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DISTRIBUTION PATTERNS OF RAPTORS IN RELATION TO DENSITY OF MEADOW VOLES

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ABSTRACT.—Densities of overwintering Red-tailed Hawks (*Buteo jamaicensis*) and Rough-legged Hawks (*Buteo lagopus*) were examined in relation to densities of meadow voles (*Microtus pennsylvanicus*) on six habitat types. Generally, densities of both raptor species were greater in habitats that had higher densities of meadow voles. However, not all habitats with high numbers of voles had high numbers of the raptors. The amount and distribution of cover also appeared to influence the distribution of the raptors. Hence, patches that support high densities of prey may not be profitable foraging sites for predators because other factors may reduce availability of prey.

Optimal foraging theory predicts that animals should maximize their net rate of energy intake (Krebs 1973, Pyke et al. 1977). For example, when the food of a predator is distributed unevenly in space, the predator would be expected to spend more time on those patches yielding greatest net gain of energy (MacArthur and Pianka 1966, Krebs 1973, Smith and Sweatman 1974, Zach and Falls 1976a, Pyke et al. 1977, Bobisud and Voxman 1979, Waage 1979). Several studies have shown that predators do concentrate their search efforts in areas of high prey density (Goss-Custard 1970, Simons and Alcock 1971, Smith and Dawkins 1971, Hassel and May 1974, Smith 1974, Smith and Sweatman 1974, Hartwick 1976, Zach and Falls 1976a, b, c). Royama (1970, 1971) hypothesized that predators learn to use the most "profitable" patches where profitable is defined in terms of biomass of prey taken by a predator per unit of hunting time, rather than strictly on the basis of prey density.

Few field studies, however, have investigated whether predators concentrate their foraging efforts on the most profitable sites. In the present study, we examined the profitability hypothesis of Royama (1970) by measuring responses of raptors to different densities of meadow voles (*Microtus pennsylvanicus*). On Toronto International Airport, meadow voles constitute more than 85% of prey items in the diets of overwintering Red-tailed Hawks (*Buteo jamaicensis*) and Rough-legged Hawks (*B. lagopus*; Baker 1977). From November to March these hawks devote most of the day to foraging and might be expected to be most numerous in areas where voles are abundant.

STUDY AREA AND METHODS

Toronto International Airport is on the western perimeter of Metropolitan Toronto, Ontario (79°37′W, 43°41′N). In addition to buildings and paved areas, it includes about 1,200 ha of farmland and assorted grasslands. The airport is surrounded by industrial and urban areas and by flat old-field communities that are largely devoid of trees and shrubs. On the basis of access roads and runways, we chose a study area of 827 ha so as to permit a total census of the raptors on the study area.

The study area was divided into six habitat types according to vegetation composition and type of land management. *Shortgrass* habitats (407 ha) were mowed and treated with herbicides regularly by airport personnel so that the average vegetation height was about 10 cm and the dominant plant species was bluegrass (*Poa* sp.). Agricultural land (273 ha) was classified into four habitat types. *Pastures* (49 ha) were grazed by cattle except in winter. By early fall, little cover remained on pastures except around clumps of weeds avoided by the cattle. *Plowed fields* (100 ha) were farmed during summer, then were plowed in early fall and left fallow over winter. *Winter wheat* (69 ha) was sown in September, and harvested the following July. There was little cover on winter wheat fields over winter. *Straw* habitats (55 ha) occurred only in 1974–75 when straw from the harvested winter wheat was left in rows in the fields over winter. The straw provided good winter cover for voles. *Old fields* (147 ha) were largely abandoned farm fields (70%) and unmanaged areas near streams and lowlands (30%). They were densely covered by perennial grasses, forbs and hawthorn (*Crataegus* spp.) seedlings. More detailed description of these habitat types is in Steele (1977).

