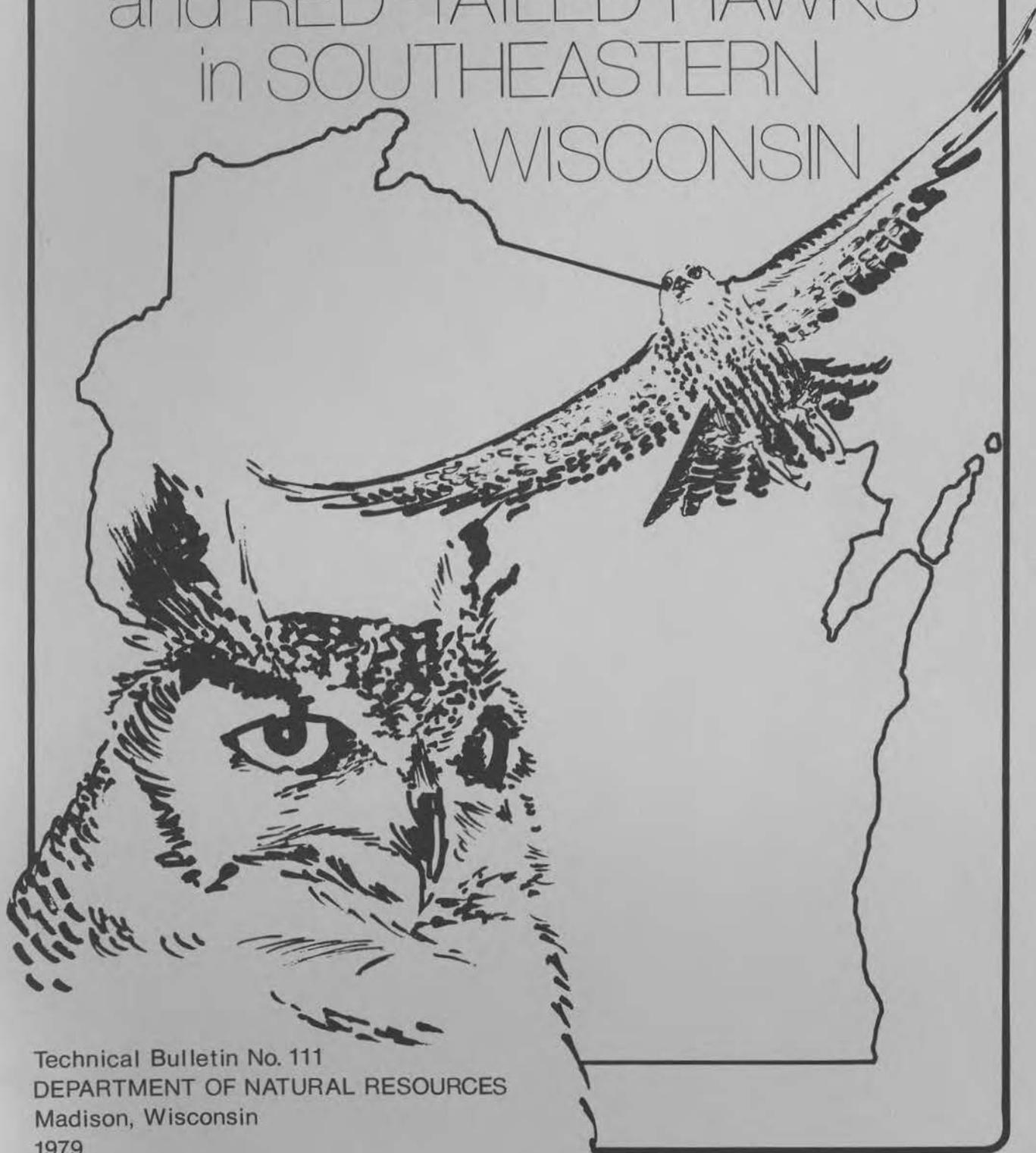


ECOLOGY of
GREAT HORNED OWLS
and RED-TAILED HAWKS
in SOUTHEASTERN
WISCONSIN



Technical Bulletin No. 111
DEPARTMENT OF NATURAL RESOURCES
Madison, Wisconsin
1979

ABSTRACT

During 1971-75, a study of great horned owls and red-tailed hawks was undertaken on a 8373-ha acre in southern Wisconsin (43° 10'N, 88° 50'W). The objectives of the study were: (1) to determine demography (numbers, distribution, and reproduction), food habits, and behavior of great horned owls and red-tailed hawks; (2) to examine the impact of these raptors on pheasants, cottontail rabbits, and small mammals; and (3) to formulate management practices that would possibly reduce predation on pheasants by raptors.

Great horned owl density was 1 resident pair per 7.5 km²; corresponding density of redtails was 1 resident pair per 4.1 km². The density of active (egg-laying) breeding pairs was 1 pair per 9.3 km² for horned owls, and 1 pair per 4.7 km² for redtails. Breeding results were 1.1 fledglings per resident pair of owls per year, and 1.3 fledglings per resident pair of redtails per year. Both raptors produced sufficient fledglings to replace lost resident adults and are maintaining population stability. The number of active pairs of horned owls (78% of the resident pairs) was related to cottontail abundance, while owl productivity was related to the combined index of staple prey. Any substantial reduction in staple prey numbers would therefore have serious consequences on great horned owl breeding success. There was little evidence to support the possibility that some owl pairs occupied territories of marginal quality. A comparison of cover within the home range of owl pairs to owl breeding success failed to show any direct relationship. Great horned owls nested predominantly in abandoned redtail nests, within the interior of large woodlots (> 15 ha), although owl preference for nesting sites was a factor of nest availability. Brood size in redtails appeared to be related to small mammal vulnerability (an index of mammal abundance plus the number of days with 10 cm or more of snow cover). Redtails nested near woodlot edges (< 30 m), without preference towards slope exposure. Self-regulated or territorial spacing between raptors pairs of the same species was found to occur for both horned owls and redtails, and regulated spacing between pairs of different species was suggested.

The year-round habitat cover preferences for great horned owls included upland and lowland hardwoods, tamarack swamps, marsh/shrub-carr, and miscellaneous cover. Owls used cover types of similar sizes during the different seasons, the average annual home range being 328.9 ha. Owls actually utilized only 40% of their maximum winter, spring, and fall home range, and 30% of their summer range. Owls hunt almost entirely from elevated perches, thus cover without available perches is not effectively used. Cover preferences of redtails included upland and lowland hardwoods, tamarack swamps, marsh/shrub-carr, and upland and lowland pastures. Average home range of redtails was 136.9 ha. Cover preferences of both raptors varied by season, sex, and breeding status. Differences in activity cycles between horned owls and redtails allow both species to coexist on the same area without adverse competition excluding one of the two raptor species.

Cottontails were the most important winter prey, followed by mice and voles. Food items utilized by raptors in spring were, in descending order, cottontails, pheasants, passerines, squirrels, and mice and voles. Populations of staple prey were relatively stable, especially the ring-necked pheasant. No responses were

observed in the number of raptor pairs to changes in prey abundance, although some dietary (functional) responses were noted. These dietary responses to population changes in staple prey in winter were primarily independently related to each other. Dietary responses in spring were somewhat directly related to the density of cottontails and pheasants, although a strong relationship with mice and voles was evident.

During winter, great horned owls removed 1.5% of the estimated 1 January pheasant population; while redtails removed a corresponding 2.3%. During spring, the 1 April pheasant population was removed at a rate of 12.2% by horned owls and 23.3% by redtails. The level of raptor predation upon pheasants to Waterloo was determined by weather conditions, particularly snow cover and spring rainfall, and by vulnerability of alternate prey species such as cottontails and small mammals. It appears that horned owls and redtails, along with other pheasant predators, depress the pheasant population below the carrying capacity of the habitat.

An original objective of the study was to remove horned owls and redtails from the study area to test for responses in the pheasant population to low predator densities. However, direct raptor removal was never attempted because: (1) a corresponding red fox removal phase was dropped due to changing attitudes towards foxes; and (2) direct raptor removal presented legal and economic restraints that questioned the value of a removal program as a logical management alternative.

Management efforts to reduce pheasant mortality caused by avian predators must include efforts to achieve maximum dispersal of winter-spring pheasants, and also a carefully planned program of habitat manipulation designed to reduce raptor-pheasant encounters. A number of management possibilities were considered, although they were based mostly on circumstantial evidence, as little field evaluation was accomplished. Management considerations were designed for state-owned lands within Wisconsin's pheasant range. The type of management practices to be considered is dependent upon whether the primary management objective of the wildlife area is wildlife production or maximizing public recreation opportunities. Management recommendations include: (1) selective removal of trees used by raptors as hunting perches; (2) establishment of tall, dense nesting cover to provide visual concealment for pheasants; (3) the placement of winter food patches near quality escape-roosting cover for pheasants; (4) avoiding the acquisition of poor quality pheasant habitat; (5) intensive management programs to benefit alternate prey staples of raptors; and (6) avoiding the stocking of pen-raised pheasants on wildlife areas where wildlife production is the primary concern.

Raptor predation on Waterloo pheasants appears to be in excess of the "surplus" population (those pheasants in excess of the carrying capacity of the habitat). Raptor predation therefore appears to be additive, rather than a compensatory form of mortality. Compensatory mortality implies that all pheasants above the carrying capacity of the habitat are surplus, and are doomed to die, if not from predation then from some compensatory form of mortality. Additive mortality implies the loss of pheasants below the carrying capacity of the habitat. Pheasant densities at Waterloo could maintain higher densities without predators, than with their presence.

ECOLOGY OF GREAT HORNED OWLS
AND RED-TAILED HAWKS
IN SOUTHEASTERN WISCONSIN

By
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Technical Bulletin No. 111
Department of Natural Resources
Madison, Wisconsin 53701
1979

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INTRODUCTION

Predation has long been recognized as a necessary natural element in the complicated systems of relationships by which life supports life (Gilbert 1970:i). Two avian predators found in Wisconsin, the great horned owl and the red-tailed hawk, have received considerable attention primarily because of their roles as predators of game animals. Various studies of these raptors have identified their staple prey as cottontails and small mammals (Errington 1932a, 1933, 1938; Errington and Breckenridge 1938; Errington, Hamerstrom, and Hamerstrom 1940) or cottontails and ring-necked pheasants (Orians and Kuhlman 1956).

In Wisconsin, studies of great horned owls and redtails have been linked to the need to determine the impact of these raptors on pheasant populations. The first Wisconsin study to quantitatively evaluate the predatory role of horned owls and redtails was that of Gates (1972). He concluded that great horned owls had a negligible effect on pheasant numbers on his Waupun Study Area in east

central Wisconsin (1972:425), but that redtails removed between 5% and 7% of the pheasants present. On a nearby study area at Waterloo, an intensive program of pheasant habitat improvement failed to produce a measurable increase in pheasant populations (Frank and Woehler 1969:809). Although the authors believed this was due to poor pheasant census techniques or limited habitat management, additional studies at Waupun by Gates (1971) and at Waterloo by Dumke and Pils (1973) indicated predation to be the limiting factor holding pheasant populations below environmental capacity. The logical sequel in examining the pheasant-predator relationship was, therefore, to investigate the identified pheasant predators.

During 1971-75, a study of great horned owls and red-tailed hawks was conducted within a 8373-ha area (WSA) that included the Waterloo Wildlife Area and surrounding private lands. Objectives of this study were: (1) to determine the demography (numbers, distribution, and reproduc-

tion), food habits, and behavior (seasonal and annual movements, habitat preferences, pair-bonds, relationships between successful and unsuccessful pairs, adult-juvenile interaction, hunting and roosting patterns, and inter- and intraspecific competition) of great horned owls and red-tailed hawks; (2) to examine the impact of these raptors on pheasants, cottontail rabbits, and small mammals; and (3) to formulate management practices that could conceivably reduce predation on pheasants by raptors. A fourth objective — to remove raptors from the study area to test for responses in the pheasant population to low raptor densities — was never attempted because: (1) a corresponding red fox removal phase was dropped due to changing attitudes towards foxes; and (2) direct raptor removal was evaluated as being neither legally nor economically feasible. A companion study dealing with the population dynamics and ecological facets of the red fox ran in conjunction with the raptor study.

STUDY AREA

LAND USE

My study area was expanded from the 6477-ha Waterloo Study area (WSA) originally used by Frank and Woehler (1969) and Dumke and Pils (1973). The WSA is located in Dodge and Jefferson counties, and is described in detail in Dumke and Pils (1973:3-4). Briefly, the WSA is rolling till plain, interspersed with southerly oriented drumlin hills and wetlands, composed of outwashed, gravel deposits. Elevation varies from 228 m to 305 m above sea level. Soils are developed from a discontinuous loess covering, glacial till, outwash, lacustrine deposits, and peat and muck of bogs, and are underlain by St. Peter sandstone and Prairie du Chien dolomite. Pre-settlement oak-savanna and wet prairie plant communities have been replaced by agricultural crops with dairy farming being the predominant land use.

The study area is a complex of state-owned (1285 ha) and private lands. Large, unbroken, seasonally flooded wetlands form the core of the study area, surrounded by agriculturally dominated uplands (Table 1, Fig. 1). Upland hardwood woodlots, dominated by red and white oaks and shagbark hickory, represent 4.5% of the total area. Lowland stands of white ash, American elm, and silver maple, and tamarack swamps represent 1.5% and 1.6%, respectively, of the area. Cropland, primarily corn and oats, occupies 56.0% of the land surface; pastures, 10.5%; and marsh/shrub-carr, 15.8%. Curtis (1959:353) considered shrub-carr to be a "... wetland plant community dominated by tall shrubs rather than alder with an understory intermediate between meadow and forest in composition...", a normal stage in the primary hydrosere succession. Dairy farming consists of the typical alfalfa-corn-oats cropping rotation. Cash crop farming in lowland sites, mainly for mint and sod production, has become increasingly important. Federally sponsored land retirement programs have virtually disappeared from privately owned lands, and non-cultivated areas outside of state-owned lands are commonly grazed (Fig.1).

CLIMATE

The study area lies about 48 km southeast of the 16- to 48-km wide



The Waterloo Study Area consists of privately owned, farmed uplands surrounding large blocks of state-owned wetlands. The interspersion of small upland and lowland hardwoods is ideal habitat for great horned owls and red-tailed hawks.

TABLE 1. Land use summary, Waterloo Study Area, 1975.¹

Land Use Types	Plant Indicators	Hectares	Percentage of Total Area
Cultivated lands	corn, oats	4 691	56.0
Pasture	grasses	876	10.5
Retired cropland (upland grass)	grasses, legumes	346	4.1
Marsh	sedges, cattails	1 069	12.8
Shrub-carr	dogwoods, willows	255	3.0
Upland hardwoods	oaks, hickory	376	4.5
Lowland hardwoods	ash, elm	124	1.5
Tamarack swamp	tamarack	138	1.6
Conifer plantation	pine, spruce	11	0.1
Strip cover ²	grasses	117	1.4
Miscellaneous ³		370	4.4
Total		8 373	99.9

¹ Land use data compiled from 1969-71 aerial photographs and ground checks (Martin, unpubl.)

² Ditchbanks (66.0 km), fencelines (32.5 km), roadsides (68.0 km), and railroad right-of-way (7.7 km).

³ Farmsteads, road pavement, gravel pits, and open water.

"tension zone" between the northern hardwood and prairie-forest floristic provinces (Curtis 1959:15-24). Climate of the WSA is typical of the prairie-forest province and is discussed in detail by Dumke and Pils (1973:4).

Weather data were obtained from the Watertown and Madison stations maintained by the National Oceanic and Atmospheric Administration (NOAA), Environmental Data Ser-

vice. Approximately 38% (31 cm) of the 82 cm of annual precipitation falls during the cold season. Snow covers the WSA approximately 95 d of the year, with the first 3 cm of snow on the ground by 27 November. Average annual snowfall is about 103 cm, and average annual temperature is 12°C; January temperatures average -9°C (Milfred and Hole 1970).

