $P < 0.001$), which nested more in trees and less in willows than Swainson's Hawks ($\chi^2 = 3.58$, df = 1, $P = 0.059$) (Fig. 1). Nest substrate overlap was greatest between Ferruginous and Swainson's Hawks (0.97), intermediate between Red-tailed and Ferruginous Hawks (0.31), and least between Red-tailed and Swainson's Hawks (0.29).

Ferruginous and Swainson's Hawks nested extensively in willows on my study area but nested commonly in trees elsewhere (Schmutz et al. 1980, Cottrell 1981, Gilmer and Stewart 1983). In the Centennial Valley, aspen stands were located at high elevation, on steep slopes, and far (>1.6 km) from the valley floor. These characteristics may have made aspen less desirable to Ferruginous and Swainson's Hawks, species more commonly associated with prairie habitat. In five drainages that contained nests of each species, Red-tailed Hawks nested highest in elevation, Ferruginous Hawks lowest adjacent to the valley floor, and Swainson's Hawks in between. Six drainages contained nests of two species. Regardless of the species combination,

the same relationship of nest location occurred with respect to elevation.

Although Ferruginous and Swainson's Hawks showed great overlap in nest substrate use (97%), nest site characteristics differed. Willow stands along foothill streams ended near the valley floor. Ferruginous Hawks nested most often in the more exposed terminal willows that provided a commanding view (large LDE). Those sites also were closest to primary foraging areas on the valley floor. Nest substrate height differed between Ferruginous and Swainson's Hawks in Alberta (Schmutz et al. 1980) and Oregon (Cottrell 1981). I did not observe this on my study area due to the uniform height of willows compared to trees.

Hawks showed no preference for slope aspect at nest sites (Red-tailed, $\chi^2 = 5.20$, $P = 0.580$; Ferruginous, $\chi^2 = 2.00$, $P = 0.572$; Swainson's, $\chi^2 = 3.74$, $P = 0.291$). I assumed that nest sites had equal probability of facing either NE, SE, SW, or NW. When building nests hawks could likely compensate for unfavorable aspects by orienting nests toward specific exposures. However, nest exposures also varied widely (Red-tailed, $\chi^2 = 0.40$, $P = 0.940$; Ferruginous, $\chi^2 = 1.20$, $P = 0.753$; Swainson's, $\chi^2 = 3.54$, $P = 0.316$). High elevation and latitude of the Centennial Valley probably reduced thermal stress to nestlings which may have made slope aspect a minor factor in nest site selection.

PRODUCTIVITY

In the Centennial Valley Red-tailed and Ferruginous Hawks began to lay eggs in late April and Swainson's Hawks began to lay eggs three weeks later. I calculated laying dates from known fledging dates (Red-tailed, $\bar{x}$ = 11 July, SD = 4.4, n = 12; Ferruginous, $\bar{x}$ = 15 July, SD = 6.8, n = 15; Swainson's, $\bar{x}$ = 5 August, SD = 5.8, n = 25). Staggered breeding cycles probably did not reduce competition for nest substrates between Swainson's Hawks and Red-tailed and Ferruginous Hawks because the latter occupied nest sites all summer. However, Red-tailed and Ferruginous Hawks may have benefited by establishing territories in the absence of Swainson's Hawks because the latter dominated in 90% of interspecific, agonistic encounters observed (n = 25). Swainson's Hawks usurped portions of occupied Red-tailed Hawk territories in Oregon (Janes 1984). Staggered cycles probably did not reduce competition for food between Red-tailed and Ferruginous Hawks because of the large overlap of nestling periods from late June to mid-July when food demand was highest.
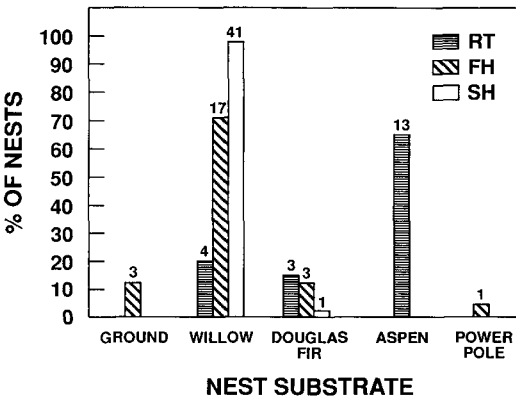

FIGURE 1. Substrates of Red-tailed (RT), Ferruginous (FH), and Swainson's Hawk (SH) nests on the Centennial Valley study area, Montana, 1987 and 1988. Sample sizes are indicated above bars.

TABLE 2. Prey of Red-tailed, Ferruginous, and Swainson's Hawks based on remains found at nests and perch sites on the Centennial Valley study area, Montana, 1987 and 1988. Prey are expressed in number (*n*) and percentage frequency (%F).

	Red-tailed		Ferruginous		Swainson's	
	n	%F	*n*	%F	*n*	%F
Mammals						
Spermophilus spp.	44	45.4	118	62.1	55	31.4
Voles[a]	12	12.3	19	10.0	43	24.6
Thomomys talpoides	6	6.2	11	5.8	13	7.4
Other small mammals[b]	3	3.1	5	2.6	4	2.3
Other mammals[c]	3	3.1	4	2.1	2	1.1
Total mammals	68	70.1	157	82.6	117	66.8
Birds						
Passeriformes	14	14.4	23	12.1	33	18.9
Piciformes	5	5.2	0	0.0	2	1.1
Galliformes	1	1.0	0	0.0	10	5.7
Other birds[d]	4	4.1	2	1.1	2	1.1
Total birds	24	24.7	25	13.2	47	26.8
Reptiles	2	2.1	0	0.0	1	0.6
Insects	3	3.1	8	4.2	10	5.7

[a] *Lagurus* and *Microtus* spp.
[b] *Peromyscus* and unidentified mice.
[c] *Lepus townsendii* and *Mephitis mephitis.*
[d] *Falco sparverius* and unidentified birds.

