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# PARTIAL LOSS OF RED-TAILED HAWK TERRITORIES TO SWAINSON'S HAWKS: RELATIONS TO HABITAT[1]

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*Abstract.* Of a population of 33 pairs of Red-tailed Hawks (*Buteo jamaicensis*) inhabiting north-central Oregon, 9 and 10 pairs lost portions of their breeding territories to later-arriving Swainson's Hawks (*B. swainsoni*) in 1977 and 1978, respectively. The loss was accompanied by aggressive Swainson's Hawk behavior and vigorous Red-tailed Hawk defense.

Analysis of the habitat relinquished by Red-tailed Hawks showed perch availability to be an important resource in the habitat relations of these species. Red-tailed Hawks abandoned areas with perches at moderate densities (0.3–0.6 perch/ha) more often than expected by chance while preferentially retaining areas with greater perch densities. The habitat lost by Red-tailed Hawks is associated with high reproductive performance.

*Key words:* Buteo jamaicensis; Buteo swainsoni; *competition; habitat selection; interspecific territoriality; Red-tailed Hawk; Swainson's Hawk; territoriality.*

## INTRODUCTION

A reduction in resource utilization by a species in the presence of ecologically similar species (or expansion in its absence) provides some of the best evidence for the role of competition in structuring communities (Schoener 1975, Diamond 1978). While such evidence indicates the relevant limiting resources, it may reveal nothing of the mechanism by which the changes in resource use occur. Interspecific territoriality among ecologically similar organisms may also be a good indicator of interspecific competition (Orians and Willson 1964). In contrast, interspecific territoriality reveals the mechanism but not necessarily the relevant limiting resources. It is uncommon to be able to explore both simultaneously, particularly among avian populations.

Many populations of Red-tailed (*Buteo jamaicensis*) and Swainson's Hawks (*B. swainsoni*) exhibit interspecific territorial behavior (Schmutz et al. 1980, Thiollay 1981, Janes 1984, Rothfels and Lein 1984). In Oregon, Swainson's Hawks return from their South American wintering areas approximately three to six weeks following territory establishment by Red-tailed Hawks in mid-March. Upon their arrival, Swainson's Hawks often usurp portions of Red-tailed Hawk territories (Janes 1984). Red-tailed Hawks typically defend these areas vigorously, but territory loss usually occurs within one to three days following the arrival of Swainson's Hawks (Janes 1984). The resulting boundaries are typically maintained by both species with little further boundary adjustments until the territorial system begins to break down as young Red-tailed Hawks fledge.

Thiollay (1981) found that Red-tailed Hawks retreated from relatively flat land that contained few potential perches in the presence of Swainson's Hawks. Abundant perches are more characteristic of Red-tailed Hawk habitat (Bent 1937; Fitch et al. 1946; Brown and Amadon 1968; Janes 1984, 1985a, 1985b), suggesting in that study that Red-tailed Hawks surrendered less preferred habitat.

In the intermountain west, Red-tailed and Swainson's Hawks tend to occupy habitat differing in perch density, topographic relief, the incidence of outcrops and cliffs, and vegetative associations (Janes 1985a, 1985b). If territory loss by Red-tailed Hawks to Swainson's Hawks is nonrandom with respect to habitat, the analysis of the lost habitat can provide a better understanding of the competitive relations among these species.

I asked several questions concerning the habitat relinquished by Red-tailed Hawks to Swainson's Hawks in north-central Oregon. Does this habitat differ from the habitat retained by Red-tailed Hawks? Which features are preferentially retained and lost? Is the habitat yielded by Red-

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tailed Hawks marginal habitat for Red-tailed Hawks in terms of reproductive success? In other words is this habitat that Red-tailed Hawks would have abandoned anyway, or are Swainson's Hawks encroaching upon potentially productive Red-tailed Hawk habitat?

## STUDY AREA AND METHODS

The 137-km$^2$ study area was located near Antelope, Oregon and consisted of a mosaic of vegetative associations dominated by sagebrush (*Artemisia tridentata*) and perennial bunchgrasses (*Pseudoroegneria spicata, Festuca idahoensis* and others). A long history of grazing reduced the abundance of the bunchgrasses, and rabbitbrush (*Chrysothamnus nauseosus* and *C. viscidflorus*), match-weed (*Gutierrizia sarothrae*), and introduced annual grasses were widespread (e.g., *Bromus tectorum, Taeniatherum caput-medusa*). Junipers (*Juniperus occidentalis*) were the only trees except for those near human habitations. A more complete description of the study area is presented elsewhere (Janes 1984).