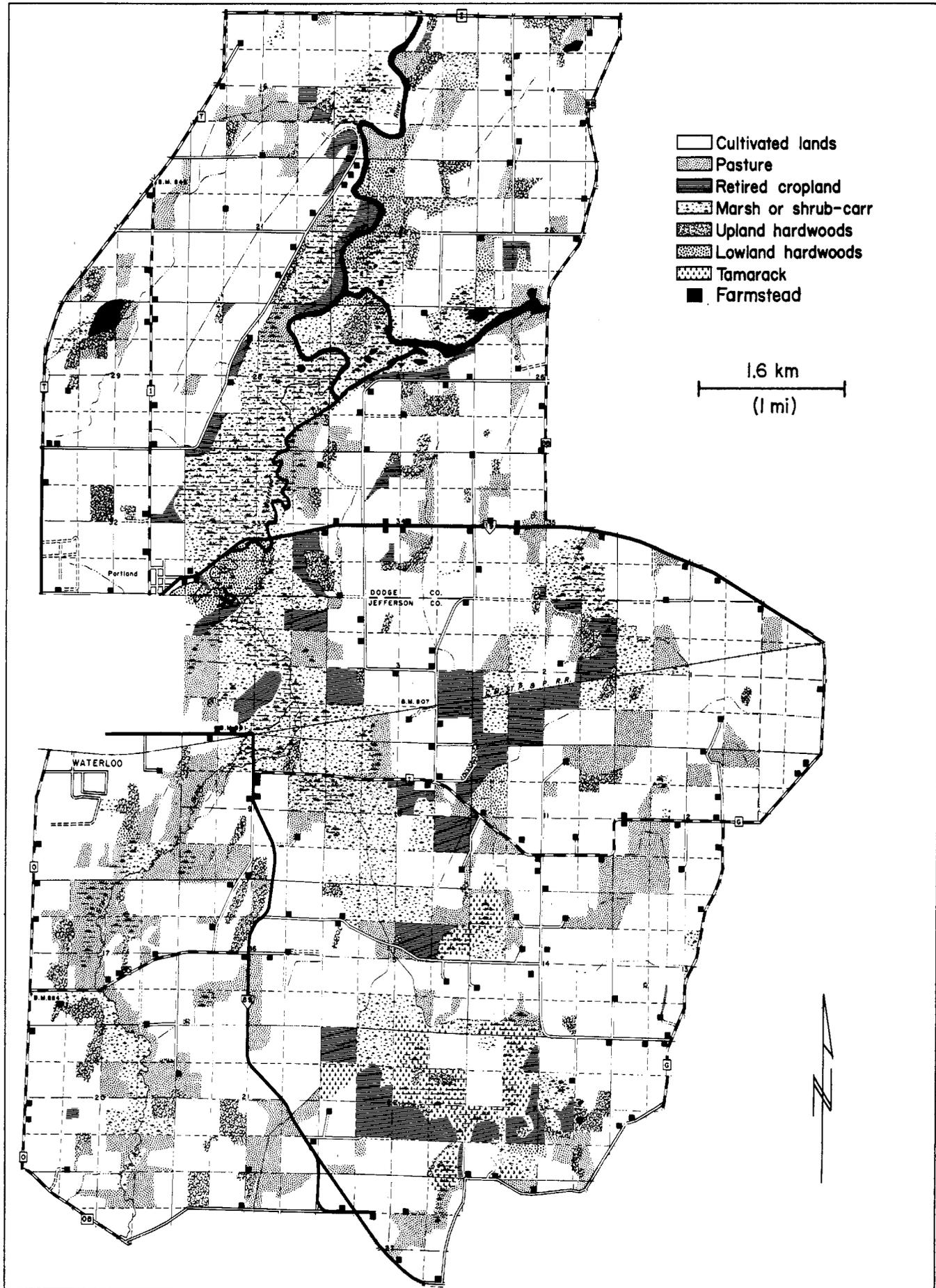


Figure 1. Land use patterns of the Waterloo Study Area.

GLOSSARY¹

To avoid the possibility of misinterpretation, breeding terminology has been taken virtually verbatim from Postupalsky (1974).

WINTER — the period, 1 January-31 March.

SPRING — the period, 1 April-30 June.

SUMMER — the period, 1 July-30 September.

FALL — the period, 1 October-31 December.

BREEDING TERRITORY — an area containing 1 or more nests within the range of 1 mated pair of birds. Each breeding territory indicates the known presence of a mated, territorial (resident) pair of potential breeders.

OCCUPIED NEST — a nest where (a) young were raised, (b) eggs were laid, (c) 1 adult was observed in an incubating position, (d) 2 adults were present on or near the nest regardless of whether or not it had been repaired during the season under consideration, and (e) there was evidence of recent repair (i.e., fresh sticks, as fresh boughs on top), droppings, and/or molted feathers on its rim or underneath.

OCCUPIED BREEDING TERRITORY — an area containing an occupied nest within the range of a territorial (resident) pair. Synonymous with occupied nest because by

definition there can be only 1 occupied nest per breeding territory.

UNOCCUPIED BREEDING TERRITORY — an area containing a nest or group of alternate nests at which none of the activity patterns diagnostic of an occupied nest were observed.

ACTIVE NEST (or ACTIVE BREEDING TERRITORY) — an occupied nest in which eggs have been laid. This category excludes pairs and subadults that establish territories and mate but do not lay eggs.

NON-ACTIVE NEST — an occupied nest in which eggs have not been laid.

PRODUCTIVE OR SUCCESSFUL NEST — an occupied nest from which at least 1 fledgling or fledgling-sized young is produced.

UNPRODUCTIVE OR UNSUCCESSFUL NEST, OR NEST FAILURE — an occupied nest from which no young fledged due to: (a) no eggs being laid, (b) eggs being destroyed or lost, (c) eggs failing to hatch, or (d) young hatching, but known to have died prior to fledgling.

MEAN BROOD SIZE — the number of young per productive or successful nest.

PERCENT NEST SUCCESS — the percent of occupied nests producing young.

PRODUCTIVITY — the number of fledglings or large young per occupied nest.

¹Listed in order of citation in the text.

METHODS

SEASONAL TIME PERIODS

The 4 traditional calendar seasons were used in this report: (1) winter, 1 January through 31 March; (2) spring, 1 April through 30 June; (3) summer, 1 July through 30 September; and (4) fall, 1 October through 31 December. These periods may not always have been the most appropriate choice biologically, nevertheless a standardized approach was essential since the raptor study was only one of several dealing with a variety of animals on the WSA. Use of calendar

seasons also facilitated comparison of WSA findings with other raptor literature.

RAPTOR SURVEY TECHNIQUES

Demography

Number and Distribution. Winter and spring great horned owl counts were made according to the techni-

ques described by Craighead and Craighead (1956:7-10,196-98). Great horned owls were actively courting by 1 January, hence territorial hooting was the principal method used to locate owls. Day-to-day hooting activity of courting horned owls was quite variable for individual pairs and was, therefore, not reliable as a sole census technique. I supplemented the hooting counts with daylight counts of owls in woodlots and at roosting site locations, and with observations of horned owls seen during other field activities. Baumgartner (1939:279) indicated that a nest count was the most



Woodlots were checked during the early spring for active raptor nests. Nests showing recent repairs were noted and later checked for incubating raptors.



All active raptor nests were examined to determine nesting success. These redtail nestlings are approximately 3½ wk old.

satisfactory method of estimating winter-spring horned owls. Nests found, however, do not provide an estimate of unsuccessful owls. Adult resident owls were believed to almost always form pair-bonds during the breeding season. Territorial hooting was thus especially useful for locating unsuccessful owls.

Helicopter surveys of owls were made during the first half of April in 1972-74. Great horned owls were particularly prone to flush from a helicopter flying 15-30 m above tree tops. A flight pattern in the form of a grid was used to systematically examine wooded areas suspected of harboring horned owls. Ground checks were subsequently used to check the efficiency of the helicopter survey, and to examine flush locations for possible nesting and/or roosting sites.

Winter red-tailed hawk counts were made by car as described by Craighead and Craighead (1956:7-10). A car was slowly driven on a standard road through the study area. Two observers tallied redtails seen within 0.8 km of either side of the road, along with data on activity (soaring, perching, defense, courtship), height, exposure, and a description of the area utilized by the hawk. Since the transect covered 62% of the total study area, redtails seen within the 0.8 km were multiplied by 1.60 to obtain a population estimate for the entire

WSA. Hawk counts by car were conducted at approximately 10 intervals from 1 December through 31 March.

Hoot censusing of horned owls and redtail censusing by car were discontinued after spring 1973 due to raptor population stability, and field observations were then used to monitor raptor populations. Since the predatory effect of horned owls and redtails was believed to be most severe during the winter-spring period (Dumke and Pils 1973:36), comparatively little raptor demographic and food habits data were collected during the summer-fall months.

Spring redtails were censused by nest counts, and by observations of paired and territory-defending (courting) adult redtails. Ground checks were made of known redtail nests and all WSA woodlots. Helicopter surveys to confirm nest activity were made after most redtails had finished laying. The helicopter proved especially useful for checking flooded areas in tamarack swamps and lowland hardwoods. It is believed that interference with incubating redtails was minimal, as they were extremely reluctant to flush unless the aircraft hovered directly overhead.

Spacing between great horned owl and red-tailed hawk nesting sites was examined using the "nearest-neighbor test" of dispersion (Clark and Evans 1954). That is, the distribution of dis-

tances from one active nest to its nearest active neighbor in any direction was compared to a distribution expected of randomly situated nests. Breeding territories were expected to be regularly spaced rather than randomly dispersed.

Reproduction. "Breeding" raptors are defined as those birds with established pair bonds that occupied a nest within a territory (Postupalsky 1974:25). "Active" raptors are territorial or resident pairs that laid eggs. Ground checks were made of raptor pairs until an active nest was found or until it became apparent that the pair would not lay. Preliminary work during the 1971 breeding season revealed that both horned owls and redtails were prone to desert as a result of human disturbance during early incubation. Once eggs hatched, desertion still occurred, but the probability of desertion was less. Craighead and Craighead (1956:239), Rusch et al. (1972), and Lattich, Keith, and Stephenson (1971) report nest desertion by horned owls and redtails because of human disturbance.

Active nests were examined only when a nestling could be observed, or when the incubation period was believed passed. Nestlings were banded with aluminum lock-on leg bands from the USFWS. Dead chicks and addled eggs were included in

counts of clutch size, and added eggs were collected for late determination of eggshell thickness. Nestlings were aged by length of the fourth primary (Petersen and Thompson 1977) and dates of clutch initiation, hatching, and potential fledging were calculated for each nest. When possible, a nest was checked more than once.

An "occupied breeding territory" is defined as an area containing 1 occupied nest and possibly 1 or more alternative nests within the range of 1 mated pair of birds. An "active" pair refers to territorial (resident) birds that have an "active" nest, or an occupied nest in which eggs have been laid. "Productive" or "successful nest" is an occupied nest from which at least 1 young fledged, or in which at least 1 young was raised to an advanced stage of development. Reproductive success or "productivity" refers to the number of fledglings (or large young) per occupied nest; it is the number of young produced per territorial pair, or the reproductive rate. Reproductive success is based on the entire territorial population of potential breeders.

Food Habits

Food habits of great horned owls and red-tailed hawks were determined from prey remains and pellets (castings). Food habits were expressed as percent biomass and percent composition. Prey remains were collected only during the winter and spring seasons (1 January to 3 June). Collections of summer-fall prey remains and pellets were unreliable indicators due to small sample size. Prey eaten by redtails were also identified from direct observation. During the breeding season, prey were collected from active nests and from tethered nestlings. Thus the diet of raptors reported here is restricted to winter and spring and is largely that of successfully breeding adults. Regurgitated pellets were also collected from adults of both sexes at roosting and hunting perches, and from nestlings in the nest or tethered.



Raptor nestlings were aged by measuring the length of the fourth primary. The aging allowed the calculation of hatching dates which could then be related to weather conditions or prey abundance.

The tethering techniques used were first described by Errington (1932b) and revised by Petersen and Keir (1976). Tethering was initiated at age 3-4 wk when adult brooding was no longer necessary to protect the nestlings from adverse weather. During 4 breeding seasons (1972-75), nestlings were tethered on elevated, screened, slatted-base platforms through the end of June. Platforms were visited 2 or more times each week to collect food remains and pellets, and to check the condition of the young. All prey remains and pellets were removed at each visit. In general, body weights of tethered nestlings steadily increased, which indicated that the adults were providing sufficient food. However, supplemental food was provided when weight losses in excess of 100 g over a 5-d span became evident. Birds showing losses of $\geq 15\%$ received supplemental feeding for a week prior to release to build up their strength.

Pellets were air-dried and their components identified by comparing them with a reference collection of the

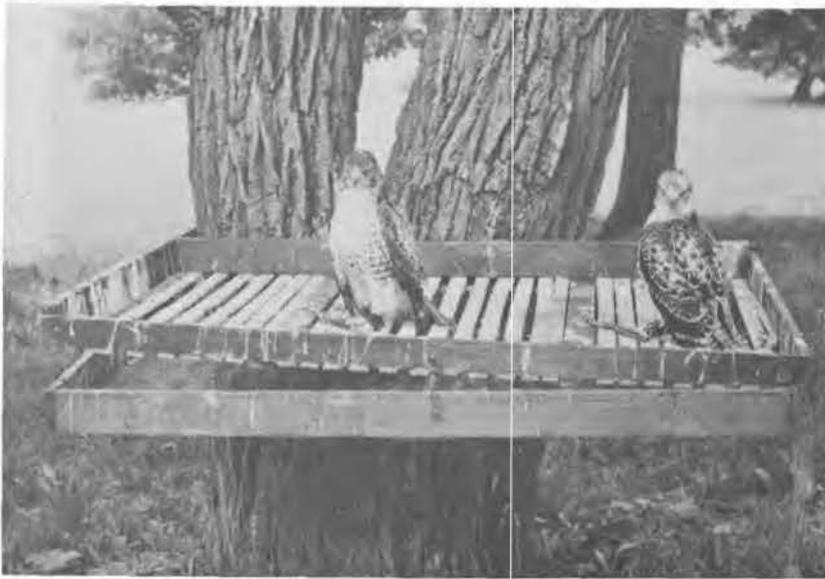
local fauna, and with specimens in the Zoology Museum, University of Wisconsin-Madison.

Great horned owl pellets are an accurate, durable, and easily collected source of food habits data (Craighead and Craighead 1956; Errington 1932b; Errington, Hamerstrom, and Hamerstrom 1940; Marti 1974). Hawk pellets present more problems because hawks digest bones more completely (Craighead and Craighead 1956; Errington 1933; Glading, Tillotson, and Selleck 1943). However, Fitch, Swenson, and Tillotson (1946) found that hawk food habits can be accurately determined only if one individual of a species was credited to a pellet (unless numbers of teeth and bones indicated otherwise).

Predation rate, the percentage of a prey population taken by a predator, has been used to indicate the impact of predation on individual prey populations (Craighead and Craighead 1956:311-26; Luttich et al. 1970:194-95; Rusch et al. 1972:286-87; McInville and Keith 1974:3-4), and represents an extension of raptor food habits data. While such estimates are crude, they do provide a realistic means of judging the impact of raptor predation.

Predation rates were calculated by first determining the seasonal food requirements of each of the two raptor populations at Waterloo. The winter season was 90, and the spring season was 91 d. Seasonal food requirements (in grams) for WSA horned owls and redtails were estimated by multiplying the daily food requirement by season length times the number of birds in the population. Craighead





Prolonged food habits were collected by tethering young raptors on elevated platforms. All tethered birds were released by the first of July.

and Craighead (1956:412) determined daily food requirements as a percent of body weight of food consumed daily. Mean body weights, determined from live-trapped resident birds, were 1850 g for female and 1400 g for male great horned owls, and 1350 g for female and 1150 g for male red-tailed hawks. Predation rates for individual prey species were calculated by multiplying seasonal food requirements of the two raptor populations times the percent biomass of each prey species in the seasonal diet. The product was then divided by the biomass for each prey species to obtain the number of animals taken over the seasonal period. A comparison of the animals taken to the total prey population available at the beginning of the period then yielded the rate of prey population removal by the avian predators during each season. The biomass killed was assumed to equal the biomass consumed.

Capture

Adult and free-flying juvenile great horned owls and red-tailed hawks were live-trapped for radio-tagging and color-marking. Trapping efforts concentrated on resident birds. Redtail trapping was avoided during migration periods. Trapping was done predominately during periods of snow cover from December through March, or during the breeding season near active nests with hatched young.

Modified prairie chicken traps (funnel-style) (F. Hamerstrom pers.

comm.), bal-chatris (Berger and Mueller 1959; Berger and Hamerstrom 1962), and Swedish goshawk traps (Meng 1971) were used for great horned owls during periods of snow cover. Dho-gaza sets (Hamerstrom 1963) and Swedish goshawk traps were used primarily during the breeding season. Owl trapping was discontinued by February to avoid potential nest desertion problems, and was resumed when nestlings were 3-4 wk old. Eight adult owls were live-trapped in prairie chicken traps and radio-tagged. No owls were trapped for color-marking.

Modified prairie chicken traps, modified automatic bow-nets (Tordoff 1954; Anderson and Hamerstrom 1967), bal-chatris, and noose carpets (Anderson and Hamerstrom 1967) were used to catch red-tailed hawks in winter. Hawks were trapped with bal-chatris and dho-gaza sets during the spring. Ten adult redtails were radio-tagged during the 4 yr. Nine birds were trapped with bal-chatris sets, 1 redtail with a dho-gaza trap, and 1 redtail was recaptured in a prairie chicken trap. Eight redtails were trapped with bal-chatris in winter for color-marking with fluorescent paints.

Traps were baited with either rock doves, domestic rabbits, starlings,

Leafy oak trees were a preferred roosting site for wintering owls. These sites were examined after the snow cover had melted to collect pellets for winter food habits.





Adult redtails were live-trapped primarily with bal-chattris baited with rock doves.



Swedish goshawk traps were also used to live-trap both hawks and owls.

laboratory mice and rats, hamsters, or dead domestic chickens. Laboratory mice and rats and hamsters were poor bait, as they were unable to cope with cold temperatures. Rock doves, captures by night-lighting from local farm buildings, proved the most effective bait. Pigeons were easily obtained, withstood temperatures down to -20°C , and were extremely durable.

Marking

Transmitters employed circuits described by Cochran (1967), with a Dunstan (1972) harness design. AVM model LA-12 receivers (AVM Instrument Co., Champaign, IL) were used with a dual-yagi directional antenna mounted on top of a 4-wheel drive vehicle. An AVM-design null-peak system was installed to provide a reading error of $\pm 1^{\circ}$, and eliminated false peak signals allowing for greater ease in triangulation (Heezen and Tester 1967). Transmitter design was a modification of designs described by Brander (1968) and Dumke and Pils (1973:43-45). Whip antennas (25.6 cm long) were initially of gold-plated steel guitar string, but were eventually replaced by the more durable Twist Flex (twisted strands of stainless steel of 0.55 mm diameter; Unitex Corp., Monrovia, CA). AVM Model SM-1 transmitters with Mallory (Tarrytown, NY), 1.35-V RM1CC (with taps) batteries, potted in dental acrylic provided a transmitter with a calculated life expectancy in excess of 900 radio-days. Analysis of telemetry data was limited to seasonal rather than monthly comparisons because the information from radio-tagged birds was quite limited.

