

DISTRIBUTION OF RAPTOR FORAGING IN RELATION TO PREY BIOMASS AND HABITAT STRUCTURE¹

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Abstract. The spatial distribution of Red-tailed Hawks (*Buteo jamaicensis*) and Northern Harriers (*Circus cyaneus*) overwintering in central Arkansas was studied in relation to perch availability, plant cover, and small rodent biomass in six habitat patch types. In general, raptor foraging was distributed nonrandomly among patch types. Red-tailed Hawks occupied corn stubble and old-field patches more frequently than expected by chance and occupied tall corn and bare patches less frequently than expected. Adult male Northern Harriers used corn stubble and wetland patches more frequently than expected and used tall corn and bare patches less frequently than expected, while adult female and juvenile harriers used wetland patches more frequently than expected and used bare patches less frequently than expected. The general distribution of Northern Harriers is interpreted as a response to prey biomass availability (rodent biomass index \times 1/plant cover density), while Red-tailed Hawk distribution is interpreted as a response to both prey biomass availability and perch availability.

Key words: *Buteo jamaicensis*; *Circus cyaneus*; foraging distribution; patch use; perch availability; plant cover density; prey biomass.

INTRODUCTION

Raptors are highly mobile predators that often inhabit markedly heterogeneous habitats. Optimal foraging theory predicts that the foraging distribution of such predators should be nonrandom, i.e., most hunting should occur in habitat patches yielding the greatest net energy gain (Pyke et al. 1977, Krebs et al. 1983). Some predator-prey models assume a direct relationship between foraging distribution and prey density (e.g., MacArthur and Pianka 1966, Poole 1974); however, according to the profitability hypothesis of Royama (1970, 1971), habitat patches yielding the greatest energy gain per unit of hunting effort may not contain the highest prey density.

Several studies have indicated that plant cover exerts a significant effect on raptor foraging success and distribution (Southern and Lowe 1968, Wakeley 1978, Baker and Brooks 1981, Stinson et al. 1981, Bechard 1982). Most of these were autecological studies conducted during the breeding season (but see Baker and Brooks 1981). Here, I present the results of a study conducted to determine the foraging distribution of overwintering Northern Harriers (*Circus cyaneus*) and

Red-tailed Hawks (*Buteo jamaicensis*) in relation to habitat characteristics and small rodent biomass.

STUDY AREA

The study was conducted at Holla Bend National Wildlife Refuge, located in Yell County, Arkansas, about 16 km southeast of Dardanelle. The refuge is managed primarily for overwintering waterfowl and includes 980 ha of contiguous cultivated fields surrounded by 670 ha of woodlands. The study was confined to the field habitats in the interior of the refuge. Six habitat patch types were identified.

Tall corn. First-growth corn (*Zea mays*) fields invaded extensively by weeds such as *Xanthium chinense*.

Corn stubble. Recently cut corn fields. These patches included short corn stalks and weeds, as well as ground litter of leaves, cobs, etc.

Soybeans. First-growth soybean (*Glycine max*) fields invaded by weeds such as *X. chinense* and *Solanum carolinense*. These were not cut or plowed during the observation periods.

Old field. Previously cultivated areas which had reverted to weedy vegetation. Common species in these fields included *Andropogon virginicus*, *Desmodium canescens*, *X. chinense*, *S. carolinense*, *Solidago* spp., and *Aster* spp.

Wetland. Uncultivated moist soil areas dominated by *Polygonum* spp. and *Scirpus* spp.

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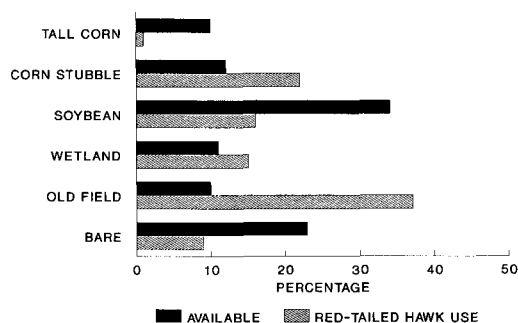


FIGURE 1. Red-tailed Hawk foraging distribution in relation to habitat patch availability.