Vole populations were estimated on the basis of live-trapping plots using standard capture/mark/recapture methods (Davis 1956). Estimates were based on the Schnabel (1938) method, using Overton's (1965) modification for known removals. The minimum number of voles known to be alive (MNA) was also tabulated (Krebs 1966). One live-trapping plot was set on each habitat type, with no plot less than 50 m from the habitat boundary, and no plot within 400 m of any other. Each plot was a 0.4-ha grid with one trap set every 10 m for a total of 55 traps per plot. Each plot was trapped every three months and at each sample period the traps were opened for five consecutive days. Sherman live traps, baited with raisins, were set one per station and protected with a 15 × 30-cm piece of plywood. Captured voles were toe-clipped and released at point of capture. From October 1974 to April 1975, plots were placed in all habitats, but from October 1975 to April 1976, plots were placed only in shortgrass, old field and pasture. Two habitat types were trapped each week and all habitat types were trapped within one month for each round of sampling.

Populations of overwintering Red-tailed and Rough-legged hawks were estimated using a total census of the study area. Censuses were conducted from a vehicle traveling over a 12.8-km route. Each census took about 45 min and included stops at designated points to obtain counts from areas difficult to observe. Accuracy in locating and counting raptors was facilitated by a map, marked off in a 200 × 200-m grid, which showed the location and extent of all habitats on the census area. When a hawk was sighted, species, grid location, and habitat were noted. Birds that could not be identified to species or could not be located on or over a specific habitat, were not included in the analysis. Fewer than 1% of birds were excluded on these two criteria.

The possibility of counting the same bird twice in any census was minimized by noting any individually distinctive features on a bird and by keeping track of all birds flying out of an area being censused and into another area yet to be censused. Both species were equally detectable on all parts of the study area, as confirmed by agreements between counts done by a stationary observer and a moving observer in two different parts of the study area each year (Baker 1977). Censuses were carried out between 10:00 and 14:30, usually twice a week. Forty-seven censuses were conducted from 1 October through 15 April in 1974–75; 62 censuses were made during the same time period in 1975–76. Each year was divided into three seasons: fall (1 October through 15 December); winter (16 December through 15 February); and spring (16 February through 15 April).

Profile analysis (Harris 1975) was used in a two-way comparison of Red-tailed and Rough-legged hawk densities across habitats and seasons within each year. The data were normalized with a log (χ + 1) transformation before testing. The profile analysis generated a curve of mean hawk density on each habitat for each season within each year and compared the slopes of the curves to determine if they were parallel (no significant interaction [$P > 0.05$] between habitat and season). When the curves were parallel, the mean density of hawks over the three seasons was used to compare across the habitats, and Scheffe's multiple comparison procedure was used to compare the means at the 0.05 probability level. When the curves were not parallel, there was a significant interaction ($P < 0.05$) between habitat and season, and the mean hawk density within each season was used in the comparisons across habitats. The means were compared using Hotteling's T^2-test followed by Scheffe's multiple comparison procedure (at $P < 0.01$ level of significance).

When the curves were parallel, a Duncan's multiple range test (Snedecor and Cochran 1967) was used to compare hawk densities across seasons (at the 0.05 probability level) based on a mean hawk density for all habitat types within each season. When the curves were not parallel, the mean hawk density within each habitat was compared across the three seasons using a one-way analysis of variance (Snedecor and Cochran 1967). The means were then compared using Duncan's test (at $P < 0.01$). All means shown in text and tables were converted from log-transformed data back to the original units (number per 100 ha) using the formula antilog ([SD^2 × 1.15] + $\bar{x}$) given by Elliot (1971).