Eight WSA redtails were color-coded with fast-drying fluorescent

spray paints ("Glowz" brand, New York Powder Co., Elizabeth, NJ) (Green pers. comm.; Keith 1964; LeDuc 1969) to test the feasibility of this technique in marking adult, resident redtails. At Waterloo, green, gold, and red paints or combinations of these colors were sprayed on the ventral surface of primaries and coverts, and on a dorsal and ventral rectrix tips of live-trapped redtails. A template with a 15-cm diameter circle, or a diamond of similar size, was placed on the underwing prior to painting to avoid excessive paint accumulation. Even though these paints were quick drying, they were used sparingly to prevent feather-matting problems that might interfere with flight.

Behavior

Behavior of adult and juvenile owls and hawks was studied by direct observation of radio-tagged and/or color-coded individuals. Behavior of several unmarked birds was also observed for short periods.

Locations of radio-tagged birds were periodically obtained through triangulation. Tagged birds were intensively monitored for a 8-hr periods, 1-3 times weekly. In addition, locations of color-marked birds were recorded whenever the birds were encountered. Home ranges was determined seasonally by the minimum-perimeter polygon method (Mohr 1974, expanded by Odom and Kuenzler 1955), i.e., outside points of a cluster of locations for an individual, were connected in such a way that all outside angles of the figure were convex. Territories are defined as a topographically localized, defended area (Hinde 1956). As the locations of an individual are often far from the

area which is actively defended, the home range must overestimate, to some unknown degree, the breeding territory of the pair. However, unless the number of locations is very small, the home range will completely contain the defended area.

The home range of each marked bird was cover-mapped, then each location was associated with a particular cover types utilized by and home, habitat use was then described by season.

Horned owls and redtails were separated into successful or unsuccessful females and successful or unsuccessful males (sexual breakdown only in redtails), on the basis of sex and breeding behavior. Actual ties to the nest or young were thought to have a considerable impact on the activities of a tagged raptor. Nesting raptors that failed to hatch their eggs or raise their young to fledging size adopted behavioral characteristics similar to non-nesting raptors, therefore unsuccessful and non-nesters were combined for comparison with successful nesters. Nesting influenced adult raptor behavior only during the breeding seasons. Birds were evaluated by sex only during summer and fall seasons.

I tested three hypotheses regarding seasonal movements and associated behavior:

The first hypothesis assumes no difference between the proportions of the various cover types within the minimum polygon home range and the proportions of radio-telemetry fixes within these particular cover types. Rejection implies that patterns of habitat use are nonrandom in regard to cover types within the home ranges. Chi-square was used as a criterion of the hypothesis.

A second hypothesis assumes no difference between the area of particular cover types of utilized by successful breeding raptors compared

Radio-transmitters with a hack-back harness system were used on both adult and juvenile raptors to gather information on behavior.



Color-marking redtails with fluorescent spray paints had limited use as an alternate marking system. Yellow (used in photo), red, and green paints were the colors tested.



to the area of the same cover types utilized by unsuccessful pairs. Rejection of the hypothesis suggests that the production of fledgling-size young depends on the presence of "essential" cover types within a home range. It has been suggested that quality of a breeding territory may influence breeding success, and that pairs holding marginal breeding territories would be expected to have lower reproductive success (Southern 1954; Lack 1966:144). Student's *t*-test was used as a criterion for accepting or rejecting the hypothesis.

My third hypothesis assumes no differences between the proportions of telemetry fixes in various cover types obtained for successful as compared to unsuccessful birds. The third hypothesis would demonstrate any habitat preferences (as indicated by Robel's et al. 1970:293 technique) by birds of a particular sex or nesting status. Chi-square was again used as a test criterion.

PREY POPULATION ESTIMATES

Small Mammals

Small mammals are defined as mammals ≤ 300 g. Population indices and species composition of small mammals were determined by using a snap-trap removal system developed at the University of Wisconsin-Madison (F. Iwen, pers. comm.). Each trap line consisted of 50 trapping stations 9.2 m apart. The size and shape of areas of homogeneous cover usually allowed traplines to be set in U-shaped patterns for ease in checking. Two lines were set out in each of the following cover types: corn, lowland hardwoods, upland hardwoods, tamarack swamps, upland grassland, and marsh/shrub-carr. Trap lines were run at 60-d intervals for 10 consecutive nights from September through May in 1972-75. A July survey was also run in 1974. Small mammal surveys totalled 114,000 trap nights (19 separate surveys).

Distance between trapping stations was paced and each trapping station marked by colored flagging. Trapping stations were selected without regard to the presence of rodent trails or burrows. All traps were baited with nonhomogenized peanut butter dis-



Radio-tagged raptors were intensively monitored at periodic intervals. Hand-held antennae were used to pinpoint roosting sites or to check on birds that failed to move for prolonged periods.



Small mammal traplines were set in a variety of cover types at Waterloo. Note the snap-trap in the foreground of photo. The trap was part of a trapline in a marsh/shrub-carr complex.

pensed from plastic catsup-and-mustard containers. The viscosity of nonhomogenized peanut butter was easily altered to meeting changing weather conditions by adding peanut oil (Smith, Chew, and Gentry 1969).

Victor "Holdfast" snap-traps manufactured by Woodstream Corp. (Lititz, PA) were used for small mammal surveys. Beginning with the September 1973 survey, rat traps were set in a 1:4 ratio with mouse traps to gain a better index to abundance of striped ground squirrels and eastern chipmunks. However, rat traps were not as effective in overall trapping ability as were mouse traps, and monthly adjustment factors were calculated so that pre-September 1973 surveys were comparable with later results. Adjustment factors were compiled from a proportional arrangement based on the 1:4 trap ratios.

Cottontail Rabbits

Cottontail density was determined from capture-mark-recapture activities at three selected sites on the study area. Densities derived from the sampled areas were used as an index to WSA cottontail abundance. Trapping was conducted in selected areas

where rabbit densities were sufficiently high to calculate statistically reliable population estimates using the regression analysis technique of Edwards and Eberhardt (1967). Densities were calculated in animals per hectare.

Cottontails were trapped during 8 fall (October-November) and winter (January-February) periods from October 1971 to January 1975. Three sites in upland hardwoods with brushy understory were trapped for 17,432 trap nights (Pils and Martin 1978). Spring densities were determined from a graphic extrapolation of the annual drop in cottontail levels between the fall and winter sampling period. WSA cottontail harvest estimates for 1967-74 were obtained from intensive interviews of study area hunters to provide a long-term rabbit index.

Ring-necked Pheasants

Pheasant population estimates used in this report were determined from data gathered by Woehler (unpubl.) who estimated pheasant population trends on the study area as part of a long-term pheasant habitat study (1968-74). He used sex ratios in winter multiplied by the number of triangulated crowing cocks in spring to

determine spring (1 April) estimates. Winter sex ratios were compiled from both December-March roadside observations and flush counts during beat-outs of winter cover units. Winter (7 December) estimates were obtained from summer-brood (number of young per hen) and intensive hunter-interview data (to determine pheasants harvested). This figure was expanded to represent the ensuing 1 January population. These surveys were designed to detract a 50% population change at the 90% level of probability.

ENVIRONMENTAL MEASUREMENTS

The severity of winter weather has been shown to influence pheasant survival (Gates 1971:24; Dumke and Pils 1973:37-38). Winter severity is measured by calculating a "winter hardness value" by combining average minimum temperatures and snow depth from 1 December to 31 March. The monthly minimum temperature is coded and multiplied by the sum of coded values for various snow depths. Monthly values are summed to provide an annual winter hardness index.

RESULTS AND DISCUSSION

RAPTOR DEMOGRAPHY

Raptor Numbers

WSA great horned owl and red-tailed hawk counts from December 1971 through spring 1973 revealed remarkably stable year-round populations of these raptors. Adult great horned owls and red-tailed hawks were present as paired residents throughout the winter and spring months. The winter-spring populations of these raptors can be looked upon as the resident populations since courtship actually began during the winter and the last redtail fledged by the end of June. Density of resident horned owls at Waterloo was 1 pair per 7.5 km². Corresponding density for redtails was 1 pair per 4.1 km².

Single great horned owls and red-tailed hawks were occasionally observed during the winter and spring. Field observations and radio-tracking suggested that these birds were probably juvenile transients, the so-called "floating population" (Craighead and Craighead 1956:16-17). In some cases, single raptors established short-term ranges but these areas were essentially undefended. Single horned owls and redtails were transient, elusive and seemingly not tied to any particular area, and little information was obtained on their numbers, food habits, or behavior.

The floating populations served as a source of replacements of lost residents. In early January 1974, the resident adult female owl of the Highway 19 pair died from transmitter harness problems. The male secured a new mate by the first week in March.

Great Horned Owls

Breeding Densities. Eleven to 12 pairs of great horned owls occupied

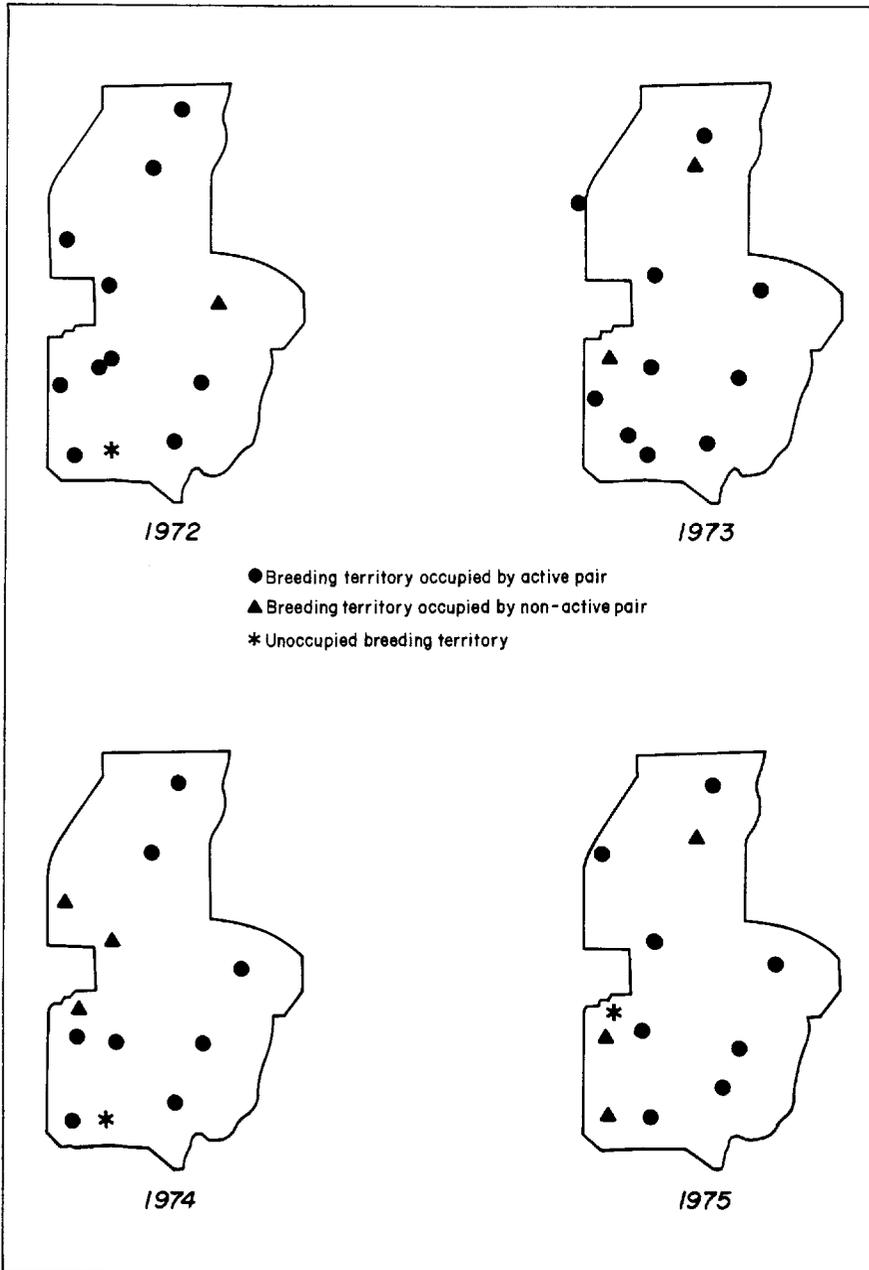


Figure 2. Locations of great horned owl nesting sites on the WSA, 1972-75.

TABLE 2. Great horned owl breeding summary for the Waterloo Study Area, 1972-75.¹

Year	No. Breeding Territories			No. Productive or Success. ²	Nests			Mean Brood Size	Productivity ⁴
	Unocc.	Occupied	Active		Percent Success	No. Unprod. or Unsucc. ³	Percent Unsucc.		
1972	1	11	10	10	91	0	9	1.6	1.5
1973	0	12	10	8	67	2	33	1.6	1.1
1974	1	11	8	7	64	1	36	1.7	1.1
1975	1	11	7	5	42	2	58	1.8	0.8
4-Year Average	0.8	11.3	8.8	7.5	66	1.5	34	1.7	1.1

¹ Nest containing 1, 2, and 3 young respectively, were: (1) 1972, 4, 5, and 1; (2) 1973, 4, 3, and 1; (3) 1974, 2, 5, and 0; (4) 1975, 1, 4, and 0.

² Number of productive nests per occupied breeding territory.

³ Number of unproductive and non-active nests per occupied breeding territory.

⁴ Number of fledglings or large young per occupied breeding territory or occupied nest.

breeding territories at Waterloo during the study (Table 2, Fig. 2). An average of 9.0 pairs per year occupied nests or laid eggs (one pair per 9.3 km²). These densities must be evaluated along with the fact that only 7.6% of the WSA was wooded. For comparison, breeding densities of great horned owls range from a pair per 1.3 km² (Errington, Hamerstrom, and Hamerstrom 1940) in the west-central region which is approximately 29% wooded (Wis. Dep. Nat. Resour. and North Central For. Exp. Stn. 1968:3) to a pair per 14.8 km² in the extreme southern portion which is 8% wooded (Orians and Kuhlman 1956:376). Gates (1972:427-28) found a mean density of < 1 breeding pair of owls per km² on the Waupun Area where 78% of the land was cultivated and only 0.3% was upland hardwoods. Craighead and Craighead (1956:214) reported a breeding density of one pair of horned owls to 13.7 km² in southern Michigan where 11% of the land was wooded. Breeding density reflects territory-size requirements (intraspecific intolerance) which are believed to vary with percent mature woodland cover; food supply was not found to limit populations size (Craighead and Craighead 1956:86).

River-edge wooded habitat in Kansas had a breeding density of 1 owl pair for 0.8 to 2.6 km (Baumgartner 1939). The owls hunted over the open prairie, consequently the breeding densities based only on river-edge timber may have been inaccurate. Olendorff and Stoddart (1974:52) studied raptors breeding in the short-grass prairie habitat of Colorado.

They reported that 80% of the cover used by nesting great horned owls was in creek bottoms. Horned owl breeding density in central Alberta (35% forested) ranged from 1 pair for 10.1 km² to 1 pair for 32.4 km² (McInville and Keith 1974:4). Apparently breeding densities depended upon the cyclic fluctuations in numbers of snowshoe hares, their major food, which is a result contrary to Craighead and Craighead (1956:86).

Prey Relationships. In response to increased prey abundance, owls show: (1) an increase in clutch size (Southern 1959; Lack 1966:141; Houston 1971); (2) earlier egg-laying dates (Lockie 1955; McInville and Keith 1974:6); and (3) an increase in the percentage of pairs breeding (Southern 1959; Lack 1956:141).

Mean clutch size of great horned owls at Waterloo, as determined by egg counts during late incubation and counts of owlets plus unhatched eggs (a minimum count), indicated little annual variability (range of 1.8-2.0 eggs, average of 1.9).

Mean clutch-initiation dates at Waterloo did not vary significantly between years: 23 February 1972, 8 February 1973, 15 February 1974, and 16 February 1975. The earliest clutch-initiation date was 29 January 1973 and the latest was 21 March 1972. Mean egg-laying period (number of days from the first clutch laid to the last) for all nests was 36 d, with a peak during the third week of February. I observed no owl re-nesting attempts.

Younger owls will breed when ample prey is available (Lack 1966:148;

McInville and Keith 1974:6). Lack (1947) found younger birds nested later and produced smaller clutches than older birds. I found little evidence that yearlings bred at Waterloo.

The Dunneison and Fuchs pairs (thought to be the same individual birds), which were the most consistent between years, initiated their nests between 13 and 26 February (4 yr) and 17 and 22 February (3 yr), respectively. Pairs less consistent between years were: Soldners pair, 29 January - 20 February (4 yr); Drager Conifers pair, 6 February - 27 February (3 yr); and Schneider pair, 28 January - 21 February (4 yr). Year-to-year clutch initiation dates for established breeding pairs showed no consistent chronological pattern.

The number of pairs actively breeding at Waterloo was significantly correlated with cottontail abundance at $P < 0.10$ ($r = 0.92$, $df = 3$). However, cottontail indices were not correlated with nest success or the number of young owls per occupied territory at $P < 0.10$ ($r = 0.55$, $r = 0.81$, $df = 3$). The staple winter prey of owls (in terms of biomass and caloric intake) was the cottontail rabbit, representing 62% to 71% of the biomass taken. In years with lower rabbit numbers (e.g., 1975), 3 of 12 pairs occupying breeding territories did not breed. Tawny owls in marginal territories also would not lay eggs during prey population lows (Lack 1966: 144-45; Southern 1970).