Bare ground. Plowed fields with little or no vegetation.

METHODS

The foraging behavior of raptors was observed for at least two successive days during the second week of each month from November through February in two nonbreeding seasons, 1986–1987 ($n = 11$ days), and 1987–1988 ($n = 10$ days). Observations were made by several field parties systematically surveying the study area on foot and by auto. During each observation period, all hours of the day between 09:00 and 17:00 CST were sampled. The location (habitat patch type) and activity of each hawk observed were recorded at 10-min intervals until the hawk was lost to view. When possible, each harrier was classified as an adult female, adult male, or juvenile using criteria described by Brown and Amadon (1968). Harriers that could not be classified (i.e., some adult females and juveniles of either sex) were recorded as “brown birds” following Colopy and Bildstein (1987). To determine raptor food habits in the study area, communal roosts of Northern Harriers and favored perch sites of Red-tailed Hawks were systematically searched for regurgitated pellets. Searches were conducted biweekly throughout each study period. The pellets were placed in plastic bags and transported to the laboratory for analysis. Prey remains were identified with the aid of a mammalian skull key (Glass 1973) and specimens in the UALR reference collection.

Relative rodent abundance in each patch type was estimated with Sherman live traps. Traplines consisting of 25–60 traps transected four patches of each type during each year of the study. Intertrap distance within each trapline was approximately 10 m. Each patch was sampled for

two consecutive days during each month of the study period, coinciding with observations of raptor foraging behavior. Traps were baited with Omolene-100 horse feed and checked morning and evening. I calculated a rodent index for each patch type based on biomass of rodents captured per trap-day (= number of traps set \times number of 24-hr periods trapped). Biomass was calculated using average weights of specimens in the UALR mammal collection.

In mid-December 1987, plant cover density was sampled at 10-m intervals along randomly located line transects in 11–12 patches of each type. There were 20–60 sample sites per patch, depending on the size of the patch. At each sample site, I counted the number of stems and leaves touching a 150-cm vertical rod (James and Lockerd 1986). These values were averaged for each patch.

Because the amount of prey biomass actually available to raptors may be dependent on both prey biomass and plant cover density, I calculated an estimated prey biomass availability index for each patch using the equation: available prey biomass = rodent biomass index \times 1/plant cover density. Bechard (1982) used a similar index substituting incident light at ground level for plant cover density (i.e., available prey biomass = estimated prey biomass \times fraction of incident light at ground level). It is likely that the two indices are comparable in most agricultural/grassland environments, where plant cover density is inversely related to incident light at ground level.

RESULTS

During the 2 years of the study, 418 Northern Harrier (230 adult female, 61 adult male, 98 juvenile, 29 brown) and 208 Red-tailed Hawk (21 adult, 18 immature, 169 undetermined) observations were recorded. Observations of soaring hawks (13 harrier and 56 red-tailed) were omitted from distribution analyses because of the difficulty of assigning a soaring hawk to a habitat patch.

FORAGING DISTRIBUTION

The null hypothesis that raptors used habitat patch types in proportion to availability was rejected for both species in both years ($\chi^2 \geq 59.74$, $df = 5$, $P < 0.001$). The methods of Neu et al. (1974) were used to determine which patch types were used more or less frequently than expected