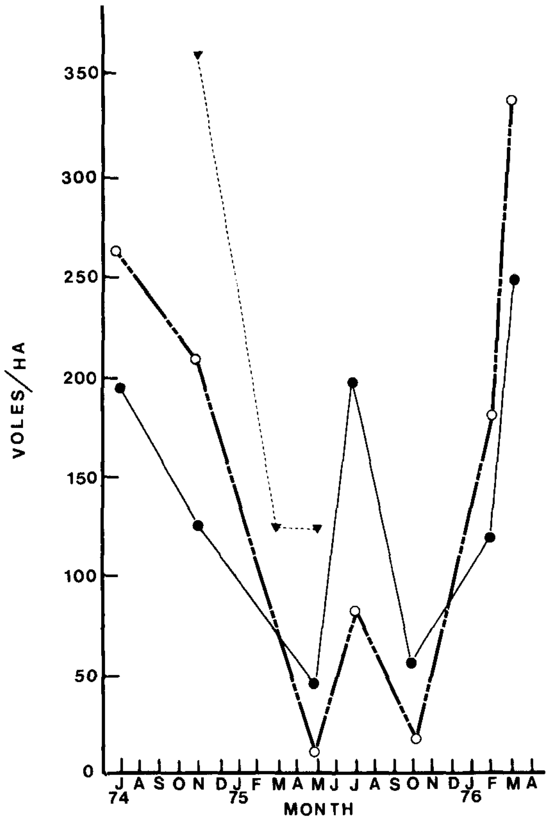

FIGURE 1. Changes in density of voles on shortgrass (open circles), old field (black circles), and straw (triangles) habitat types from June 1974 to April 1976.

RESULTS

CHANGES IN VOLE POPULATIONS WITHIN AND AMONG HABITATS

Statistical comparisons of vole densities among habitats were impractical due to large confidence limits on the Schnabel indices. However, the MNA and Schnabel estimates showed similar trends and values, so the Schnabel estimates were accepted as reasonable and are presented here to show trends and relative densities (Fig. 1).

We classified the various habitats into those with a density of at least 10 voles/ha (shortgrass, old fields and straw) and those with a density of at most 5 voles/ha. Substantial changes in vole population levels occurred on the habitats with high densities of voles. Numbers were high in the fall of 1974, declined over winter to a low level in the spring of 1975, increased moderately in the summer of 1975, declined to a low in the fall of 1975, and increased substantially over the winter of 1976 (Fig. 1). At times,

TABLE 1. Comparisons of mean densities (number per 100 ha) of Red-tailed and Rough-legged hawks among six habitat types in 1974–75 and 1975–76.[a,b]

Species of raptor	Habitat types					
1974–75	SG	OF	P	ST	PF	WW
Red-tailed Hawk (N = 47)[c]	3.8	2.5	1.7	1.6	1.0	1.0
1974–75	SG	ST	OF	P	WW	PF
Rough-legged Hawk (N = 47)	3.4	2.8	2.5	1.1	0.3	0.2
1975–76	SG	OF	P	PF	WW	
Red-tailed Hawk (N = 62)	1.3	0.8	0.3	0.0	0.0	

[a] Means joined by lines are not significantly different ($P > 0.05$).
[b] SG = shortgrass; OF = old field; P = pasture; ST = straw; PF = plowed field; WW = winter wheat.
[c] N = number of censuses.

the density of voles differed markedly among these habitats. The straw habitat was present only during the first year, and it had the highest density of voles during that time (Fig. 1). When vole numbers were high, the vole density on shortgrass was greater than on the old field habitats, but this difference was reversed at periods when voles were scarce (Fig. 1). Furthermore, the voles fluctuated in abundance on shortgrass much more than on old fields.

Within the remaining habitats, we never caught enough voles to obtain a Schnabel estimate. In 1974–75, the maximum MNA estimate in four trapping sessions in pasture was four voles/ha, but in 1975–76 no voles were captured on pasture. No voles were ever captured or seen on plowed fields or on fields with winter wheat.

HAWK DENSITY COMPARISONS

During 1974–75, the changes in densities of Red-tailed and Rough-legged hawks on each habitat were parallel from fall through spring. Thus, we compared densities across habitats using mean hawk densities for the three seasons on each habitat. Generally, in 1974–75, hawks of both species were significantly more numerous ($P < 0.05$) on the high-vole-density habitats than on the low-density habitats, but there were some exceptions (Table 1). Red-tailed Hawk density on straw was not significantly different ($P > 0.05$) from those on pasture or plowed fields, and Rough-legged Hawk densities on both old field and straw were not significantly different ($P > 0.05$) from pasture (Table 1).