Productivity was not correlated *individually* with any of the 3 staple prey species — cottontails, pheasants or small mammals. A Kendall Rank



Owlets around 4 wk old were either tethered on platforms for food habits information or simply banded and returned to the nest.

Correlation Coefficient Test (Siegel 1956:213-23) was used to measure the relationship of owl productivity to a combined prey-abundance index. Each staple prey species was ranked by abundance (from 1 through 4) within each year of the 4-yr study period. The results were averaged by year to determine the combined prey-abundance index (1972-75 indices were 3.3, 3.9, 2.7, and 1.0, respectively). The combined prey index was found to be highly correlated with owl productivity ($T = +1.00$, $P = 0.042$, $r = 0.92$, $df = 2$). Therefore, while the number of great horned owl pairs which bred was directly related to only cottontail abundance, owl productivity was directly associated with the abundance of *all* the staple winter-spring prey species.

Productivity. Productivity was used as the common denominator for measuring raptor reproductive success. Great horned owl productivity on the WSA ranged from 1.5 (younger per occupied breeding territory) in 1972 to 0.8 in 1975. The mean productivity of 1.1 young was very similar to the 1.2 young observed by Orians and Kuhlman (1956:376) in extreme southern Wisconsin. Number of fledglings per nesting attempt (active pairs) at Waterloo averaged 1.5

(range 1.3—1.7). Young fledged per successful nest, or the mean brood size, was quite constant, ranging from 1.6 to 1.8, and averaging 1.7.

Any expression of reproduction success should logically consider all pairs occupying breeding territories whether or not they actually laid eggs. In 1975, a major segment of the breeding population, 33% of the 12 pairs of resident owls, were non-active. Orians and Kuhlman (1956:380) found that 24% of the great horned owl pairs did not lay eggs over a 3-yr period. At Waterloo, an average of 22% of the pairs did not lay.

Henny (1972:16) estimated the recruitment rate required for population stability in great horned owls at 1.47 fledglings per nesting attempt, or 1.73 fledglings per successful nest. The weighted recruitment rate was based on a nesting success of 78% of active nests calculated from published great horned owl nesting studies (Henny 1972:14). Henny's "recruitment standard" essentially ignores unsuccessful pairs, therefore the standard would be too high if taken to mean young per occupied nest (productivity). The error is not large for a population in which only a small and relatively constant proportion of pairs does not breed in any one year.

At Waterloo, the mean number of fledglings per nesting attempt was 1.46; 83% of the active nests were successful, yielding 1.70 fledglings per successful nest. Based upon Henny's (1972:14-16) standard, and the apparent stability in the number of occupied breeding territories on the WSA each year during 1972-75, the great horned owl population appears to be maintaining itself.

Mortality of Eggs and Young. I have little data concerning survival of young owls because nests were not inspected during incubation and early brooding to prevent nest desertion, and because of high percentage of nestlings were tethered (normally at age 4-5 wk) to obtain food remains and pellets (35 of 51 owlets tethered; 69%). Known losses of eggs and nestlings (Table 3) resulted from nest disintegration (4 eggs, 3 nestlings) and human interference (not by investigator) (2 eggs, 2 nestlings). In addition, 2 of 9 (22%) radio-tagged owl fledglings probably starved during late summer. Disintegration of nests most often occurred when breeding owls chose old squirrel or crow structures for nesting. First year mortality rates from banded nestlings has been calculated as 51% (Hickey 1952:116) and 40% (Stewart 1969:159). More recently, Henny (1972:15) has recalculated Stewart's data and obtained a first year mortality rate of 53% with shooting being the primary cause of death.

The extent of environmental pollutant contamination in great horned owl eggs as a possible mortality factor was not examined due to a small sample size. However, Seidensticker and Reynolds (1971:415) found that shell thickness of great horned owl eggs in Montana has actually increased in recent years. Similar results were obtained in California using eggshell weights (Hickey and Anderson 1968:272).

Nest Site Selection. The great horned owl is known for its wide adaptability in selecting nest sites. Owls have been reported nesting on the ground, on bare cliff ledges, in badger dens (Bent 1938:222), and even in a hollow log lying on the ground (Karalus and Eckert 1974:241). Bendire (1892) suggested that tree hollows were the preferred nesting site in Wisconsin before widespread logging. Large stick nests of redtails and other hawks now seem to be the preferred nesting sites in eastern North America (Errington 1932c:218; Baumgartner 1938:276; Orians and Kuhlman 1956:379; Hagar 1957:266). Twenty-four (69%) of the 35 WSA owl nests were in redtail nests. Fox squirrel nests (4), crow nests (4), and artificial or man-made sites (2) were also used



Great horned owls primarily used old redtail nests for nesting. The egg tooth can still be seen on the upper mandible of both owlets.



Artificial owl nests were constructed and placed in areas where suitable nesting sites were lacking. The life time of such nests was estimated at 15-20 y.

(Table 4). Great horned owls have also successfully used artificial nesting structures in Kansas (Conway 1972:19), and in South Dakota (Dunstan 1970:32).

I found no evidence to suggest that WSA great horned owls built or repaired their selected nests. Breast feathers, apparently from the incubating owls, were usually present in owl nests containing eggs. After hatching, prey debris and crushed pellets lined the nest bowl. No nest sanitation attempts by the adult owls were observed.

On the WSA owl nests were situated between 8.5 m and 21.3 m from the ground, with a mean of 12.9 m. Orians and Kuhlman (1956:373) reported a mean nest height of 17.4 m for the species.

Great horned owl nests were generally found in white (9) or red oak (7) trees; however, this was thought to be a reflection of redtail nest site preference. Other trees used for nesting were tamaracks (5), black cherry (4), white ash (4), shagbark hickory (2), and one each in silver maple, black willow, basswood, and aspen. Orians and Kuhlman (1956:373) found American elm as the preferred nesting tree even though the species was outnumbered by sugar maple and white oak. Dutch elm disease has virtually eliminated American elms at Waterloo. Although redtails have used dead elms for nesting, these trees were definitely not preferred sites for either raptor.

Slope (directional of nest sites did not differ significantly from a randomly selected sample of slope

TABLE 3. Mortality of great horned owl eggs and nestlings near Waterloo, Wisconsin, 1972-75.

Cause of Mortality	Number of Occurrences				Total	Percent
	1972	1973	1974	1975		
<i>Egg stage</i>						
Eggs falling from nest (nest disintegration)		2	2		4	36
Human interference ¹				2	2	18
<i>Nestling stage</i>						
Young falling from nest (nest disintegration)	1		1	1	3	27
Human interference ¹		2			2	18
Total	1	4	3	3	11	99

¹ Does not include investigator-caused mortalities.

TABLE 4. Nest types utilized by great horned owls at Waterloo, 1972-75.

Year	Redtail nest	Squirrel nest	Crow nest	Artificial nest	Nest of Unknown hawk	Total
1972	8		1		1	10
1973	6	3	1			10
1974	8					8
1975	2	1	2	2		7
Total	24	4	4	2	1	35
Percent	69	11	11	6	3	100

exposures, suggesting no exposure preference ($P > 0.10$, $\chi^2 = 10.2$, $df = 7$). Great horned owls did show a preference for nesting locations within the interior of woodlots (> 30 m from edge) when compared to open-grown trees, gallery forests, or woodlot edges ($P < 0.10$, $\chi^2 = 38.7$, $df = 4$). Hagar (1957:267) reported similar findings in New York.

Hagar (1957:267) suggested that owls preferred woodlots larger than 7.7 ha, usually composed of a mature deciduous forest with a scattering of conifers for roosting. At Waterloo,

owls primarily nested in the larger woodlots within their breeding territory, although again, I believe owl preference for nesting sites was influenced by nest availability. Some owl pairs had little choice when selecting suitable nests, while other pairs had 3 or 4 redtail nests to choose from within their territory. The mere presence of a redtail nest does not insure its use by breeding owls. In 1973, the Semrau pair selected a crow's nest (and were eventually unsuccessful), even though a well-constructed redtail nest was less than 3 m away.

Red-tailed Hawks

Breeding Densities. The WSA lies well south of the northern limits of the redtail winter range through central Wisconsin as described by Orians (1955:40). Redtails breeding at Waterloo were not observed to migrate in the fall. Resident redtails maintained pair-bonds and territories throughout the year, although territories were only defended during the summer and early fall. The spring and fall WSA redtail migrations were primarily over-flights, and only four migrant redtails were known to have established winter ranges. These wintering redtails migrated before courtship began in mid-February. Only one redtail in immature (brown tail) plumage was observed during the winter. Fitch, Swenson, and Tillotson (1946:205) and Craighead and Craighead (1956:217) observed redtails in California and Michigan as paired and permanent residents on definite hunting and nesting territories year-round, although territories again were only weakly defended during the summer and early fall. Evidence from Wisconsin (Orians and Kuhlman 1956: 372; Gates 1972:423) and central Iowa (Weller 1964:59) also indicated that wintering redtails remain in the same areas to nest.

The resident redtail population on the WSA showed little change over the 4 yr (Table 5, Fig. 3). The number of occupied breeding territories averaged 20.3, or 1 pair per 4.1 km². McInville and Keith (1974:6) observed a similar population stability in redtails over 5 yrs in Alberta. Craighead and Craighead (1956: 222) found little annual change in the number and distribution of a collective raptor population nesting in southern Michigan.

Recent evidence suggests an increase in redtail populations in the midwest over the past 20 yr. Migration counts in central North America have measured a 70% increase between the 1948-66 period and 1967-74 (United States Department of the Interior 1976:6-7). Also, the more adaptable and aggressive red-tailed hawks have replaced red-shouldered hawks as the dominant diurnal, breeding raptor on the Craighead's (1956) Michigan study area (Brown 1964:82; Postupalsky, pers. comm.). Henny and Wight (1972:243-44), however, found no change in redtail mortality or productivity based upon 1926-64 band recovery data.

In Green County, occupied breeding territories averaged 1 pair per 7.5 km² (Orians and Kuhlman 1956:376), in Dane and Columbia counties, 1 pair

Figure 3. Locations of red-tailed hawk nesting sites on the WSA, 1972-75.

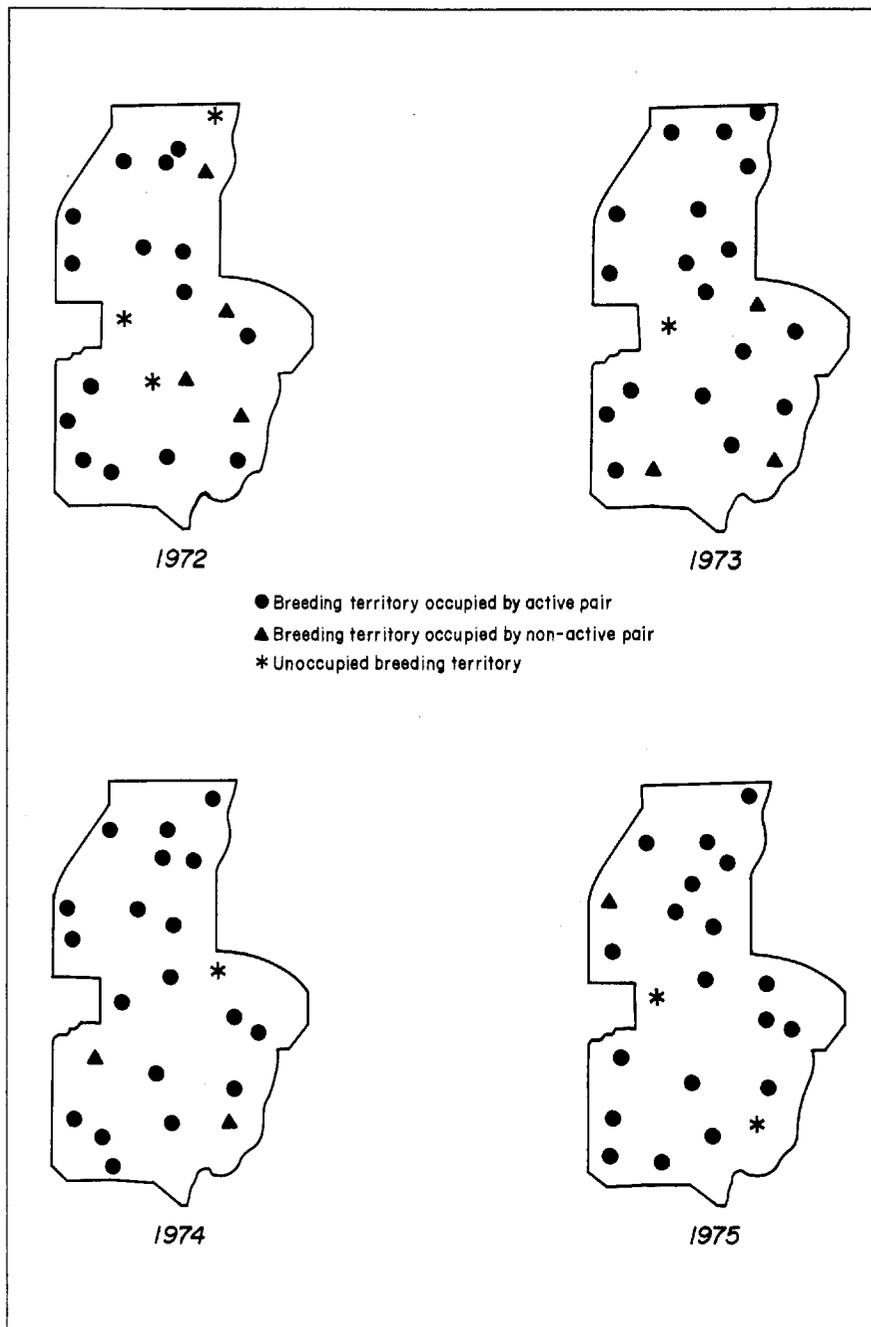


TABLE 5. Red-tailed hawk breeding summary for the Waterloo Study Area, 1972-75.¹

Year	No. Breeding Territories			Nests				Mean Brood Size	Productivity ⁴
	Unocc.	Occupied	Active	No. Productive or Success. ²	Percent Success	No. Unprod. or Unsucc. ³	Percent Unsucc.		
1972	3	19	15	10	53	5	47	1.8	1.0
1973	1	21	18	14	67	4	33	2.1	1.3
1974	1	21	19	18	86	1	14	1.9	1.6
1975	2	20	19	16	80	3	20	1.3	1.1
4-Year Average	1.8	20.3	17.8	14.5	72	3.3	28	1.8	1.3

¹Nests containing 1, 2, 3, and 4 young respectively, were: (1) 1972, 3, 7, 1, and 0; (2) 1973, 3, 7, 3, and 1; (3) 1974, 4, 12, 2, and 0; and (4) 1975, 11, 5, 0, and 0.

²Number of productive nests per occupied breeding territory.

³Number of unproductive and non-active nests per occupied breeding territory.

⁴Number of fledglings or large young per occupied breeding territory or occupied nest.

per 6.8 km², assuming winter populations equalled breeding populations (Kabat and Thompson 1963:24). In other states, occupied red-tail breeding territories averaged 1 pair per 7.2 km² in Michigan (Belyea 1976:20), 1 pair per 5.2 km² in New York (Hagar 1957:263), 1 pair 7.6 km² in Alberta (McInville and Keith 1974:6), and 1 pair per 8.7 km² in Montana (Johnson 1975:733). To the best of my knowledge, the highest reported density of breeding redtails was 1 pair per 1.3 km² in California (Fitch, Swenson, and Tillotson 1946:207).

Table 6 compares redtail breeding parameters from throughout North America. Percent of active breeding pairs ranges from 65% (New York, Hagar 1957) to 100% (Michigan, Craighead and Craighead 1956:214). The percent of active breeding pairs from almost all multi-year studies (≥ 2 years) strongly indicates that "normally" between 87% and 91% of resident, territorial pairs will breed each year.

Densities of redtails from extreme southern Wisconsin averaged an active pair per 8.2 km² (Orians and Kuhlman 1956:214), while Gates (1972:427) reported a pair per 10.6 km² in east-central Wisconsin. In New York (Hagar 1957:270), Alberta (McInville and Keith 1974:6), southern Michigan (Belyea 1976:20), and Montana (Johnson 1975:733), active breeding densities were 1 pair per 7.9, 8.5, 7.9 and 9.8 km², respectively.

Reproduction. Redtail clutch sizes and brood sizes were similar for the first 3 yr of the study (1972-74); in 1975 they were marked by smaller sizes. Mean clutch size varied from 1.8 (1975) to 2.3 (1973) eggs, while brood sizes ranged from 1.3 (1975) to 2.1 (1973) young. Mean WSA redtail

clutch (2.1) and brood size (1.8) were similar to the 6-yr mean clutch (2.1) and brood size (2.1) observed by McInville and Keith (1974:6) in Alberta. Mean annual WSA redtail clutch sizes were not significantly correlated with any staple spring prey population level ($P > 0.10$, $r = 0.18$ to 1.70, $df = 3$).

An index to prey vulnerability (abundance plus risk factors) during late winter was determined from the number of days with 10 cm or more of snow in February and March. It was hypothesized that breeding redtails were physiologically better able to produce larger clutch sizes when little snow cover was present during the late winter. The relationship between brood size and the prey vulnerability index approached significance at the 10% level ($P = 0.12$, $r = 0.88$, $df = 2$). McInville and Keith (1974:18-19) found a similar relationship between ability of great horned owls to nest (physiological condition) and prey vulnerability. Annual redtail brood size was only weakly correlated with the combined prey index ($P > 0.20$, $r = 0.80$, $df = 3$).