Previously, I evaluated the habitat relations among Red-tailed Hawks, Ferruginous Hawks (*B. regalis*) and Swainson's Hawks at six sites in the Columbia River Basin and the Great Basin, including the Antelope site considered here (Janes 1985a, 1985b). Twelve habitat features were important in distinguishing habitats occupied by the three species, and I used these as a basis for evaluating the habitat lost by Red-tailed Hawks to Swainson's Hawks.

I measured habitat on each of the 768, 16.2-ha (1/16 section) habitat blocks comprising the study area. I defined perches as utility poles and trees $\geq$2 m tall and counted the number present in each block. Outcrops and cliffs were also potential perches, but since they could not be quantified in the same manner as trees and utility poles, they are treated as separate variables. I assigned each block to one of three categories: no outcrops or cliffs, outcrops present but not cliffs (outcrops with a vertical face $\geq$5 m), and cliffs present. I also estimated the percent cover of shrubland, native bunchgrass habitat, and cropland (almost entirely dryland wheat) to the nearest 5% using 1:8,000 aerial photographs in conjunction with ground surveys. I assessed topographic relief by counting the number of 6.1 m (20′) contour lines intersected by a circle inscribed within each block and tangent to its boundaries using U.S.G.S. 7.5′ topographic maps.

I assessed territorial boundaries of Red-tailed Hawks both prior to and again after the arrival of the Swainson's Hawks, as well as the territorial boundaries for Swainson's Hawks, during the 1977 and 1978 breeding seasons. I ascertained territorial boundaries based on a minimum of 10 hr of observation of a pair (20 bird-hours) and often considerably more. By plotting the cumulative percentage of the maximum observed territory as a function of observation time, I found that 9.1 hr of observation of both members of a pair defined 95% of a territory (Janes 1984). I considered the habitat blocks most closely conforming to territorial boundaries to comprise a territory for the purpose of habitat analysis.

A hawk territory must meet a variety of needs including a nest site, prey, and an adequate flight environment. These diverse needs often require diverse habitat features all in an area sufficiently small to provide easy access to the pair. Consequently, it is appropriate to consider territories as a whole and not as a set of independent habitat blocks (Janes 1984, 1985a, 1985b). However, treatment of territories as a unit was not possible here. The habitat blocks lost by Red-tailed Hawks comprised small portions of larger territories. To compare this habitat with habitat retained by Red-tailed Hawks, it was necessary to compare habitat blocks and not territories even though this approach increased the variance within each variable and risked the loss of sensitivity in the statistical analyses sufficient to detect important patterns.

I compared the habitat blocks occupied by Swainson's and Red-tailed Hawks using a discriminant function analysis and compared these results with earlier analyses of territories (Janes 1985a, 1985b). When treating territories as the unit of measure, variables reflect the proportion of the territory containing the feature. For example, "Perch Density 50+" was the proportion of the habitat blocks comprising a territory with 50 or more perches. Upon finding that the analysis provided results qualitatively similar to the earlier studies, albeit with reduced powers of discrimination, I calculated discriminant scores for the habitat blocks lost by Red-tailed Hawks to Swainson's Hawks. To obtain a clearer picture of the nature of the habitat relinquished by Red-tailed Hawks, I then compared the habitat lost with that retained by Red-tailed Hawks using a second discriminant function analysis.