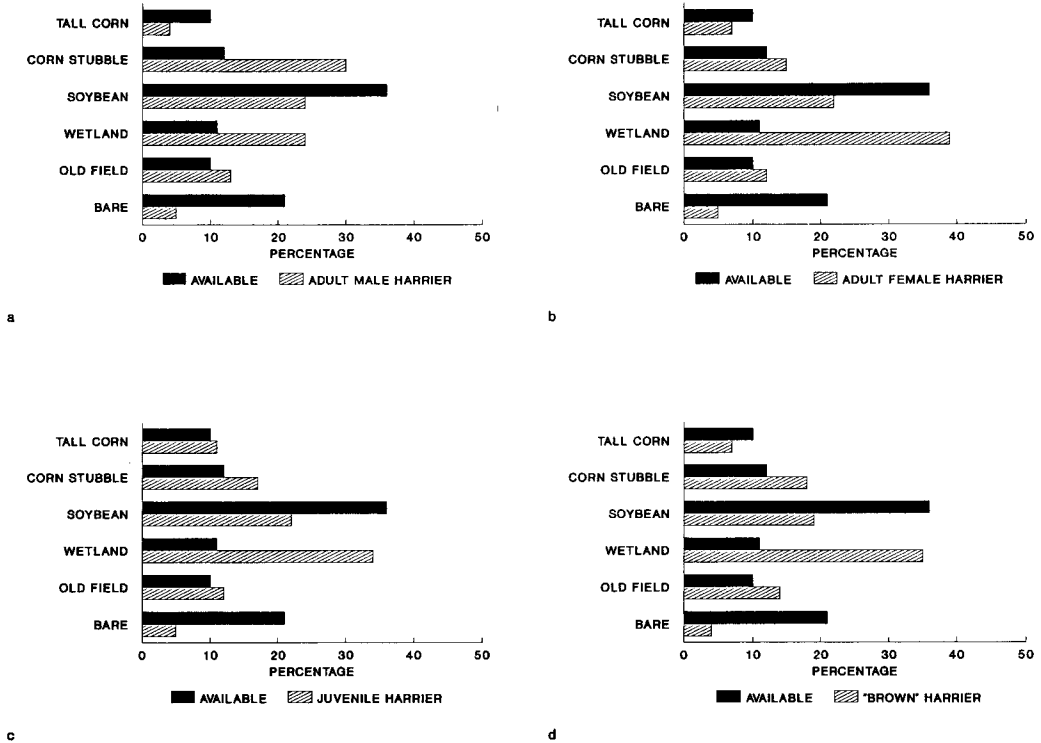


FIGURE 2. Foraging distribution of (a) adult male, (b) adult female, (c) juvenile, and (d) “brown” Northern Harriers in relation to habitat patch availability.

by chance ($\alpha = 0.05$). During both years, Red-tailed Hawks used corn stubble and old-field patches more than expected and used tall corn and bare patches less than expected (Fig. 1). Adult male Northern Harriers used corn stubble and wetland patches more than expected, and, like Red-tailed Hawks, frequented tall corn and bare patches less than expected (Fig. 2a). The foraging distribution patterns of adult female (Fig. 2b), juvenile (Fig. 2c), and brown Northern Harriers (Fig. 2d) were similar; each used wetland patches more than expected and bare patches less than expected.

RELATIVE RODENT BIOMASS

Five rodent species were trapped at Holla Bend during the study period. *Mus musculus* accounted for 42% of the total captures, followed by *Sigmodon hispidus* (28%), *Oryzomys palustris* (22%), *Peromyscus maniculatus* (5%), and *Reithrodontomys fulvescens* (3%).

Trapping results were combined for both years because between-year variation in trap indices was less than within-year variation. Rodent bio-

mass indices varied widely among habitat patch types (Table 1). Differences among patch types were highly significant ($\chi^2 = 41.89$, $df = 5$, $P < 0.0001$, Kruskal-Wallis test). Tall corn patches yielded significantly greater rodent biomass than any other period type, and patches of bare ground yielded significantly less rodent biomass than any other patch type ($P < 0.05$, Tukey’s nonparametric multiple comparison test). Of the remaining patch types, wetland yielded greater rodent biomass ($P < 0.05$, Tukey’s nonparametric multiple comparison test) than old field, corn stubble, or soybean (Table 1).