Mean dates of redtail clutch initiation were: 3 April 1972, 10 March 1973, 21 March 1974, and 30 March 1975. The earliest clutch initiation date was 2 March (1974); the latest 22 April (1975). The mean egg-laying period (number of days from the first clutch laid to the last) was 36 d, with the peak laying activity occurring during the third week in March. Little year-to-year consistency in clutch initiation dates was observed in breeding redtails thought to be the same individual birds each spring. Mean clutch initiation dates were directly associated with the number of days with 10 or more cm of snow in late winter (February and March). The two

variables were correlated at $P = 0.05$ ($r = 0.95$, $df = 2$).

The number of fledglings produced per occupied breeding territory ranged from 1.0 (1972) to 1.6 (1974), averaging 1.3. Redtail productivity was not significantly correlated ($P > 0.10$, $df = 3$) with a combined prey index ($r = 0.72$), cottontail abundance ($r = 0.77$), pheasant abundance ($r = 0.24$), or the index to small mammal abundance in May ($P > 0.10$, $r = 0.78$).

Productivity at Waterloo was higher than the 1.2 fledglings per occupied territory recorded in Green County (Orians and Kuhlman 1956:376), but was less than productivity reported by McInville and Keith (1974:6) and Johnson (1975:376) (Table 6).

Estimated "recruitment standard" rate for population stability in red-tailed hawks north of the 42° latitude was 1.33-1.38 fledglings per breeding age female, or 1.84 young per successful nest (Henny 1972:245). All breeding redtails were assumed to be at least 2 yr old, while about 22% of the territorial birds did not lay eggs and were assumed to be yearlings (Henny and Wight 1972:245). An inherent weakness in Henny's calculations is his assumptions that: (1) all adults breed, and (2) all non-breeders are yearlings. At Waterloo, all non-breeders possessed fully molted red-colored tails, indicating that they were at least 2 yr old (after the redtail aging techniques described by Hamerstrom 1971). "Recruitment standards" for redtails, therefore, are at best crude approximations and must be used with caution.

The number of fledglings produced per nesting attempt at Waterloo ranged from 1.1 (1975) to 1.8 (1974), averaging 1.5. Fledglings produced per successful nest averaged 1.8, ranging from 1.3 (1975) to 2.1 (1973). Even

TABLE 6. Comparison of red-tailed hawk breeding parameters.¹

Source (Area)	Years exam.	Density of resident redtails in km ² per pair		Percent Active	Percent occupied nests successful (range)	Percent active nests successful (range)	Brood size (range)	Productivity ² (range)
		Occupied terr.	Active breed. pairs					
WSA (Southern Wisconsin)	1972-1975	4.1	4.7	88	72(53-86)	81(66-95)	1.8(1.3-2.1)	1.3(1.0-1.6)
Orians & Kuhlman (1956)								
(Extrem. South. Wisconsin)	1954-1955	7.5	8.2	91	62(55-68)	67(64-70)	1.9(1.7-2.1)	1.2(0.9-1.4)
Gates (1972)								
(East-central Wisconsin)	1962-1964	unk.	10.6	unk.	unk.	65(50-78)	1.8(1.6-1.9)	unk.
Craighead & Craighead(1956)								
(Southern Michigan)	1948	19.2	19.2	100	100	100	0.8	0.8
Belyea (1976)								
(Southern Michigan)	1971-72,75	unk.	7.8	unk.	unk.	53(40-62)	1.4(1.1-1.6)	unk.
Hagar (1957)								
(SE New York)	1952	5.2	7.9	65	39	59	1.5	0.6
Seidensticker & Reynolds (1971)								
(South-central Montana)	1966-1967	unk.	unk.	unk.	unk.	50(unk.)	1.7(1.5-1.9)	unk.
McInville & Keith (1974)								
(Alberta)	1967-1971	7.6	8.5	89	unk.	unk.	2.1(1.9-2.5)	1.5(0.9-2.1)
Johnson (1975)								
(SW Montana)	1971-1972	8.7	9.8	88	53(53-54)	60(59-62)	2.5(2.3-2.7)	1.4(1.3-1.5)
Wiley (1975)								
(Southern California)	1973	unk.	unk.	unk.	unk.	74	1.6	unk.

¹Parameters for multi-year studies represent mean figures.

²Number of young per occupied breeding territory.

with the poor 1975 breeding season, the red-tailed hawk at Waterloo was reproducing at replacement levels.

Mortality of Eggs and Young.

Documentation of losses of redtail eggs and nestlings was also limited by the lack of nest inspection during incubation and early brooding, and by the number of redtail nestlings tethered for food habits study (30 of 101 fledglings tethered; 30%). A life-equation developed by Luttich, Keith, and Stephenson (1971:83) reported a 29% mortality for nestlings from hatching to 6 wk of age (near fledging), 11% from 6 to 10 wk, and 18% from 10 to 12 wk old.

Human interference (not by the investigator) was believed to be responsible for most redtail nest desertion, although the evidence was mostly circumstantial. Early incubation and the beginning of the spring farming operations coincided rather well. Red-tail nest sites along fencelines next to cropland seemed particularly vulnerable to human-caused desertion. The loss of eggs due to nest disintegration and predation (suspected to be crows) was slight (Table 7). The difficulty in documenting losses during the egg stage is also evident from the dearth of published material. Fitch, Swenson, and Tillotson (1946) reported investigator interference and predation by blue jays (which may also be the result of human interference), Luttich, Keith, and Stephenson (1971:77) cited investigator-caused losses, and Craighead and Craighead (1956:279) again indicated man as the leading cause of nest desertion.

A mean of 19% of the active redtail pairs failed to produce fledglings. Nestling mortality at Waterloo implicated starvation/fratricide and falls from the nest as the primary causes of death (Table 7). Starvation/fratricide, however, was only observed in 1975 when a continuing shortage of mammalian prey was apparent. Great horned owls killed 2 redtail fledglings in 1971; no other predation on young was observed during 1972-75. Luttich, Keith, and Stephenson (1972:82) disclosed predation as the leading cause of nestling mortality with horned owls the primary predator.

Myiasis, an infection of a blood-sucking, fly larvae of the genus, *Protocalliphora*, was commonly encountered on red-tailed hawk nestlings at the WSA. The maggots were observed in the ears of young at 46% of the successful nesting sites in 1974, and at 100% of the successful nests in 1975. Hamerstrom and Hamerstrom (1954) noted that these maggots are quite commonly found in several species of hawks and seldom cause permanent disabilities or mortalities of their hosts.



The widespread use of organic pesticides after World War II has been linked to the decline of certain raptor populations (Anderson and Hickey 1972). The weight and thickness of WSA redtail eggs were measured to provide an index to a possible raptor-pesticide syndrome. Compared to pre-1946 eggs (pre-pesticide) from Anderson and Hickey (1972), redtail eggs from Waterloo exhibited no signs of eggshell thinning. In fact, Waterloo redtail eggs were significantly heavier ($6.727 \text{ g} \pm 0.025$; $n = 5$) and thicker ($0.460 \text{ mm} \pm 0.094$; $n = 7$) than pre-1946 eggs ($P < 0.05$). Toxicants are acquired from prey consumed, therefore the level of pesticide contamination or resulting stress is dependent on the raptor's diet. Prey species high in the food chain contain greater concentrations of pesticides when compared to low-level or primary consumers, thus fish- and bird-eating raptors are more affected than raptors feeding primarily on herbivorous mammals and insects (Snyder and Snyder 1975:196). Redtails feed mainly on mammals, therefore it can be expected that their level of pesticide contamination would be low. Redtails in southern Wisconsin do not appear to have measurably suffered from pesticides.

Nest Site Selection. WSA red-tailed hawks usually began nest construction or repairs in late February to early March. Repairs were also ob-

served during mild January weather, and frustration nests (Postupalsky 1974:26-27) were commonly constructed after nesting failures. White oaks were used most frequently for nests (38%), followed by red oak (15%), black willow (13%), shagbark hickory (8%), white ash (7%), American elm (7%), black cherry (4%), soft maple (3%), catalpa (3%), and tamarack (1%).

To measure redtail nest site preference, sites were grouped into up-

land hardwoods (47 nests), lowland hardwoods (18), and tamaracks (1). A comparison between cover types with nests and the actual occurrence of that cover type showed little preference for tamaracks (1 nest per 138 ha), and equal preferences for lowland hardwoods (1 nest per 7 ha) and upland hardwoods (1 nest per 8 ha). Nine of 18 redtail nests found in lowland hardwoods were in woodlots, 6 were in gallery forests, and 3 were in open-grown trees. Comparable figures in upland hardwoods were 37, 3, and 7 nests, respectively. Woodlot nesting sites are believed to be preferred, although statistical significance could not be demonstrated. Average size of lowland hardwood stands with nests was 10.3 ha, compared to 2.6 ha for upland hardwood stands with nests. Overall potential nesting sites in lowland hardwoods were less available because of the smaller number of available lowland stands. Therefore, even though a larger number of red-tails nested in upland hardwoods, a preference for nesting in lowland hardwoods seemed to exist. The tree species used for nesting apparently were dependent upon availability, as significant preferences could not be demonstrated.

Redtails did not prefer a particular slope exposure ($P > 0.10$, $\chi^2 = 11.1$, $df = 7$). Breeding birds using woodlot nesting sites preferred woodlot edges ($< 30 \text{ m}$ from edge) ($P < 0.10$, $\chi^2 = 28.7$, $df = 4$). I believe a free avenue of approach is an important factor in nest site selection, and if birds nest in the interior woodlots, they are usually on the edge of small openings or in trees towering above the forest canopy. Tubbs (1974:127), commenting on the breeding biology of the common buzzard, the European ecological counterpart of the red-

TABLE 7. Mortality of red-tailed hawk eggs and nestlings at Waterloo, 1972-75.

Cause of Mortality	Number of Occurrences				Total	Percent
	1972	1973	1974	1975		
<i>Egg stage</i>						
Human interference ¹	6				6	26
Eggs falling from nest		2			2	9
Crow predation		2			2	9
<i>Nestling stage</i>						
Human interference ¹	2				2	9
Young falling from nest		2	2		4	17
Starvation/fratricide				5	5	22
Unknown			1	1	2	9
Total	8	6	3	6	23	101

¹ Does not include investigator-caused mortalities.



Redtails preferred to nest near the edges of woodlots, in sites that allowed a free avenue of approach for the adults to the nest.



Redtails typically constructed sturdy nests, the bowls usually lined with corn husks and cobs.

tailed hawk, stated: "... regularly used nests generally possess such obvious advantages as ease of access through the canopy, a reasonable field of view, and a degree of shelter. Thus, most such nests were located on the margin of a wood or on the edge of a substantial clearing...."

The typical redtail nest was located 15.5 m above the ground in a somewhat open tree, 20.2 m in height and with a DBH of 64 cm. Mean nest dimensions were 36 cm high, and 56 cm by 64 cm wide, Fitch et al. (1946:211) found that redtail nests varied in size according to the type of

support, with the larger nests built in the main forks of the tree trunk and smaller nests constructed far out on lateral branches, Fitch, Swenson, and Tillotson (1946:211) also felt "... some birds tend to build larger nests than do others...." Nests were constructed of twigs obtained from the surrounding trees, with the bowl having a mean diameter of 20.3 cm, and usually being lined with corn husks (sometimes even corn cobs). Green vegetation, usually newly emerging deciduous tree leaves and small branches or twigs of conifer, was found when young were present, perhaps for

nest sanitation. When flies were present during late May and early June, adults were observed removing uneaten prey from the nest.

Nest Arrangement

Clark and Evans (1954) characterized the spatial relationships among immobile objects as being either random, aggregated, or regular in distribution. In a completely random arrangement, the ratio (R) of observed to expected mean distances to the nearest neighbor is 1.0, for a completely aggregated dispersion $R = 0$, and in a completely regular distribution $R = 2.15$. A comparison of the annual dispersion of owls to owl nests, hawks to hawk nests, and raptors to raptor (nearest nest regardless of species) nests was used to test the hypothesis that regular distribution was characteristic of territorial raptors at Waterloo. McInville and Keith (1974:6-8), using the same procedure, found regular or territorial spacing (inter- and intraspecific) among great horned owls and red-tailed hawks in Alberta. At Waterloo, regular intraspecific dispersion was indicated among horned owls and among red-tails during 3 of the 4 yr (Table 8). From 1973 to 1975, the calculated ratios among WSA horned owls and redtails were significantly greater than 1.0 indicating a regular or territorial spacing ($P < 0.01$). Interspecific dispersion ratios between all active raptor nests were significantly regular only in 1974 and 1975 ($P < 0.05$). Failure to demonstrate regular distribution of all raptor nests during 1972 and 1973 can be partially attributed to: (1) the failure of dispersion calculations to consider non-active breeding raptors; and (2) the failure to use a common density-base so that all nearest-neighbor distances would be standardized to the greatest density of the area, i.e., the total owl and hawk pairs (to account for intraspecific interaction between the owls and the hawks). Spatial arrangement among birds (nests) is never random. In spite of the seemingly random dispersion during some years, territoriality among nesting horned owls and redtails did exist, and territorial interactions between owls and hawks were suggested.

TABLE 8. Dispersion of nests of great horned owls and red-tailed hawks near Waterloo, Wisconsin, 1972-75.¹

Species and Year	No. Nests	Mean distance in kilometers to nearest neighbor \pm standard error		Nest dispersion ratio R = A/B
		Observed (A)	Expected (B)	
<i>Great horned owls</i>				
1972	10	1.74 \pm .24	1.45 \pm .24	1.20
1973	10	2.17 \pm .77	1.45 \pm .24	1.50**
1974	8	2.40 \pm .23	1.63 \pm .31	1.47**
1975	8	2.96 \pm .42	1.72 \pm .34	1.72**
Mean		2.32	1.56	1.49
<i>Red-tailed hawks</i>				
1972	15	1.27 \pm .14	1.18 \pm .16	1.08
1973	18	1.71 \pm .14	1.08 \pm .13	1.58**
1974	19	1.45 \pm .14	1.05 \pm .13	1.38**
1975	19	1.58 \pm .14	1.05 \pm .13	1.51**
Mean		1.51	1.09	1.39

¹Dispersion ratios for all active nests of both species were: 1.08, 1.17, 1.24*, and 1.21* from 1972 to 1975, respectively. Asterisks indicate significant difference from a random distribution (* = $P < 0.05$; ** = $P < 0.01$).

TABLE 9. Small mammal abundance near Waterloo, Wisconsin, 1972-75.¹

Survey	All species	Captures per 1 000 Trap Nights			
		Meadow vole	Deer mouse ²	Cinereous shrew	Giant mole shrew
1972					
January	25.0	0.8	18.8	4.7	0.8
March	17.3	0.8	6.7	7.7	0.8
May	14.0	4.8	6.0	0.3	0
July	NA	NA	NA	NA	NA
September	136.7	10.2	59.0	27.0	24.3
November	131.3	9.3	81.3	17.3	14.0
1973					
January	46.8	0.8	32.2	13.2	0.5
March	14.5	0.8	11.2	2.3	0
May	57.8	16.7	16.2	17.3	2.5
July	NA	NA	NA	NA	NA
September	122.6	19.2	30.8	29.0	26.0
November	106.7	6.5	45.4	26.3	12.7
1974					
January	14.0	4.2	3.8	5.6	0
March	20.0	3.3	7.7	7.7	0.2
May	45.0	10.0	7.9	22.9	0.8
July	84.2	13.3	22.3	21.0	20.0
September	104.4	11.9	20.2	25.8	34.8
November	85.2	7.3	41.0	13.1	19.0
1975					
January	31.9	1.5	12.3	12.3	1.9
March	11.7	0.6	1.9	5.4	1.5
May	9.0	1.3	3.1	3.5	0.4

¹Each bimonthly index represents 6 000 trap nights in 6 different cover types: upland hardwoods, lowland hardwoods, tamaracks, marsh/shrub-carr, retired cropland (or permanent pasture), and cropland.

²Northern white-footed mouse and prairie deer mouse combined.

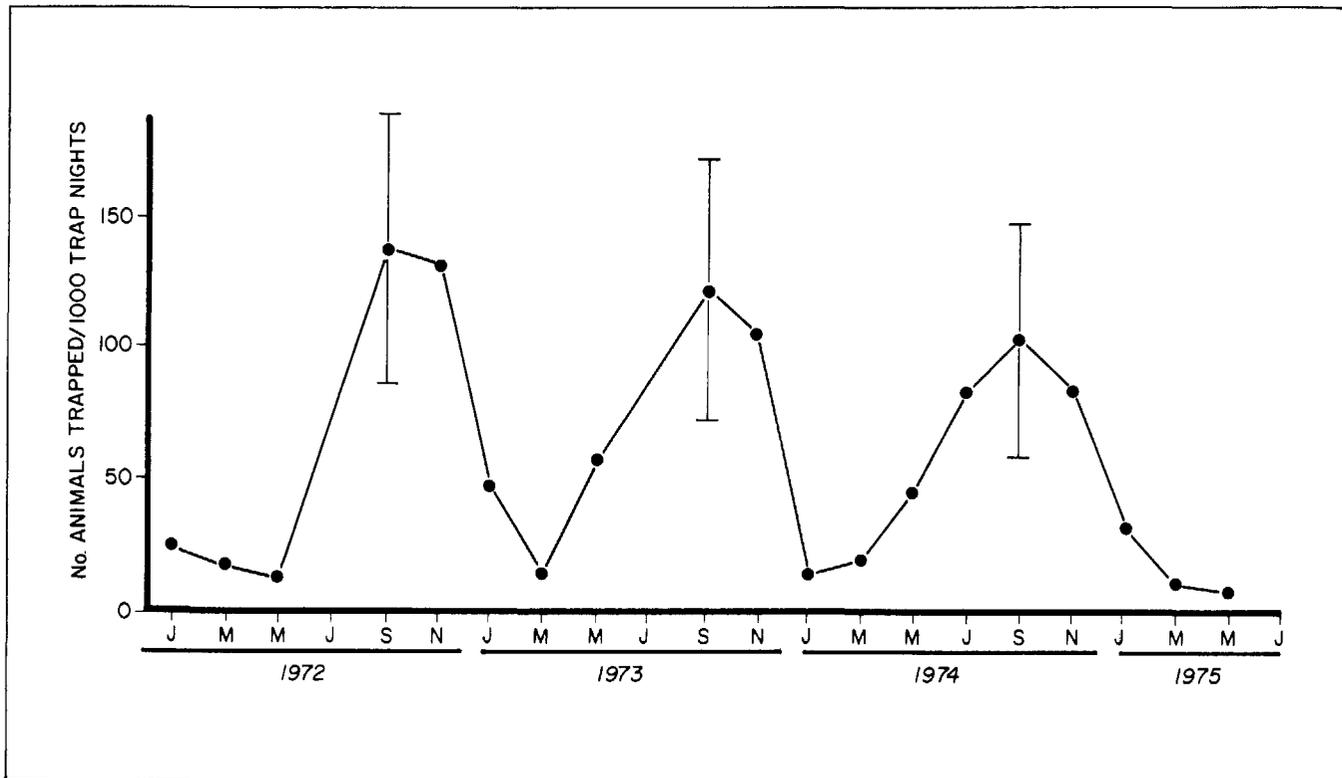


Figure 4. Indices to and 95% confidence limits ($df = 9$) for abundance of small mammals on the WSA, 1972-75.