To evaluate habitat differences concerning just

TABLE 1. Discriminant function analysis comparing the habitat blocks occupied by Swainson's Hawks with those occupied by Red-tailed Hawks following boundary adjustments. This analysis, which treats habitat blocks as separate sampling points, is contrasted with previous results (Janes 1985a, 1985b) which treat each territory (with its component habitat blocks) as a sampling point. The two analyses provide qualitatively similar results though the analysis treating habitat blocks separately is less able to distinguish between Red-tailed and Swainson's Hawk habitat as indicated by the canonical correlation. Positive coefficients indicate features associated with Red-tailed Hawks.

| Sampling unit | | | |
|---|---|---|---|
| Habitat block | | Territory[a] | |
| Variable/standardized discriminant function coefficient | | | |
| Outcrop/cliff | 0.899 | Outcrop | 0.865 |
| Topographic relief | 0.343 | Perch density 50+ | 0.591 |
| Perch density | 0.303 | Perch density 5–9 | 0.456 |
| Cropland cover | 0.268 | Topographic relief 5–9 | −0.360 |
| Shrub cover | −0.223 | | |
| Canonical correlation | 0.297 | | 0.686 |
| $\chi^2$ | 56.84 | | 29.87 |
| df | 5 | | 4 |
| $P <$ | 0.0001 | | 0.0001 |

[a] Janes (1985b).

perches, I used a Chi-square goodness-of-fit test with habitat blocks assigned to one of five density categories: 0, 1–4, 5–9, 10–49, and ≥50 perches. I used the procedure of Neu et al. (1974) to evaluate significant deviations within each category.

In addition to noting territorial boundary adjustments at the periphery of a territory in 1977 and 1978, I also recorded behavior and resolution of conflicts involving more centrally located portions of a territory between 1975 and 1983. This included attempts by Swainson's Hawks to evict a pair of Red-tailed Hawks from a territory or the occupancy of a traditional Swainson's Hawk territory by Red-tailed Hawks. I defined a traditional territory as one with three or more years of continuous occupancy by a species during the breeding season.

## RESULTS

Of the 33 Red-tailed Hawk pairs studied, 10 lost one or more habitat blocks to Swainson's Hawks in 1977, and 9 lost habitat blocks in 1978. A total of 49 separate habitat blocks was relinquished in the two-year period. Twelve were surrendered both years. In comparison, territorial adjustments also occurred along boundaries not contested by Swainson's Hawks, but these involved the loss or gain of fewer habitat blocks, usually only one, rarely two.

Discriminant function analysis treating habitat blocks as independent samples revealed qualitative results similar to previous analyses employing territories (Table 1). In both analyses, features related to outcrops and cliffs yielded the greatest habitat difference between Red-tailed and Swainson's Hawks. Likewise, perch density was important while vegetative associations were relatively unimportant.

When this discriminant function was applied to the habitat blocks abandoned by Red-tailed Hawks, the mean score differed significantly from the habitat blocks retained by Red-tailed Hawks ($t = 2.79$, df = 493, $P < 0.01$; Fig. 1). Habitat blocks lost by Red-tailed Hawks were more characteristic of Swainson's Hawk habitat blocks ($t = 1.58$, df = 222, $P > 0.05$).

A separate discriminant function analysis comparing the relinquished habitat blocks with those retained by Red-tailed Hawks provided a more direct evaluation of the habitat lost (Table 2). Perch-related variables still figured prominently and vegetative associations were still relatively unimportant, but with important differences. Perch density became the most important discriminating variable. Outcrops and cliffs fell to secondary importance while topographic relief all but disappeared as an important discriminating feature.

A closer analysis of perch density revealed the densities most strongly contested by the two species. A Chi-square goodness-of-fit test again showed that Red-tailed Hawks abandoned habitat blocks in a non-random manner with respect to perch density ($X^2 = 19.23$, df = 3, $P < 0.001$; Fig. 2). They preferentially lost blocks with 5–9 perches and retained those with 10 or more