For 1975–76, fall, winter, and spring curves of mean hawk densities were parallel for Red-tailed Hawks, but not for Rough-legged Hawks. Thus, for Red-tailed Hawks we compared densities across habitats as in 1974–75, whereas, for Rough-legged Hawks we compared across habitats within each season.

During 1975–76, Red-tailed Hawks were significantly more abundant ($P < 0.05$) on those habitat types (shortgrass and old field) that had high densities of meadow voles than on the three agricultural habitats (Table 1). However, there were no significant differences ($P > 0.05$) between shortgrass and old field nor among the three agricultural habitats. Rough-legged Hawks did not differ significantly ($P > 0.05$) among any habitats during fall (Table 2). In winter, Rough-legged Hawks were found only on the two habitats with high densities of voles. In spring, these raptors were significantly more abundant ($P < 0.01$) on shortgrass and old field than on any of the agricultural habitats (Table 2).

For both Red-tailed and Rough-legged hawks in 1974–75 and for Red-tailed Hawks in 1975–76, we compared densities across seasons by using the sum of the five habitat means within each season. The curves of densities of Rough-legged Hawks were not parallel in 1975–76, so for that period we used the habitat means for each season and compared the seasons within each habitat.

Red-tailed Hawks were significantly more abundant ($P < 0.05$) in fall than in winter 1974–75, but all other comparisons were not significantly different ($P > 0.05$). Rough-legged Hawks were significantly more abundant in winter ($P < 0.05$) than in fall and in

TABLE 2. Comparison of mean densities (number per 100 ha) of Rough-legged Hawks for five habitat types within each season in 1975–76.[a,b]

Season	Habitat types				
	SG	OF	WW	PF	P
Fall (N = 20)[c]	1.1	1.1	1.0	1.0	0.0
Winter (N = 22)	1.3	1.2	0.0	0.0	0.0
Spring (N = 20)	2.5	2.6	1.2	1.3	1.1

[a] Means joined by lines are not significantly different ($P > 0.01$).
[b] SG = shortgrass; OF = old field; P = pasture; PF = plowed field; WW = winter wheat.
[c] N = number of censuses.

TABLE 3. Comparison of seasonal mean densities (number per 100 ha) of Red-tailed and Rough-legged hawks in 1974–75 and 1975–76.[a]

Species of raptor	Seasonal mean densities (no./100 ha)		
Red-tailed Hawk (1974–75)	Fall (N = 16)[b] 2.5	Spring (N = 16) 1.7	Winter (N = 15) 1.4
Rough-legged Hawk (1974–75)	Winter (N = 15) 3.5	Spring (N = 16) 2.6	Fall (N = 10) 2.3
Red-tailed Hawk (1975–76)	Spring (N = 20) 1.0	Fall (N = 20) 0.4	Winter (N = 22) 0.2

[a] Means joined by lines are not significantly different ($P > 0.05$).
[b] N = number of censuses.

spring 1974–75, but fall and spring were not significantly different ($P > 0.05$; Table 3).

In 1975–76, Red-tailed Hawks were significantly more abundant ($P < 0.05$) in spring than in winter and in fall, but winter and fall densities were not significantly different ($P > 0.05$; Table 3). Rough-legged Hawk densities in spring 1975–76 were significantly higher ($P < 0.01$) than in fall and winter on old fields and plowed fields, but their densities in the latter two seasons did not differ significantly (Table 4). On shortgrass, densities were again higher in spring than in fall ($P < 0.01$), but they did not differ significantly between winter and spring or between fall and winter (Table 4). Densities did not differ significantly between any pair of seasons on pasture or winter wheat.