RAPTOR FOOD HABITS

Prey Populations

Small Mammals. A total of 6470 small mammals was captured during 1972-75. An annual cycle in small mammal abundance was observed (Fig. 4), with annual highs consistently occurring during September, and lows in January (1974), March (1973), and May (1972 and 1975). While annual cycles were readily evident in the small mammal indices, no multi-year cycle, such as the 4-yr cycle reported by Hamilton (1937) in meadow voles, was noted for an individual species or for all small mammals combined. The WSA study may have been too short (3.5 yr) to observe such long-term cycles. Also, since small mammals were sampled at 60-d intervals, it was possible for some peaks or lows to have occurred at other times than indicated. Numerically, the annual highs as well as the lows were similar (Table 9). Confidence intervals at the 95% level ($df = 9$) for the annual highs were calculated using the days of the 10-d trapping period as replications (Fig. 4).

Twelve small mammal species were captured. In order of decreasing abun-

dance they were: northern white-footed mouse, prairie deer mouse, cinereous (or masked) shrew, giant mole shrew, meadow vole, southern saddle-backed shrew, Hudsonian meadow jumping mouse, house mouse, striped ground squirrel, eastern chipmunk, Franklin's ground squirrel, and Hanson's harvest mouse. Due to difficulties of making positive identification of skeletal remains in raptor pellets, abundance indices of northern white-footed mice and prairie deer mice were combined. Biomonthly indices for the four most abundant species are given in Table 9.

Deer mice were found in all cover types (40% of animals trapped), but were most abundant in areas containing woody vegetation (Table 10). Upland grasslands and marsh/shrub-carr were used to a lesser extent. Northern white-footed mice are seldom found more than 15 m from woods (Jackson 1961:217). Prairie deer mice prefer open areas and are more plentiful in sparse grassy cover (Jackson 1961:214) such as the cornfields sampled on WSA.

Meadow voles ranked only fourth in abundance (11% of total small mammals trapped), but were the most important small mammal prey species of raptors. Jackson (1961:231) observed that voles prefer rank growth of grasses chiefly in lowland fields and

meadows. At Waterloo, meadow voles were decidedly more abundant in upland grassland and marsh/shrub-carr cover types (Table 10). Although meadow voles are found in wooded areas, their abundance is related to the amount of graminoid cover present (Getz 1961).

Meadow jumping mice represented only 3% of the 6470 animals trapped at Waterloo. Jumping mice hibernate from the first heavy frost in the fall until warmer weather in late spring (Jackson 1961:264). Burt (1957:136) reported that this species prefers moist grassy habitat. At Waterloo, however, it was more frequently trapped in well-drained grassy areas (Table 10).

House mice were trapped only during the July through November surveys and then only represented 2% of the catch. The species inhabits almost every county in Wisconsin (Jackson 1961:258), but at Waterloo, it apparently was unable to withstand the winter weather except near human habitations. House mice comprised 80% of the small mammals trapped in weedy cornfields and were captured most frequently during the late summer and fall.

The cinereous shrew ranked second in abundance on the WSA, and represented 24% of the small mammals trapped. It is a highly active

TABLE 10. *Distribution (in percent) of rodent species trapped among six cover types, Waterloo Study Area, 1972-75.*

Species	Upland Hardwoods	Corn	Lowland Hardwoods	Tamaracks	Upland Grassland	Marsh/shrub-carr
Deer mice	16	20	25	23	7	9
Meadow voles	T	2	3	13	39	42
Jumping mice	T	12	8	12	54	15
House mice	—	80	3	T	12	4
Cinereous shrews	1	1	17	25	23	33
Saddle-backed shrews	—	—	T	16	5	77
Giant mole shrews	2	3	12	13	36	34
Other species	24	39	5	10	22	—

animal (Jackson 1961:28) that displayed considerable variation in seasonal abundance at Waterloo (Table 9). Hoffmeister and Mohr (1957:56) recorded the cinereous shrew's diet as chiefly insects, snails, and worms which might account for the infrequency with which it was trapped during late winter and early spring at Waterloo. Cinereous shrews were commonly caught in every cover type except upland hardwoods and cornfields.

The southern saddle-backed shrew, a close relative of the cinereous shrew, was much more abundant (4%) than expected for an animal more commonly found in northern Wisconsin (Burt 1957:56). The saddle-backed shrew prefers tamarack and marsh/shrub-carr.

Another insectivore trapped at Waterloo was the giant mole (short-tailed) shrew. Hoffmeister and Mohr (1957:60) observed giant mole shrews in close association with woody vegetation, although grassy areas near woods were also used. At Waterloo, 15% of the trapped animals were shrews, predominantly in upland grasslands and marsh/shrub-carr vegetation.

Eastern chipmunks and thirteen-lined ground squirrels, while considered potentially important raptor prey items, were seldom trapped (0.4%) even though rat traps were used in 11 out of 19 bimonthly surveys. I noted that the thirteen-lined ground squirrels occurred predominantly in grassy roadside cover, which was not adequately sampled. Eastern chipmunks, while quite abundant in some upland hardwoods, apparently were not captured by the rat traps set at Waterloo (0.1/1000 trap nights). March 1976), using similar techniques, caught eastern chipmunks more frequently (8.4/1000 trap nights) in south central Wisconsin woodlots.

TABLE 11. *Small mammal captures per 1 000 trap-nights by cover type on the Waterloo Study Area, 1972-75.*

Cover Type	1972	1973	1974	1975*	Mean 1972-74
Upland hardwoods	35	26	27	5	29
Corn	78	59	14	11	50
Lowland hardwoods	76	66	64	18	69
Tamaracks	87	66	79	28	77
Upland grassland	92	76	83	17	84
Marsh/shrub-carr	91	124	85	28	100
Mean	76	67	59	18	67

*Included January, March, and April surveys only.

TABLE 12. *WSA cottontail abundance indices, 1967-74.*

Year	Harvest Factor ²	Cottontail Density ³ (no./ha)		
		Fall ¹	Winter	Spring
1967	1.12			
1968	0.75			
1969	0.73			
1970	0.62			
1971	0.69	8.7		
1972	0.89	11.0	6.8	8.7
1973	0.82	7.2	9.5	9.0
1974	0.17	3.5	3.8	3.7
1975			3.1	3.1

¹ From Pils and Martin (1978:30). The two indices are correlated at $P < 0.10$, $r = 0.90$, $df = 3$.

² Number of cottontails harvested/total hunter-days.

³ Surveys not conducted in 1967-70.

TABLE 13. Ring-necked pheasant populations on the Waterloo Study Area, 1968-75.¹

Year	Spring Population		Winter Population	
	Total No.	No. per km ²	Total No.	No. per km ²
1968	757	9.0	1 393	16.6
1969	867	10.3	1 147	13.7
1970	602	7.2	1 481	17.7
1971	841	10.0	1 190	14.2
1972	860	10.3	1 295	15.5
1973	695	8.3	1 270	15.2
1974	747	8.9	867	10.4
1975	527	6.3	—	—
Mean				
1968-71	767	9.2	1 303	15.6
1972-75	707	8.5	1 144 ²	13.7

¹Data from Woehler (unpubl.).

²1972-74 mean only.

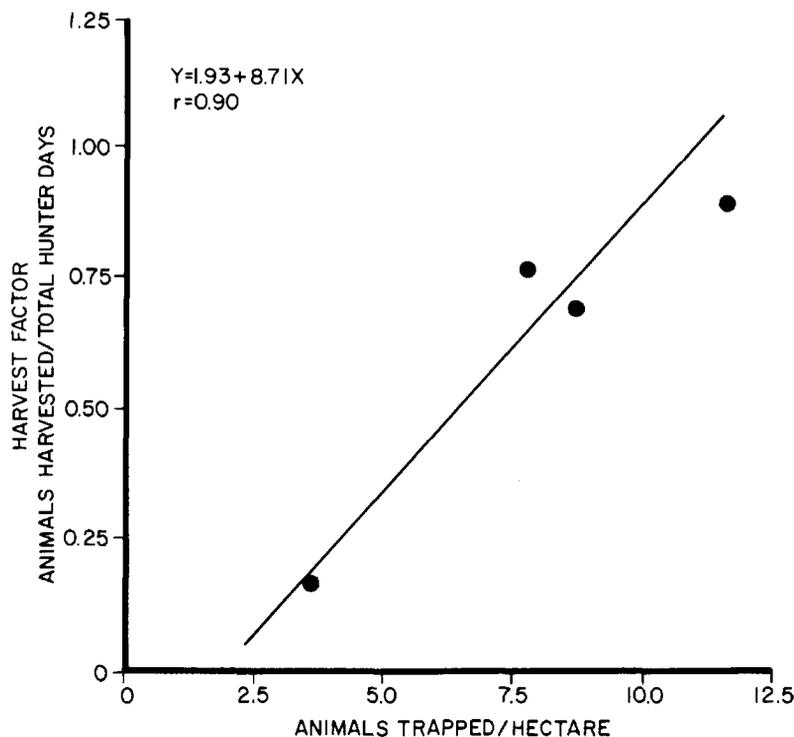


Figure 5. Relationship of WSA fall cottontail abundance indices to harvest (kill) factor, 1972-75.

In sum, there were pronounced variations in small mammal abundance among cover types (Table 11). Upland hardwoods and cornfields generally had low small mammal indices throughout the study, whereas upland grasslands and marsh/shrub-carr continually had high rodent indices. Numbers of small mammals within a cover type were generally stable between years, except for small mammals in cornfields. This may have been due to plowing and other agricultural practices which would periodically disrupt the habitat from a small mammal's point of view.

Cottontail Rabbits. A total of 331 individual cottontails, with 724 recaptures, were taken on the 3 selected upland hardwood trapping sites (Pils and Martin 1978:31). A mean fall density of 8.1 cottontails per ha was similar to the 8.9 cottontails taken per ha during the fall at a 34.6-ha woodlot in southwestern Wisconsin (Trent and Rougstad 1974:459).

The fall-winter live-trapping index, expressed as "mean cottontails per ha", was correlated with WSA cottontail harvest estimates (number of rabbits harvested per total hunter-days) at $P < 0.10$ ($r = 0.90$, $df = 3$) (Fig. 5; Table 12). Harvest factors were used as the most reliable long-range index to cottontail abundance. Over the 1967-73 period, cottontail abundance ranged from 0.62 to 1.12 rabbits per ha (mean of 0.80). A relatively severe cottontail decline occurred in 1974, when the harvest factor fell to 0.17 rabbits per ha. Mean number of cottontails live-trapped per ha in 1974 was 3.5, compared to a mean of 9.2 (range = 7.2-11.6) during the previous 3-yr span.

Ring-necked Pheasants. Pheasant population estimates were available from 1968 through the spring of 1975. The 1972-75 spring and winter population means declined 8% and 12% respectively, from the 1968-71 means for spring and winter (Table 13). The decline resulted from abnormally low 1974 winter and 1975 spring pheasant populations. An average 1974 spring density indicated that a severe decline occurred from 1 April 1974 to 7 December 1974. The 1974 pre-hunt pheasant population (1 October 1974) was reported by Woehler (unpub.) to be also abnormally low. The 1974 pheasant decline must have resulted from factors operating during the spring and summer seasons. The most reasonable explanation was that the continued inundation of wetlands in the spring of 1974 created a redistribution of the spring breeding population away from traditional wintering areas and adjacent nesting areas resulting in poor productivity (Woehler pers.

comm.). Over the 8-yr period, a 40% mean loss in the pheasant population occurred between winter and spring (1 April) estimates. The range of losses observed between individual estimates was broad, 28-48%.

Winter sex ratio estimates were considered to the weakest WSA pheasant population parameter measured. Sample sizes used to calculate hens per cock range from as few as 81 total birds in 1973 to 554 total birds in 1969. At the 95% confidence level, the indicated winter sex ratios, and spring pheasant population estimates based on these sex ratios, could have been off by $\pm 25\%$ to $\pm 43\%$. Because of sample variability and unevaluated biases in observing techniques, the calculated spring pheasant population estimates must be interpreted with some caution.



Winter Raptor Diets

Great Horned Owls. The cottontail rabbit was the most important prey of great horned owls during all 3 winters. Cottontails comprised 62-71% (average of 66%) of the total biomass consumed (Table 14). Mice (mostly deer mice) and meadow voles ranked second (in percent biomass) in the horned owl's winter diet. From 13% to 18% (average of 15% of the total biomass consumed consisted of mice and voles.

Craighead and Craighead (1956:137) considered microtines as the major winter prey of horned owls in an area of low cottontail abundance. However, a recalculation of their data from percent composition (in Craighead and Craighead 1956:131) to percent biomass (using WSA species biomass figures) in-

dicated mice and voles comprised 27% of the biomass consumed compared to 41% of the biomass for cottontails.

Ring-necked pheasants were the only other prey species making a major contribution to the horned owl's winter diet at Waterloo, ranging from 5% to 9%, averaging 6%. Craighead and Craighead's (1956:131) data indicate that pheasants comprised 11% of the biomass consumed in winter by horned owls over a 2-yr period.

At Waterloo, the remaining winter prey and average percent biomass were: Norway rats, 5%; carnivores and insectivores, 3%; and passerines and related bird species, 2%. Domestic chickens eaten by owls were believed to be carrion deposited in fields by local farmers when spreading manure. Farmers at Waterloo commonly dis-

posed of dead chickens, ducks, and small pigs in this manner.

Red-tailed Hawks. The winter diet of the red-tailed hawks at Waterloo was quite similar to that of great horned owls (Table 15). Cottontail rabbits were also the major winter prey item, averaging 44% of the biomass consumed, followed by mice and voles averaging 28%, and finally the ring-necked pheasants averaging 10%.

Little information has been published on winter diets of redtails. Craighead and Craighead (1956:133) again considered microtines as the major winter prey, with rabbits, pheasants, and small birds representing small, but important secondary components. I recalculated Craighead

TABLE 14. Winter food habits of great horned owls on the WSA, 1973-75.¹

Prey	Percent Composition				Percent Biomass			
	1973	1974	1975	Mean	1973	1974	1975	Mean
Cottontail rabbits	12	8	10	9	67	62	71	66
Norway rats	1	5	1	3	2	10	2	5
Mice & voles	71	81	75	77	13	18	14	15
Squirrels & muskrats		tr ²	1	tr		1	2	1
Carnivores & insectivores	5	3	7	5	4	2	2	3
Passerines & related bird species	10	3	6	5	4	1	3	2
Domestic chickens	tr	tr		tr	2	1		1
Pheasants	2	1	1	1	9	5	7	6
Lower vertebrates			tr				tr	tr
Total	101	101	101		101	100	101	

¹ Total prey items were 294, 671, and 400 for 1973 through 1975; biomass totals were 66,245 g, 113,353 g, and 70,981 g, respectively.

² Less than 0.5%.

TABLE 15. Winter food habits of red-tailed hawks on the WSA, 1973-75.¹

Prey	Percent Composition				Percent Biomass			
	1973	1974	1975	Mean	1973	1974	1975	Mean
Cottontail rabbits	8	3	3	4	59	34	54	44
Norway rats		tr ²		tr		1		tr
Mice & voles	73	80	73	77	19	29	38	28
Squirrels & muskrats		1		tr		11		6
Carnivores & insectivores	15	11	21	14	2	3	5	3
Passerines & related bird species	3	3	3	3	1	4	3	3
Domestic chickens	1			tr	10			3
Domestic ducks		tr		tr		5		3
Pheasants	1	1		tr	9	13		10
Lower vertebrates		tr		tr		tr		tr
Total	101	99	100		100	100	100	

¹Total number of prey items were 80, 237, and 95 for 1973 through 1975; biomass totals were 13,254 g, 27,111 g, and 7,178 g, respectively.

²Less than 0.5%.