Raptor diets were determined from 407 Northern Harrier pellets and 102 Red-tailed Hawk pellets. *Sigmodon hispidus* was the most frequently occurring mammal in the diet of both raptors. Together, the five rodent species listed above accounted for at least 82% (by frequency) of the diet of Red-tailed Hawks, and at least 40% of the diet of Northern Harriers. The remaining diet of harriers included 42% birds and 18% unidentified mammals. Other items in the Red-tailed Hawk diet included unidentified mammals

TABLE 1. A comparison of the rodent biomass index among habitat patches (four patches of each type during both years of the study). Means not connected by bars are significantly different ($P < 0.05$, Tukey's multiple comparison test).

Patch	Mean biomass index (\pm SD)	n	Trap-days
Tall corn	11.40 \pm 2.39	8	1,600
Wetland	8.74 \pm 1.94	8	1,240
Old field	5.20 \pm 1.38	8	1,328
Corn stubble	3.84 \pm 1.28	8	1,216
Soybean	2.10 \pm 1.08	8	1,600
Bare	0.02 \pm 0.01	8	1,444

(10%), reptiles and arthropods (3%), birds (3%), and *Sylvilagus floridanus* (2%). Relative importance of species in the diets cannot be inferred with confidence from these data because small animals were probably underrepresented in the regurgitated pellets (see Wakeley 1978). However, the data provide confidence that the rodent species surveyed in this study were prominent in the winter diet of both raptor species.

RELATIVE PLANT COVER DENSITY

There was a significant ($\chi^2 = 48.54$, $df = 5$, $P < 0.0001$, Kruskal-Wallis test) difference among patch types with respect to plant cover density (Table 2). Plant cover density did not differ between corn stubble and soybean patches or between old field and wetland patches ($P > 0.05$, Tukey's nonparametric multiple comparison test). However, tall corn and bare ground each differed significantly ($P < 0.05$, Tukey's nonparametric multiple comparison test) from all other patch types with respect to plant cover density (Table 2). Plant cover was greatest and most variable among tall corn patches, followed by wetland and old field, respectively.

RELATIONSHIPS AMONG RAPTOR DISTRIBUTION, RODENT BIOMASS, AND HABITAT STRUCTURE

A stepwise regression analysis (Zar 1984) was used to test the effect of rodent biomass, plant cover density, prey biomass availability, and perch availability (dummy variable indicating presence or absence of perches) on raptor counts. Prey biomass availability was the only variable that had a significant effect on counts of adult male harriers ($F = 37.89$, $n = 15$, $P < 0.0001$, $R^2 = 0.86$), adult female harriers ($F = 10.94$, $n = 15$, $P < 0.01$, $R^2 = 0.85$), juvenile harriers (F

TABLE 2. A comparison of plant cover density among habitat patches. Means not connected by bars are significantly different ($P < 0.05$, Tukey's multiple comparison test).

Patch	Mean plant cover density (\pm SD)	n	Sample sites
Tall corn	20.16 \pm 8.31	12	312
Old field	11.91 \pm 3.65	12	292
Wetland	10.08 \pm 3.91	11	265
Soybean	3.83 \pm 1.53	12	332
Corn stubble	3.80 \pm 1.60	12	257
Bare	0.75 \pm 1.05	12	320

$= 14.58$, $n = 15$, $P < 0.001$, $R^2 = 0.89$), and brown harriers ($F = 21.03$, $n = 15$, $P < 0.0001$, $R^2 = 0.92$). Both prey biomass availability and perch availability had a significant effect on Red-tailed Hawk counts ($F = 15.03$, $n = 15$, $P < 0.001$, $R^2 = 0.88$).

DISCUSSION

I found no direct relationship between raptor foraging distribution and prey biomass. Both raptor species preyed heavily on small rodents, yet did not hunt extensively in rodent-rich patches of tall corn. Red-tailed Hawks and adult male Northern Harriers actually avoided these areas. Tall corn patches contained the most dense vegetation in my study area, and several authors (e.g., Southern and Lowe 1968, Wakeley 1978) have reported the raptor foraging distribution to be inversely related to the plant cover density. However, I found no significant relationship between raptor foraging and plant cover density. This is largely due to raptor avoidance of patches of bare ground. Similarly, Bildstein (1987) reported that both Northern Harriers and Red-tailed Hawks overwintering in Ohio avoided plowed fields. Notably, bare patches in my study area contained significantly fewer rodents than did any other patch type.