DISCUSSION

Hawks of both species generally distinguished between gross differences in prey densities among different habitat types in that they were more abundant on habitats with high numbers of voles. They did not, however, use different habitat types strictly on the basis of densities of voles. For example, both species of hawks were consistently more numerous on shortgrass than on straw or old fields, even though voles were most abundant on straw and often more numerous on old field than on shortgrass.

TABLE 4. Comparison of seasonal mean densities (number per 100 ha) of Rough-legged Hawks within each of five habitat types in 1975–76.[a]

Habitat types	Seasons: Spring (N = 20)[b]	Winter (N = 22)	Fall (N = 20)
Shortgrass	2.5	1.3	1.1
Old field	2.6	1.2	1.1
Pasture	1.1	0.0	0.0
Plowed field	1.3	0.0	1.0
Winter wheat	1.2	0.0	1.0

[a] Means joined by lines are not significantly different ($P > 0.01$).
[b] N = number of censuses.

The density of hawks in relation to prey populations may depend not only on the numbers of prey, but also on the vulnerability of the prey to predation. On the airport, vole density was correlated with total dry weight of vegetation (g/m^2), and the dry weight of vegetation did not differ significantly between shortgrass and old field habitats, whereas, the straw habitat had significantly higher dry weight than shortgrass, but not more than old field (Steele 1977). Therefore, using dry weight of vegetation as a measure of the total amount of cover, the straw habitat had more cover than shortgrass. In addition, radiotelemetric studies showed that voles in the straw habitat were most active along the rows of straw (Steele 1977). Finally, the vegetation was taller on old fields than on shortgrass, and both old fields and straw habitats had less bare ground than did shortgrass (Steele 1977). All these factors suggest that for a given density, it would be easier for the raptors to detect and capture voles on shortgrass habitat than on old fields or straw.

Craighead and Craighead (1956) also reported higher buteo densities on habitats with sparse ground cover even though vole populations on these habitats declined to lower densities than on other patches, which had a greater amount of cover. Tawny Owls (*Strix aluco*) captured more small mammals on patches with little ground cover (Southern and Lowe 1968), and Ferruginous Hawks (*Buteo regalis*) spent more time hunting on patches with sparser ground cover than on patches with both more cover and more biomass of prey (Wakeley 1978).

The pattern and amount of cover on the straw habitat may have affected Red-tailed Hawks more than Rough-legged Hawks and this difference may be related to differences in their hunting behavior. When foraging, Red-tailed Hawks perch more than Rough-legged Hawks (Schnell 1968, Baker 1977). There were no perches within the straw habitat and voles would be relatively immune to aerial predation unless they moved away from the rows of straw. If a vole did move into the open, a hawk hovering over the area would probably be more successful in capturing voles than would a hawk perched some distance away. Therefore, Rough-legged Hawks may have had better hunting success than Red-tailed Hawks in this habitat.

The number of voles on pasture, plowed fields or winter wheat was very low throughout the study, although both species of raptors did use these habitats in small numbers, particularly in 1974–75. Since hawks were more abundant in 1974–75 than in 1975–76, this suggests that the raptors may use areas of low prey density because of mutual interference on areas of high prey density. Mutual interference may have accounted for low densities of Redshanks (*Tringa totanus*) feeding on areas where prey was scarce (Goss-Custard 1970). Similarly, MacArthur and Pianka (1966) suggested that, as food becomes more scarce, predators such as buteos that spend more time searching than pursuing (Rudebeck 1950, 1951) should decrease the number of patches searched. Since the number of raptors declined as the number of voles declined (Baker 1977), we could not compare these two hypotheses.

It is possible that raptors seen in areas where voles were scarce were not foraging there. However, systematic observations of the birds indicated that they spent most of their time on the airport during daylight hours actively foraging. Foraging seemed to occur with equal intensity on habitats with both high and low numbers of voles. We found no evidence that the different habitat types provided differentially suitable daytime resting areas or shelter.