TABLE 16. Spring food habits of great horned owls on the WSA, 1972-75. Number of active nests examined during 1972-75 were: 10, 10, 8, and 8, respectively.¹

Prey	Percent Composition					Percent Biomass				
	1972	1973	1974	1975	Mean	1972	1973	1974	1975	Mean
Cottontail rabbits	19	9	11	15	12	47	41	51	51	47
Norway rats	2	5	3	7	4	1	7	3	6	5
Mice & voles	14	37	42	28	34	1	5	6	2	4
Squirrels & muskrats	5	2	2	3	3	5	3	2	4	3
Carnivores & insectivores	2	1	3	2	2	4	tr	tr	4	2
Passerines & related bird species	43	33	32	34	34	8	10	10	8	9
Shorebird, rails, & allies	1	6	1	2	3	tr ²	5	1	1	2
Domestic chickens		1			tr		3			1
Domestic ducks	5		tr		tr	13		1		3
Pheasants	9	6	6	7	6	20	25	24	20	23
Wild ducks	1	1	1	1	tr	2	2	2	2	2
Lower vertebrates	1	tr		1	tr	tr	tr		tr	tr
Invertebrates		tr	tr	1	tr		tr	tr	tr	tr
Total	102	101	101	101		101	101	100	98	

¹Total number of food items were 259, 775, 552, and 327 in 1972 through 1975; biomass totals were 133,063 g, 214,858 g, 154,469 g, and 124,925 g, respectively.

²Less than 0.5%.

and Craighead's (1956:133) data in terms of biomass. The winter diet of their redtails averaged 70% microtines, 21% cottontails, 4% pheasants, and 3% small birds.

The similar diets of horned owls and redtails would suggest competition for prey. Food competition is reduced due to different activity cycles (Klopfer 1969:10). Great horned owls and red-tailed hawks have been characterized as tolerant, complementary species, occupying similar niches without

adverse competition and feeding on many of the same prey species (Bent 1938:296; Fitch 1947; Orians and Kuhlman 1956:383-84). Direct competition between horned owls and redtails must be of limited magnitude, otherwise greater differences in food and habitat requirements should have been eliminated, at least on the basis of the "competitive exclusion principle" commonly known as "Gause's Rule" (Hardin 1960).

Spring Raptor Diets

Great Horned Owls. WSA great horned owls continued to eat cottontails in spring (Table 16), but at a lower rate than in winter. Average biomass of cottontails consumed declined from 66% in winter to 47% in spring. A recalculation of spring horned owl's diets from Craighead and Craighead (1956:131, 403) also indicated a biomass decline (41% to

TABLE 17. Spring food habits of red-tailed hawks on the WSA, 1972-75. Number of active nests examined during 1972-75 were 18, 20, 21, and 21, respectively.¹

Prey	Percent Composition					Percent Biomass				
	1972	1973	1974	1975	Mean	1972	1973	1974	1975	Mean
Cottontail rabbits	8	6	7	4	6	48	41	36	25	38
Norway rats	1		tr ²		tr	1		tr		tr
Mice & voles	27	44	40	19	37	5	9	7	3	7
Squirrels & muskrats	19	6	11	12	10	13	13	17	11	14
Carnivores & insectivores	10	8	5	2	6	2	4	1	tr	2
Passerines & related bird species	18	23	22	49	26	6	10	8	17	10
Shorebirds, rails, & allies		tr	tr	tr	tr		tr	tr	tr	tr
Domestic chickens	tr		1		tr	5		4		2
Domestic ducks	1				tr	5				tr
Pheasants	2	3	5	7	4	12	20	25	38	23
Wild ducks		tr	tr	tr	tr		1	tr	3	1
Lower vertebrates	16	9	5	7	8	3	2	1	2	2
Invertebrates			3		1			tr		tr
Total	100	99	98	100		100	100	98	99	

¹Total number of food items were 146, 449, 325, and 169 in 1972 through 1975; biomass totals were 29,637 g, 87,848 g, 76,851 g, and 36,454 g, respectively.

²Less than 0.5 %.

19%) from winter to spring. Lagomorphs are generally considered the major prey species of horned owls in the Midwest with cottontails most important in the agricultural areas (Errington 1932a; Errington, Hamerstrom, and Hamerstrom 1940:785; Orians and Kuhlman 1956:381). Jackrabbits become an important item in the prairie regions (Korschgen and Stuart 1972:272), and snowshoe hares are the main prey item in the conifer-hardwood and boreal forests (Rusch et al. 1972:289-91).

Pheasants made up a greater portion (23%) of the biomass consumed by horned owls in spring than found in winter. Passerines and related bird species (9%), Norway rats (5%), mice and voles (4%), squirrels and muskrats (3%), and domestic ducks (3%) represented the other major items eaten. One pair of horned owls near a local poultry hatchery where poor animal husbandry was practiced made heavy use of domestic ducks during 1972.

Norway rats contributed a fair proportion of the horned owl's winter-spring diet, but this rodent was never captured during small mammal trapping. Radio-telemetry findings indicated that local farm buildings were the source of rats. During their active hours, radio-tagged horned owls were frequently found near farm buildings. Similar findings were reported by Baumgartner (1939:280).

of red-tailed hawks at Waterloo also indicated continued high utilization of cottontails, but average percent biomass consumed declined from 44% in winter to 38% in spring (Table 17). Rabbits remained the main redtail prey species. Consumption of mice and voles also declined, from 28% in winter to 7% in spring. Utilization of pheasants increased from 10% to 23%. Increases were also noted in utilization of squirrels and muskrats (from 6% to 14%) and passerines and related bird species (from 3% to 10%).

During 1975, a decline was observed in mammalian prey taken and a corresponding increase occurred in passerines and pheasants consumed.

Spring mammalian avian prey ratios for 1972-75 were 3.0:1, 2.4:1, 2.2:1, and 0.7:1, respectively.

Spring redtail diets from other Wisconsin-based studies confirmed the heavy use of cottontails (Errington 1933:27; Orians and Kuhlman 1956:376; Gates 1972:430). Errington (1933:27) did not find any consumption of pheasants in south-central Wisconsin. However, Orians and Kuhlman (1956:376) and Gates (1972:430) found heavy spring utilization of pheasants, 43% and 46% biomass, respectively (recalculated values).

The meadow vole was the small mammal most commonly preyed

TABLE 18. Percentage meadow vole biomass in mice and vole biomass from the diets of great horned owls and red-tailed hawks on the WSA, 1972-75.

Year	Percent Meadow Vole Biomass			
	Great Horned Owls		Red-tailed Hawks	
	Spring	Winter	Spring	Winter
1972	38	—	67	—
1973	79	89	79	91
1974	79	78	89	85
1975	54	59	58	82
Mean	63.5	75.3	73.3	86.0

TABLE 19. *Mammalian:avian prey ratios (number of mammals for each avian) in the diets of great horned owls and red-tailed hawks at WSA, 1972-75.*

Season and Raptor Species	1972	1973	1974	1975	Mean
<i>Winter</i>					
Great horned owls		7.4	24.3	13.4	15.0
Red-tailed hawks		19.0	20.5	30.7	23.4
<i>Spring</i>					
Great horned owls	0.7	1.2	1.5	1.3	1.2
Red-tailed hawks	3.0	2.4	2.2	0.7	2.1

TABLE 20. *Biomass of prey (in grams) brought daily to tethered young.*

Species	1972	1973	1974	1975
Average biomass of prey killed per day per brood				
Great horned owl	348	291	326	345
Red-tailed hawk	259	245	308	218
Average biomass of prey killed per day per nestling				
Great horned owl	232	194	217	230
Red-tailed hawk	196 ¹	164	205	145

¹ Adjusted prey biomass based upon 1973-75 tethering results.

upon by raptors at Waterloo (Tables 14-17). Lowest percentages of voles were consumed during spring 1972 and the winter and spring of 1975 (Table 18). Deer mice became increasingly important during meadow vole lows, but they never became the main small mammal prey. The meadow vole has been commonly accepted as the major small mammal in horned owl and redtail diets from the Midwest (Craighead and Craighead 1956:284, Orians and Kuhlman 1956:376,381; Gates 1972:430; Korschgen and Stuart 1972:276), although deer mice have also been reported as the main small mammal prey, generally in more wooded areas (Errington 1933; Errington, Hamerstrom, and Hamerstrom 1940:788).

Ratios of mammalian:avian prey consumed, based on percent composition in the diets, illustrated greater consumption of mammals by both raptors in winter and by redtails in spring (Table 19). Concomitant with population declines in cottontails and small mammals, a decline in consumption of mammals by redtails was

quite obvious during the spring of 1975. Heavy winter utilization of small mammals by both raptors was a reflection of the abnormally mild temperatures and light, low snow cover that prevailed during the three winters examined.

Alternate prey that acts to decrease predation pressure on another prey animal are referred to as "buffer species" (Dasmann 1964:99). Buffer species usually refer to nongame animals reducing predatory pressure on game populations by acting as alternate prey (Leopold 1933:237-39). "Generalized" as compared to "specialized" predators have a greater opportunity to be influenced by buffer species. A complex community in turn, will have a greater variety of buffer prey available. Buffer species are known to affect the diets of great horned owls and red-tailed hawks (Errington 1938; McInville and Keith 1974:11). Snowshoe hares were found to act as a buffer species in reducing horned owl and redtail predation on ruffed grouse, sharp-tailed grouse, and waterfowl in Alberta (McInville and

Keith 1974:11). In a more complex ecological community such as Waterloo, small mammals, cottontails, and migrating passerines appear to buffer the winter-spring losses of pheasants to horned owls and redtails.

Tethering Results

Pellets and prey remains collected at tether sites were used primarily to obtain spring diets of both young and adults. Large, partially consumed prey items were commonly delivered to tethered young, and there was little evidence to suggest that the adult diet differed from the prey items brought to tethered young.

Biomass of prey brought to tethered young varied with: (1) the number of young at the tether site; (2) apparent differences in hunting skills of individual adults; and (3) annual fluctuations in prey populations. Snyder and Snyder (1973:463) stated brood size was not related to prey supplied to accipiter nestlings since adults were believed to be hunting at maximum capacity. McInville and Keith (1974:11) and the present study, however, indicated considerable dependence between amounts of prey biomass delivered and brood size. Findings for Alberta great horned owls ranged from 293 g of prey daily for a brood of 1 to 860 g for a brood of 3; daily amounts for redtail broods were 410 g and 730 g for brood sizes of 1 and 3 (McInville and Keith 1974:11). WSA data was limited to brood sizes of 1 and 2. Biomass of prey delivered daily increased from 296 g to 360 g in horned owls (an increase of 21%) and from 219 g to 313 g in redtails (an increase of 43%) as brood size increased from 1 to 2. Sample sizes for broods of 1 and 2 young were 15 each for great horned owls and 11 and 8, respectively, for red-tailed hawks.

TABLE 21. Winter and spring predation rates of great horned owls on ring-necked pheasant populations on a 8 373-ha area near Waterloo, Wisconsin.¹

Predation Parameters	1972		1973		1974		1975	
	Spring	Winter	Spring	Winter	Spring	Winter	Spring	
Number of Owls Present								
Adults	22	24	24	24	22	22	22	
Fledglings	13		9		10		9	
Nestlings	16		13		12		10	
Number of Owl-days on Area ²								
Adults	2 002	2 160	2 184	2 160	2 002	1 980	2 002	
Fledglings	611		558		550		513	
Nestlings	781		360		432		331	
Number of Pheasants Available	860	1 295	695	1 270	747	867	527	
Pheasants Consumed ³								
Number	90	22	91	13	91	15	68	
Percent	10.5	1.7	13.1	1.0	12.2	1.8	12.9	

¹ Assume that biomass killed equals biomass consumed.

² Number of owl-days for fledglings and nestlings based upon calculated mean fledgling date of 15 May 1972, 30 April 1973, 9 May 1974, and 8 May 1975.

³ Average daily food requirement of adults and fledglings based on 130 g/day in spring and 137 g/day in winter. Average daily food requirement of nestlings is based on results from tethered owlets.

Quantitative determination of hunting skills of individual raptors was difficult, although some circumstantial evidence was available. Adults of some tethered young were definitely more aggressive towards the investigator than others, and fewer cases of starvation of tethered young were observed with aggressive parents. Aggressive adults generally delivered more prey biomass and a greater variety of prey items to tethered young than did less aggressive parents. It is possible that the more aggressive adults occupied the "better" hunting grounds. McInville and Keith (1974:11) found that daily delivered biomass was influenced by the dominant cover surrounding nest sites. This could not be substantiated at Waterloo because of the generally homogeneous land use.

Year-to-year differences in average daily biomass killed per brood and per nestling were suggested although the lack of a systematic sampling procedure precludes statistical verification (Table 20). However, spring 1975 appears to be the 4-yr low in average daily biomass per redtail nestling. Owl data suggest a similar rate of consumption in all years except perhaps 1973. In Alberta, where raptor diets were greatly influenced by cyclic snowshoe hare density, pronounced annual variability was found in biomass of prey delivered daily to tether nestling (McInville and Keith 1974:11). Circumstantial evidence suggests that the opportunistic feeding of WSA horned owls and redtails, and the

relative stability of available prey, mask the variations in biomass of prey delivered daily to tethered nestlings. WSA redtails were not noticeably affected until the relatively severe decline of small mammals and cottontails in the spring of 1975.

The prolonged tethering of raptor nestlings was conducted throughout the 4-yr study at Waterloo. Seventeen (24%) of 71 tethered young (30 red-tailed hawks and 41 great horned owls) died while tethered. Eleven birds (15%) died of starvation. Ten of these nestlings (14%) starved during the first 2 springs. In the springs of 1974 and 1975, supplemental feeding and rotation of tethered birds on the platform helped reduce the starvation rate to only 1 nestling. Exposure losses (2 birds) occurred when nestlings were placed on the platform too early. Adults did not brood their offspring once the nestlings were tethered to the platform. Nestlings less than 4 wk old apparently are not feathered well enough to be protected from adverse weather. Handling and cannibalism were other causes of mortality (2 and 1 birds, respectively). One bird was lost to predation, presumably by a mammal.

Impact on Raptors

Changes in prey abundance can lead to changes in predator density (numerical response) or diets (functional response) (Solomon 1949). Numerical responses are produced by

changes in rates of birth, rates of survival, and movements of predators (Holling 1965). Buffering, territoriality, and learning tend to complicate numerical and functional responses and hence predator-prey relationships are difficult to analyze (Keith 1974:25). Keith believed that a characteristic of generalized predators is that a direct dietary response to changes in prey populations occurs (a density-dependent relationship). Craighead and Craighead (1956:321) concluded that raptor predation was regulated by prey density and was therefore density-dependent. The functional responses of Alberta horned owls and redtails to changes in snowshoe hare numbers were strongly density-dependent. The rate of predation on hares, however, (percentage of the hare population consumed) was density-independent as related to horned owls and inversely density-dependent with regard to redtails during hare population increases (Keith 1974:31; Adamcik and Keith 1974). Alberta great horned owls responded numerically to changing numbers of hares, but no numerical response was observed in the redtail population (Keith 1974:31). Numerical responses by Alberta raptors may have been tempered by the duration of the birds' occupancy of their home range. Great horned owls were year-round residents while redtails migrated south during the winter.

A characteristic of the boreal and aspen parkland forests that typified the Alberta raptor studies was the highly cyclic phenomenon of major

raptor prey species, primarily the snowshoe hare. Raptor populations inhabiting more southern hardwood forests and prairies (such as the WSA and the southern Michigan area of Craighead and Craighead 1956) rely on prey species with less variation and almost certainly, variations contained no cycling component. Coefficients of variation (C.V.) were determined for the staple prey species of Alberta raptors (recalculated from McInville and Keith 1974:4) as compared to C.V. values in WSA prey staples. Alberta hares exhibited high variation (C.V. = 112%) along with meadow voles (83%), while Richardson's ground squirrels (51%) and ruffed grouse (40%) were less variable. At Waterloo, the coefficient of variation for cottontails, the major raptor prey, was relatively stable when compared to Alberta hares (44%), whereas meadow voles duplicated findings from Alberta (82%). Pheasants exhibited a low C.V. of 17%.

The relative stability of southern hardwood forest prey, plus the stability in the WSA breeding populations of horned owls and redtails would indicate that only limited functional responses could be anticipated at Waterloo. Numerical responses would only be observed on a long-term basis, primarily the result of land use changes that would in turn affect prey abundance. Newton (1976:278-81) found that stable densities of diurnal raptors is related to stability of prey populations and nesting site availability.

Winter. Functional responses in Waterloo raptors were measured by comparing annual changes in Waterloo staple prey populations with the utilization of these same prey items by great horned owls and red-tailed hawks. Functional responses by WSA horned owls and redtails to changes in staple prey densities in winter were primarily density-independent. Only the winter utilization of pheasants by redtails appeared density-dependent ($P < 0.10$, $r = 0.94$, $df = 1$). Consumption of cottontails by either raptor was not directly related to cottontail density over the three winters examined. Craighead and Craighead (1956:322) concluded that the cottontail was the most vulnerable cold-weather prey regardless of density. A density-independent dietary relationship was also suggested since winter utilization of mice and voles by WSA raptors was not correlated with abundance of small mammals in winter.

Prey density apparently had little effect on prey vulnerability. Craighead and Craighead (1956:170) considered prey density together with prey risk factors in determining prey vulnerability. Prey density or

availability was considered the dominant factor affecting vulnerability. Prey risk factors included: (1) availability of food and protective cover; (2) concentration and dispersion of prey; (3) movement, activity, and habits; (4) age of individuals; (5) size and strength; (6) health of individuals; (7) speed, agility, and escape reactions; and (8) inter- and intraspecific strife (Craighead and Craighead 1956:177). Prey risk factors are strongly interrelated, with only the first two factors subject to management.