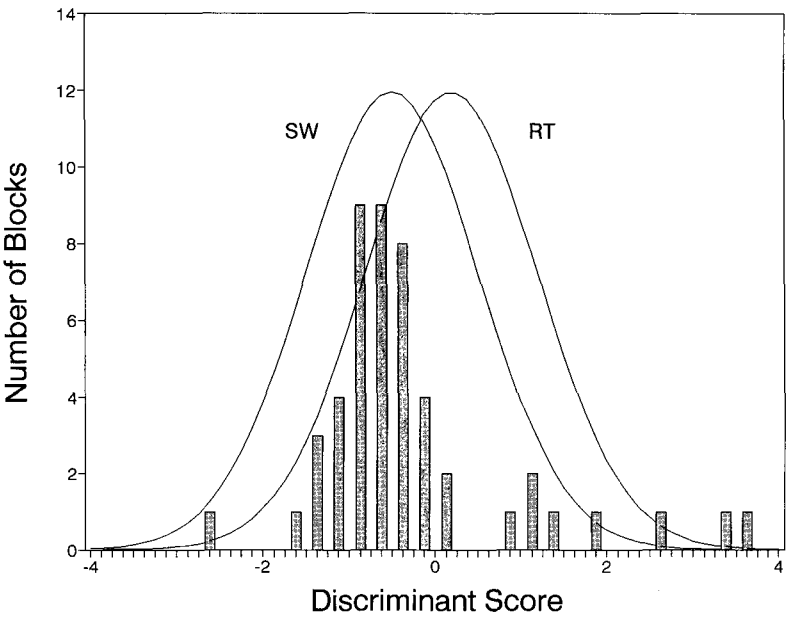


FIGURE 1. Distribution of discriminant function scores for habitat blocks relinquished by Red-tailed Hawks (bars) when applied to the discriminant function comparing habitat blocks occupied by Red-tailed Hawks following boundary adjustments and Swainson's Hawks. The curves represent normal curves generated from the means and variances of discriminant function scores for each species.

perches. Limited sample size made it necessary to combine blocks with 10–49 and ≥50 perches for the analysis. Loss of blocks without perches and those with 1–4 perches was random. The relinquished habitat blocks also differed from Swainson's Hawk habitat relative to perch density ($X^2 = 23.89$, df = 3, $P < 0.001$; Fig. 2). As above, the lost area contained more blocks with 5–9 perches and fewer blocks with 10 or more perches than expected by chance.

In more than 150 pair-years of observations of Swainson's Hawks at the Antelope site, I never observed Swainson's Hawk aggression lead to territory abandonment by Red-tailed Hawks with eggs or young. In contrast, pairs of Red-tailed Hawks occupied traditional Swainson's Hawk territories on three occasions. The newly established territories encompassed the entire territory of the previous occupants. On two occasions, pairs of Swainson's Hawks attempted to establish territories in the traditionally held area but were unsuccessful. These Swainson's Hawks subsequently established territories in adjacent areas unoccupied by buteos but failed to breed. I observed no Swainson's Hawks contesting the Red-tailed Hawks in the remaining case, but my visits were too infrequent to be certain.

## DISCUSSION

In the intermountain region of western North America, Red-tailed Hawk territories differ from those of Swainson's Hawks (and Ferruginous Hawks) primarily by inclusion of a greater percentage of habitat blocks with outcrops, cliffs, and moderate to high densities of trees and utility poles (≥5 per block; Janes 1985a). An analysis of habitat relations among Red-tailed Hawks and Swainson's Hawks on the Antelope site revealed

TABLE 2. Discriminant function analysis comparing the habitat blocks relinquished by Red-tailed Hawks with those retained. Positive coefficients indicate features preferentially retained.

| Variable/standardized discriminant function coefficient | |
|---|---|
| Perch density | 0.847 |
| Outcrop/cliff | 0.572 |
| Shrub cover | −0.377 |
| Bunchgrass cover | 0.271 |
| Cropland cover | 0.192 |
| Topographic relief | −0.076 |
| Canonical correlation | 0.161 |
| $\chi^2$ | 12.91 |
| df | 6 |
| $P <$ | 0.05 |