Ferruginous Hawks were most productive (1.77 young/occupied site, 2.21 young/active site), with Red-tailed Hawks intermediate (1.50, 1.65), and Swainson's Hawks least (1.26, 1.38). Reduced productivity has been reported for buteo nests spaced ≤0.3 km apart (Schmutz et al. 1980) and for nests in view of other nests (Cottrell 1981). Neither factor decreased productivity for active nests on my study area (spacing: t = 0.85, df = 64, P = 0.892; visual isolation: t = 0.67, df = 84, P = 0.604). No Red-tailed Hawk nests were located ≤0.3 km from other nests and data were combined due to small sample sizes. Poole and Bromley (1988) suggested that adverse weather may affect raptor reproductive success more than nest spacing in the Canadian arctic. A similar situation may exist in the Centennial Valley where spring and early summer snowstorms commonly occur. Snowstorms may indirectly affect raptor productivity by reducing above ground activity of prey, specifically ground squirrels (*Spermophilus armatus* and *S. elegans*).

FOOD HABITS

Dietary overlap was greatest between Red-tailed and Ferruginous Hawks (0.98), intermediate between Red-tailed and Swainson's Hawks (0.93), and least between Ferruginous and Swainson's Hawks (0.86). However, some differences in diet composition existed among species (Table 2). Ferruginous Hawks consumed more ground squirrels than Red-tailed Hawks (x^2 = 7.32, df = 1, P = 0.007), which consumed more ground squirrels than Swainson's Hawks (x^2 = 5.23, df = 1, P = 0.022). Both Red-tailed and Swainson's Hawks consumed more birds than Ferruginous Hawks (x^2 = 6.09, df = 1, P = 0.014; x^2 = 10.80, df = 1, P = 0.001, respectively).

In the Centennial Valley ground squirrels estivated in mid-July and became less available to the later-nesting Swainson's Hawk. At this time, however, young passerines were beginning to fledge. Swainson's Hawks might compensate for reduced ground squirrel numbers by preying on birds. Although both Red-tailed and Swainson's Hawks consumed more birds than Ferruginous Hawks, the three avian orders (Table 2) were taken in different proportions (x^2 = 7.88, df = 2, P = 0.020). Red-tailed Hawks consumed birds associated with aspen stands (Starling [*Sturnus vulgaris*] and Common Flicker [*Colaptes auratus*]) while Swainson's Hawks consumed birds associated with grassland (Western Meadowlark [*Sturnella neglecta*], Vesper Sparrow [*Pooecetes gramineus*], and Sage Grouse [*Centrocercus urophasianus*]).

In summary, the buteo hawks partitioned habitat resources, specifically nest sites. Red-tailed and Ferruginous Hawks, two species with the greatest overlap in nesting chronology and prey use, had the least similar nest sites. Ferruginous and Swainson's Hawks, two species with the greatest nest substrate overlap, had the lowest dietary overlap observed. Although these two species nested in willows extensively, differences in site characteristics were noted. Hawk diets appeared to reflect prey availability.

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AGGRESSION AND DOMINANCE IN HOUSE FINCHES[1]

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Key words: Aggression; reversed sexual dominance; House Finch; Carpodacus mexicanus; eastern population.

Among wintering birds, males generally dominate females and adults dominate immatures (Gauthreaux 1978). Reversed sexual dominance, when females dominate males during the nonbreeding season, is uncommon. Notable examples include species of raptors where females are larger than males (Amadon 1975) and shorebirds that have undergone sexual role reversals, e.g., Spotted Sandpipers (*Actitis macularia*; Maxson and Oring 1980). Among passerines, reversed sexual dominance is rare and occurs mainly among the *Carpodacus* finches (Thompson 1960a, Samson 1977).

Females dominate males during winter in native, western populations of House Finches (*Carpodacus mexicanus*; Thompson 1960a, Kalinoski 1975). Among recently introduced eastern populations, studies of unmarked birds at sunflower feeders suggest that females also dominate males (Brown and Brown 1988, Shedd 1990), but these studies offer little insight into factors other than sex (and associated plumage) that are known to influence dominance behavior in birds (e.g., body

size, mass, subcutaneous fat reserves or other morphological or physiological parameters). In this study, our objective was to examine phenotypic correlates of dominance among eastern House Finches. In contrast to previous studies of eastern populations, we used wild-caught, individually-marked House Finches that we maintained in captivity. This approach allowed us to measure morphological and physiological parameters and control for group size, sex ratio, and hunger. It also allowed a comparison of field and laboratory results.

MATERIALS AND METHODS

We captured House Finches throughout Pickens County, South Carolina during early January 1989 with mist nets. Birds were housed in individual cages (visually isolated from each other) with unlimited access to sunflower seeds, millet, and water until dominance trials began. Light on/off cycles simulated the natural photoperiod. We banded finches with uniquely numbered aluminum leg bands and color bands, and measured (to the nearest 0.5 mm) relaxed wing chord length, tarsus length, bill length (exposed culmen), medial rectrix length, abdominal fat class (Helms and Drury 1960), and body mass (to the nearest 0.1 g). We scored males for plumage brightness on the forehead, eyebrow, crown and nape, malar, throat, breast, abdomen, back, wrist (lesser secondary and marginal coverts), and rump. Body regions received a maximum of 3 points in each region