How predators determine which patches are the most profitable has not been established. Experimental studies of foraging in White-crowned Sparrows (*Zonotrichia leucophrys*; Simons and Alcock 1971) and Ovenbirds (*Seiurus aurocapillus*; Zach and Falls 1976b) have shown that predators learn to concentrate their search efforts on predictable high-prey-density patches on the basis of initial searches. On the airport, vole densities on each habitat were predictable, so once the hawks had found the profitable habitats, they continued to hunt on them. Densities of hawks changed significantly between seasons, but, with the exception of Rough-legged Hawks in 1975–76, these changes were parallel on all habitats. The exception occurred in the fall of 1975 when there were few Rough-legged Hawks on any habitat type.

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RECENT PUBLICATIONS

A Complete Checklist of the Birds of the World.—Richard Howard and Alick Moore. 1980. Oxford University Press, New York. 701 p. $49.50. For most families of birds, the ultimate authority on taxonomy, nomenclature, and distribution is the 15-volume *Check-list of Birds of the World* started by the late J. L. Peters and continued under several editors. Birders and most non-curatorial ornithologists, however, are content with a simpler reference, and indeed would prefer to have it as an affordable single volume. Several such works have been produced in recent years, among them those by Gruson and Forster (see *Condor* 78:279), Morony, Bock, and Farrand (see *Condor* 77:521), and Walters (see *Condor* 82:141). Here is yet another, perhaps overall the most useful one of the lot. It lists all living species of birds down to subspecific level and gives, briefly, the range of each subspecies. References are given for each family or subfamily, often in considerable numbers, inspiring confidence in the authors' ability to find their way through taxonomic jungles. Good typography and layout make for easy legibility, but one should watch for occasional misspellings. The index is a great asset because it includes specific names.

Edward Lear's Birds.—Susan Hyman. 1980. William Morrow and Co., New York. 96 p. $37.95. Lear's artistic career has been overshadowed by his popularity as the author and illustrator of limericks and nonsense verse. A painter and lithographer, he contributed illustrations to many zoological works, including the monographs of John Gould. Thanks to his talent and significant innovations, he became one of the finest and most important bird artists in European culture. This side of his life is the subject of the present book. A handsome, oversize volume, it provides a long biographical essay, concentrating on Lear's career as a naturalist and artist. It is lavishly illustrated, not only with bird plates, but also drawings for limericks and nonsense—one can hardly believe that the same man did both, their styles are so different. The color reproduction is first-rate. This book should be seen by those who enjoy fine bird art or study its history. Bibliography, index.

Atlas of Breeding Birds of the London Area.—edited by David J. Montier. 1977. Batsford, North Pomfret, VT. 288 p. $57.00. The summer distribution of all breeding birds in the London Area was mapped (on a 2×2 km grid) by a large corps of birders in a five-year project organized by the London Natural History Society. The results of that uniquely intensive survey are presented here. Each of the 120 species found is devoted a full-page map and page of text that discusses past and present breeding status and distribution. All phases of the project appear to have been carried out carefully and thoroughly. While this volume will chiefly interest those who had a hand in the work, it should be seen as a model for similar surveys elsewhere. Appendixes, references, indexes.

Birds of Karkar and Bagabag Islands, New Guinea.—Jared M. Diamond and Mary LeCroy. 1979. Bulletin of the American Museum of Natural History, Vol. 164, Art. 4. New York. 65 p. Paper cover. $4.30. Karkar and Bagabag are volcanic islands off the northeast coast of New Guinea. They "have been colonized by a very nonrandom sample of the New Guinea and Bismarck [Archipelago] avifaunas, and therefore afford an opportunity to obtain insight into the general problem of species differences in colonizing ability." This report first discusses the zoogeographic origin, species composition, species turnover, niche shifts, and other general features of the avifaunas. Species accounts then give measurements, information on habits, and remarks on taxonomy. The study is a valuable contribution to the ornithology of New Guinea. References.