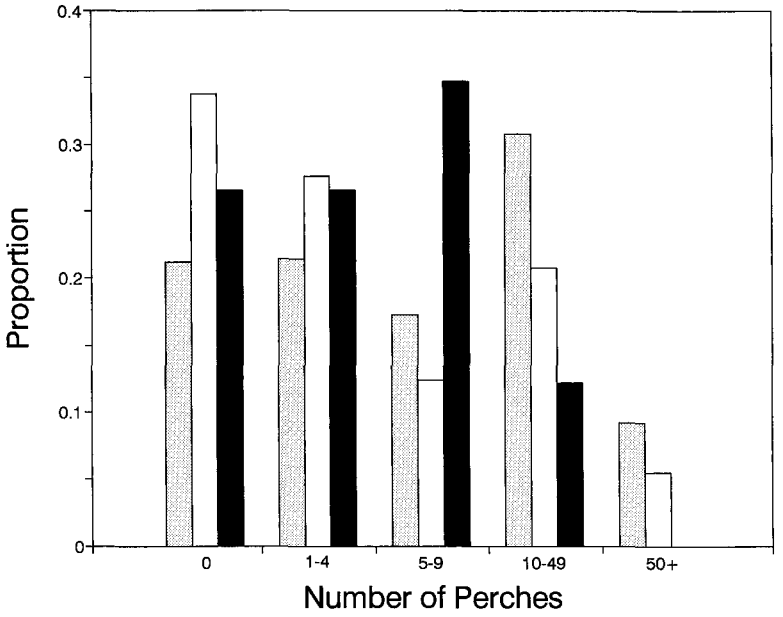


FIGURE 2. Distribution of habitat blocks comprising Red-tailed Hawk territories following boundary adjustments (gray bars), Swainson's Hawk territories (white bars) and the area relinquished by Red-tailed Hawks to Swainson's Hawks with respect to perch density (black bars).

similar habitat preferences (Janes 1985b). In both analyses, the principal habitat gradient was perch density. Similar habitat preferences have also been noted by Smith and Murphy (1973), Schmutz et al. (1980), and Thiollay (1981). The results of this study reinforce previous findings that perches are important in the competitive relations among Red-tailed Hawks and Swainson's Hawks.

The importance of perches to Red-tailed Hawks is reflected in reproductive performance. Previous work at this site has shown that the mean number of young fledged per territory is positively correlated with several perch-related features including the incidence of habitat blocks containing outcrops, cliffs, and perch densities of 1–4 perches/habitat block and greater (Janes 1984). At least in part, this can be attributed to differences in foraging behavior. Red-tailed Hawks most often seek prey from elevated perches (Fitch et al. 1946; Brown and Amadon 1968; Thiollay 1981; Janes 1984, 1985a). In contrast, Swainson's Hawks rely more on flight to detect prey (Bowles and Decker 1934; Bent 1937; Fitzner 1978; Thiollay 1981; Bechard 1982; Janes, unpubl. data). Consistent with these observations, Red-tailed Hawks preferentially retained habitat offering plentiful sites from which to detect prey.

However, not all results conformed to expectations based upon Red-tailed Hawk preference for perches. It was anticipated that Red-tailed Hawks would tend to retain habitat blocks containing not only outcrops and high perch densities but also blocks with moderate perch densities (5–9 perches/block). Moderate perch densities are associated with high Red-tailed Hawk reproductive performance (Janes 1984). Instead, Red-tailed Hawks retreated from habitat blocks with moderate perch densities more than expected by chance alone (Fig. 2). Thus Swainson's Hawks were able to displace Red-tailed Hawks from high quality habitat and not just habitat that Red-tailed Hawks might tend to abandon even in the absence of Swainson's Hawks.

The nature of encounters between these species supports this interpretation. Swainson's Hawks were aggressors in 82% of interspecific encounters ($n$ = 149) and consistently displaced Red-tailed Hawks (Janes 1984, 1985b). In part, the superiority of Swainson's Hawks in aerial encounters corresponds to morphology (Janes 1985a, 1985b). Swainson's Hawks possess a high

aspect ratio and low wing loading compared with Red-tailed Hawks, which theoretically permits them to gain a higher position more quickly than Red-tailed Hawks under most flight conditions. A higher position enables a bird to initiate an attack.

While Swainson's Hawks can displace Red-tailed Hawks from peripheral portions of Red-tailed Hawk territories even if these areas are of high quality, they are apparently less successful in displacing Red-tailed Hawks from areas more centrally located in Red-tailed Hawk territories. This must also restrict Swainson's Hawk habitat distribution by limiting access to areas suitable to both species.

This study contributes further evidence supporting the importance of perches in the competitive relations among Red-tailed Hawks and Swainson's Hawks. These hawks not only tend to select different habitats upon territory establishment, but interspecific territorial behavior initiated by Swainson's Hawks and subsequent territorial boundary adjustments by Red-tailed Hawks contribute to increased habitat differences. Red-tailed Hawks also appear to restrict the habitat distribution of Swainson's Hawks by successfully resisting Swainson's Hawk aggression in core areas of their territories, and on occasion by usurping traditional Swainson's Hawk territories.

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