While the linear model used to test the effects of independent factors on raptor distribution may be oversimplified, the significant effect of the prey availability index on raptor counts, together with the high R^2 values associated with these models, clearly suggest that the birds were more responsive to the composite of prey density and plant cover density than to either factor alone. Previous studies of Red-tailed, Rough-legged (*Buteo lagopus*; Baker and Brooks 1981), and Swainson's hawks (*Buteo swainsoni*; Bechard 1982) produced similar results and conclusions. Re-

cently, Collopy and Bildstein (1987) reported that the hunting success of Northern Harriers was lower in an area with dense vegetation than in an area with sparse vegetation. Presumably, small rodents are less vulnerable to detection and capture in dense vegetation, and thus raptor hunting profitability (and distribution) is a function of both prey abundance and vegetation density.

Despite the similar distribution pattern of both raptor species, there was a striking difference between them; Red-tailed Hawks favored old-field patches over wetland patches, while all Northern Harrier groups favored wetland patches over old-field patches. These two patch types were similar to one another with respect to plant cover, but rodent biomass was significantly higher in wetland patches than in old-field patches. The results of the regression analysis indicate that the most plausible explanation for Red-tailed Hawks not using wetlands to a greater extent is that perch sites were absent from most wetland areas. All old-field patches in my study area included either fence posts or large trees where Red-tailed Hawks were observed to perch. In contrast, most wetland patches included no trees or other perch sites. Bildstein (1987) also reported that, when compared to the distribution of Northern Harriers, the distribution of Red-tailed Hawks was more closely linked to the presence of perch sites. Because the Red-tailed Hawk possesses a relatively low wing aspect ratio, it is poorly adapted to hunting in flight. Consequently, it hunts primarily from an elevated perch and prefers areas that provide a relative abundance of potential perching sites (Janes 1984). This species uses habitats with a scarcity of perches only where topographic relief is high (Janes 1985). Topographic relief enhances declivity currents and thus provides favorable conditions for aerial foraging (Preston 1981). The relationship between Red-tailed Hawk and Northern Harrier foraging distribution is further complicated by the reliance of Northern Harriers on avian prey in this study. Although there were no obvious differences in avian prey abundance among old-field and wetland patches, subtle differences may have contributed to the observed difference in foraging distribution between the two raptor species.

There were some differences in patch use between adult male Northern Harriers and all other groups of Northern Harriers. Adult males frequented corn stubble and avoided tall corn, while adult females and juveniles used each of these

patches in proportion to their availability. Although all harriers spent a disproportionate percentage of time foraging in wetland areas, adult males spent 14–18% less time in wetland areas than did the other harrier groups (Figs. 2a–d). Thus, adult female and juvenile harriers foraged in tall, dense vegetation (e.g., tall corn, wetland) more frequently and foraged in short, sparse vegetation (e.g., corn stubble) less frequently than did adult males. This is consistent with the observations of Schipper et al. (1975) and Bildstein (1987) who found that harrier females occupied taller and denser vegetation than males. Northern Harriers hunt by coursing low over the ground, surprising prey in their path. Females and juveniles are darker in color than adult males, thus contrasting more sharply against the sky. Females are also less maneuverable than males (Janes 1985). Females and juveniles may therefore benefit more than adult males by foraging in taller, denser vegetation that helps conceal them from prey (Schipper et al. 1975).

My results and those of others (e.g., Southern and Lowe 1968, Wakeley 1978, Baker and Brooks 1981, Bechard 1982) indicate that raptor foraging distribution represents a response to a suite of environmental factors, including habitat characteristics and prey abundance. Models of predator-prey relationships that assume a direct relationship between prey density and prey capture (e.g., Poole 1974) are probably inappropriate for most raptors. To better predict raptor foraging distribution, models should include factors (e.g., vegetation structure) in addition to prey abundance that influence prey availability.

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