I hypothesized that small mammals were more vulnerable to raptor predation during winters of low snow cover and high abundance (number of days with 10 cm or more snow cover multiplied by the average abundance of small mammals during January-March). The number of days with ≥ 10 cm of snow cover were: 45 d, 1972; 25 d, 1973; 31 d, 1974; and 41 d, 1975. Tested against raptor consumption of mice and voles, the relationship suggested significance at the 15% level for great horned owls ($r = 0.86$, $df = 1$) and was significant at the 5% level for red-tailed hawks ($r = 0.90$, $df = 1$). Snow in excess of 10 cm lessened small mammal vulnerability. The high raptor use of small mammals when there was little snow cover suggests that protective cover replaced prey density as the dominant factor affecting small mammal vulnerability. In addition, the unusually high utilization of small mammals was believed to affect the consumption of other prey. The nearly uniform density-independent relationships (for all prey staples except the utilization of pheasants by redtails) observed during the 3 winters may have been the result of high vulnerability of small mammals. Consumption of other prey was modified because small mammals acted as buffer species.

Spring. The proportion of cottontails in great horned owls' diet in spring was not correlated with rabbit abundance ($P > 0.15$, $r = -0.84$, $df = 2$), although the utilization of rabbits seemed related to abundance for red-tailed hawks ($P < 0.15$, $r = 0.87$, $df = 2$). Raptor utilization of small mammals was examined separately for meadow voles, and for all mice and voles combined. The fraction of the owl's diet that voles comprised was not directly related to vole abundance ($P < 0.20$, $r = 0.79$, $df = 2$), although vole consumption by redtails was linearly related ($P < 0.05$, $r = 0.95$, $df = 2$). When all mice and voles were considered, the linear relationships were stronger for both horned owls ($P < 0.10$, $r = 0.91$, $df = 2$). Great horned owls, in particular, consumed considerable numbers of deer mice, which accounted for the stronger correlation

with mice and voles combined. The proportion of the owl's diet that was pheasants seemed weakly related to their numbers in spring ($P = 0.11$, $r = 0.89$, $df = 2$); however, no direct pheasant-redtail relationship was indicated ($P > 0.15$, $r = -0.83$, $df = 2$).

The winter-spring utilization of staple prey species by WSA horned owls and redtails is related to factors in addition to prey density. It is, therefore, possible to influence prey vulnerability, and in turn, the consumption of certain prey by raptors, with the intentional manipulation (management) of prey risk factors.

Impact on Prey

Pheasants. Predation rates were used to determine the seasonal impact of predation on WSA pheasants by great horned owls and red-tailed hawks. Waterloo pheasant populations remained extremely stable during 1968-75 with a winter C.V. of 15% and a spring C.V. of 17%. The stable pheasant population indicates a well-established game bird, apparently capable of adjusting to environmental changes (i.e., overcoming severe winter and spring weather; showing little cyclic fluctuations).

Great horned owls removed from 1.0% to 1.8% (mean of 1.5) of the 1 January 1973-75 pheasant populations during the 90-d winter seasons (Table 21). Spring owl predation rates on pheasants ranged from 10.5% to 13.1%, with a mean of 12.2%. Horned owl utilization of pheasants at Waterloo was consistently higher during the spring season. Neither the winter nor the spring owl predation rates on pheasants were correlated with pheasant density ($P > 0.10$, $r = 0.53$, 0.89 , $df = 2$). The small amount of rate variation would question the validity of any attempts at correlation.

Red-tailed hawks consumed from 0.0% to 4.1% (mean of 2.3%) of the 1 January pheasant populations estimated during the 3 winters (Table 22). The proportion of the pheasant population removed by redtails in spring was also substantially higher than in winter, ranging from 7.3% to 41.5% of the 1 April pheasant population with a mean of 23.2%. Winter predation rates by redtails were significantly correlated with pheasant density ($P < 0.10$, $r = 0.92$, $df = 2$). However, during the spring, redtail predation rates on pheasants showed a significant negative correlation due to changes in pheasant risk factors ($P < 0.05$, $r = 0.95$, $df = 2$).

Dumke and Pils (1973:1) determined the seasonal distribution of pheasant mortality and specific

TABLE 22. Winter and spring predation rates of red-tailed hawks on ring-necked pheasant populations on a 8 373-ha area near Waterloo, Wisconsin.¹

Predation Parameters	1972		1973		1974		1975	
	Spring	Winter	Spring	Winter	Spring	Winter	Spring	
Number of Hawks Present								
Adults	38	40	42	42	42	40	40	
Fledglings	20		30		34		21	
Nestlings	22		32		37		27	
Number of Hawk-days on Area ²								
Adults	3 458	3 600	3 822	3 780	3 822	3 600	3 640	
Fledglings	200		1 080		816		315	
Nestlings	990		835		352		1 570	
Number of Pheasants Available								
Pheasants Consumed ³	860	1 295	695	1 270	747	867	527	
Number								
Percent	63	35	132	52	184	0	219	
	7.3	2.7	19.1	4.1	24.7	0.0	41.5	

¹ Assume that biomass killed equals biomass consumed.

² Number of hawk-days for fledglings and nestlings based upon calculated mean fledgling date of 19 June 1972, 26 May 1973, 6 June 1974, and 15 June 1975.

³ Average daily food requirement of adults and fledglings based on 120 g/day in spring and 130 g/day in winter. Average daily food requirement of nestlings is based on results from tethered hawklets.

TABLE 23. Number of days with snow cover ≥ 10 cm, 1960-75.¹

Months	Mean Days with ≥ 10 cm Snow Cover		
	1960-75 Base	1969-72	1973-75
November	0.1	0.5	0
December	7.5	13.3	8.7
January	13.1	23.0	2.0
February	8.5	14.0	10.0
March	5.1	4.0	7.0

¹ Data compiled from monthly summaries of the NOAA's Madison station.

causes of deaths from 244 radio-tagged hen pheasants at Waterloo during 1967-71. They found that raptors had their greatest impact on pheasants during the winter. Raptor predation per 1000 pheasant-days for winter was 1.97 (mortality rate for the 90-d winter period or $q_{90} = 16.2\%$), as compared to 0.65 ($q_{91} = 5.8\%$) in the spring, 0.37 ($q_{92} = 3.3\%$) in the summer, and 0.73 ($q_{92} = 6.5\%$) during the fall (R. T. Dumke, per. comm.). A 4-yr breakdown of seasonal losses indicated "winter" (14 December to 15 April) mortality rates of hen pheasants from all causes ranged from 32.1% to 68.8%. A wide range of mortality rates, 18.2-62.9% was also observed during the reproductive period, 15 April to 28

TABLE 24. Comparison of winter hardness index to winter pheasant mortality and predation losses from raptors.

Year	Winter Pheasant Mortality ¹ (15 December - 14 April)	Winter Raptor Predation Rates ² (1 January - 31 March)	Winter Hardness Index (1 December - 31 March)
1968-69	32.1		722
1969-70	48.8		1 052
1970-71	68.8		1 720
1968-71 Mean			1 165
1971-72			672
1972-73		4.4	504
1973-74		5.1	621
1974-75		1.8	557
1972-75 Mean		3.8	561
1949-75 Mean			672

¹ From Dumke and Pils (1973:18).

² Represent combined great horned owl and red-tailed hawk predation rates on pheasants.

August (Dumke and Pils 1973:18). Gates (1972:432) also found that losses of pheasants to avian predation were greater in winter. He estimated 7% of the 1 January pheasant population was consumed by red-tailed hawks from early January through late March. Redtail predation during the spring and summer periods accounted for 5% of the 1 May pheasant population (Gates 1972:431).

In contrast to the findings of Gates (1972) and Dumke and Pils (1973), Craighead and Craighead (1956:281) found negligible winter pheasant mortality prior to 15 March. They determined that great horned owls removed approximately 2% of the overwintering pheasants during the mid-December to mid-March period. During the early spring, dispersal and breeding activities of pheasants were believed to increase their vulnerability to raptor predation, and, consequently, pheasants were "frequently" preyed upon (Craighead and Craighead 1956:300).

Utilization of pheasants by great horned owls and red-tailed hawks at Waterloo during 1972-75 supported the Craigheads' findings since combined raptor predation rates on pheasants consistently indicated heavy spring losses. The combined mean of winter rates was 3.8% compared to a spring mean of 35.3% (discussed later in text). I believe the low pheasant losses at Waterloo during the winters of 1973-75 resulted from a lack of snow cover, which in turn brought about: (1) increased small mammal vulnerability, and (2) altered pheasant behavior. The mean number of days with 10 cm or more of snow cover for November-February, 1973-785 was consistently lower than during the 1969-72 period (Table 23). A comparison of monthly means in the 1969-72 period to 1960-75 averages indicated that the pheasant telemetry-mortality study was conducted during winters with abnormally high snow cover which protected small mammals from raptors.

Thus, the relatively high mortality of pheasants in winter observed by other workers was probably related to the severity of winter weather. Winter severity was measured by Gates (1971:24) and Dumke and Pils (1973:37-38) using a combination of minimum monthly temperatures and snow cover to obtain "winter hardness" indices. Higher hardness indices were obtained in winters with lower temperatures and deeper and more persistent snow cover. Theoretically, the higher the hardness index for the 1 December to 31 March period, the greater the stress on pheasants, and, consequently, the higher the pheasant mortality. Fall-to-spring pheasant mortality was

found both by Gates (1971:747) and Dumke and Pils (1973:38) to be strongly correlated with winter hardness indices. The annual WSA winter hardness indices from the 1972-75 period were stable and averaged 17% below the 1949-75 average of 672 (Table 24). The uniformly low raptor predation rates on pheasants in 1972-75 compared with the low, stable winter hardness indices over the same time period, support the findings of Gates (1972) and Dumke and Pils (1973).

Gates and Hale (1974:27) found that winter behavior of pheasants was affected by snow depth. During winters with heavy snow cover, pheasants gathered in flocks of 15 to 70 birds near a reliable food source. However, during winters of low snow cover, pheasants remained in small groups or were scattered individually over a wide area. The most reliable food source on the WSA was corn-sorghum patches planted by DNR personnel, usually near traditional pheasant wintering sites. Frank and Woehler (1969:310) found that planting winter food patches at Waterloo brought about localized responses that were "swift and dramatic"; winter flocks of pheasants were established at sites that formerly were without wintering birds. The movement of pheasants to, and the concentration of pheasants in, localized areas can alter their risk of exposure to predation. Gates (1972:425) reported a situation in which 85-100 pheasants were concentrated in a 0.06-ha grove of willow brush adjacent to several black willow trees at a time when over .6 m of snow covered the ground. A pair of redtails removed 8 hen pheasants from this site over an 11-d span. The redtails were trapped and dispatched, only to be replaced by another redtail 3 d later. The single redtail was also removed and again was replaced in 5 d by another pair of redtails. It appears that raptors are able to recognize and take quick advantage of vulnerable flocks of pheasants concentrated in or around food sources with inadequate winter cover.

Food is recognized as the most critical need for wintering pheasants; it is thus of great importance in pheasant-management schemes (Gates and Hale 1974:52). However, it is conceivable that food patches draw pheasants into a more vulnerable situation than would exist under more normal circumstances. An intensive program of habitat management for pheasants at Waterloo, with heavy emphasis on development and maintenance of winter food patches, failed to produce a *measurable* increase in pheasants over an 11-yr period (Frank and Woehler 1969:810; Dumke and Pils 1973:i). Gates and

Hale (1974:i) determined that the daily pheasant movement between winter food and cover was 0.4 km or less; a food source would be serviceable or effective for pheasants only within that radius. R. T. Dumke (pers. comm.) found 12 radio-tagged hen pheasants that were preyed upon by raptors during the 1968-71 winters. All but one of these pheasants were taken within 0.4 km or within the effective range of existing winter food patches. Only 1 radio-tagged pheasant was actually taken in a corn-sorghum food patch, whereas 6 were taken in shrub-carr, 2 in herbaceous cover, and 1 each in an alfalfa field, canary grass, and open oak woodlot.

In the winter of 1973, 26 WSA winter food patches were rated as having a moderate-to-heavy pheasant utilization based upon track counts. These food patches, together with the surrounding area up to 0.4 km, comprised only 16% of the entire study area. An inspection of the food patches revealed that 21 were within 90 m of suitable raptor hunting perch trees. Adjacent permanent cover was lacking in 11 of the 26 patches. Of the 15 patches with adjacent cover, only 4 had permanent cover in the form of brushy ditch banks. Although pheasants will travel up to 0.4 km to acquire food, such movement makes them more conspicuous and exposes them more frequently to raptor predation. The relatively severe winters of 1968-71 brought about a concentration of pheasants and increased their movements to, and their dependency on, food patches. Because the food patches had little adjacent escape cover or were located near raptor hunting perches, the pheasants became more vulnerable to raptor predation. During the mild winters of 1972-75, pheasants at WSA were well dispersed. This lack of concentration plus the increased availability of mice and voles as buffer species, reduced winter predation rates on pheasants to insignificant levels.

The high losses of pheasants in spring were believed to be related to prey risk factors (vulnerability) resulting from the loss of nesting cover and high spring water conditions. During 1971-72, virtually all private agricultural lands retired under federal feed-grain programs were brought back into production. Dumke and Pils (1979) ranked upland grasslands (feed-grain lands) as the most important nesting cover for pheasants at Waterloo. However, prior to mid-May, nesting pheasants preferred residual vegetation in wetlands and strip cover on the Waupun area (Gates and Hale 1975:15). Cover preferences of WSA hen pheasants initiating nests between 1 April and 16 May

TABLE 25. Mean monthly departures from normal precipitation during two spring periods at Waterloo.¹

Month	Mean Monthly Departures from Normal Precipitation	
	1968-71 Period	1972-75 Period
March	-1.65	3.96
April	-0.99	4.52
May	-0.53	3.15
June	2.87	-3.78

¹ Precipitation in centimeters; data compiled from monthly summaries of the NOAA's Madison station.

TABLE 26. Comparison of spring rainfall with spring pheasant mortality and predation losses from raptors.

Year	Spring Pheasant Mortality ¹ (15 April - 27 August)	Spring Raptor Predations Rates ^{2,3} (1 April - 30 June)	Total Spring Rainfall (1 March - 30 June)
1968	44.0		14.6
1969	62.9		15.6
1970	42.6		12.1
1971	18.2		7.2
1972		17.8	8.3
1973		32.2	18.2
1974		36.9	17.3
1975		54.4	16.2
1968-71 Mean	41.9		
1972-75 Mean		35.3	

¹ From Dumke and Pils (1973:18).

² Represent combined great horned owl and red-tailed hawk predation rates on pheasants.

³ Not significantly ($P > 0.10, r = 0.79, df = 2$) related to spring rainfall.

TABLE 27. Winter and spring consumption of cottontails by raptor pairs on the WSA.¹

Parameters	1972	1973		1974		1975	
	Spring	Winter	Spring	Winter	Spring	Winter	Spring
Number of Raptor Pairs Present							
Great Horned Owls	11	12	12	12	11	11	11
Red-tailed Hawks	19	20	21	21	21	20	20
Mean Number of Cottontails Used by Each							
Great Horned Owl Pair	18	13	12	12	16	15	15
Red-tailed Hawk Pair	13	11	11	6	11	10	7
Estimated Total Number of Cottontails Consumed	446	364	378	268	403	359	296

¹ Assume that biomass killed equals biomass consumed.

were almost equally divided among upland grassland, wetlands, strip cover, and hay fields (Dumke and Pils 1979). The percentage of hen pheasants starting clutches prior to 10 May is thought to be primarily associated with the physical condition of the hens in late winter and early spring; reproduction of pheasants tended to be earlier in springs when the hens had not undergone winter depletion in body reserves (Gates and Hale 1975:13). The mild winters of 1972-75 should have encouraged pheasants to nest earlier in residual cover of wetlands and upland grasslands. However, the mean 1972-75 hatching date (12 June) which was not different from the 1968-71 mean (14 June), did not suggest nesting was unusually early.

Hen pheasants were assumed to be physiologically capable of initiating earlier clutches following the mild winters of 1972-75, however, suitable residual nesting cover was extremely restricted in those springs. Mean monthly departures from normal precipitation during 1972-75 were unusually high during March, April, and May. Comparable data for 1968-71 indicated that precipitation was consistently below normal (Table 25). In 1972-75, wetland vegetation that normally could have provided suitable nesting cover was either flattened or inundated. About 80% of the WSA wetland acreage occupied river flood plains and was subject to overflow, strongly suggesting that such vegetation was very poor pheasant nesting cover (Table 26). WSA wetlands provided suitable nesting cover only in springs of normal or low precipitation such as during 1968-71. Gates and Hale (1975:21) found that wetlands that remain consistently wet after the middle of May were of little value to pheasants as nesting cover and cannot be considered a significant asset to pheasant production.

Moreover, the critical shortage of suitable pheasant nesting cover during 1972-75 forced the birds to search more actively for a good place to nest. An increase in pheasant movements, the concentration of birds along the peripheries of flooded wetlands, and the loss of much protective cover resulted in an increased vulnerability of pheasants to raptor predation. Although great horned owls and red-tailed hawks are not selective hunters in terms of food preferences, as opportunistic, "generalized" predators, they will take full advantage of the situation when prey become highly vulnerable.

Pils and Martin (1978:40) determined that red foxes removed 9.1% of the 1 April pheasant population by 30 June, therefore, raptors (taking 35.5%) and foxes combined removed 45% of the pheasants during the 90-d

spring season. Although this rate of loss seems high, computation of a life equation suggests that the Waterloo Pheasant population can, in fact, hold its own. Mortality factors from tagged pheasants (Dumke and Pils 1973:27) were used to estimate seasonal survival intervals (survival equals 1 minus mortality) after Trent and Rongstad (1974:462). Mortality of tagged pheasants due to raptors and foxes was replaced by survival rates derived from this study and Pils and Martin (1978) with some modifications made for foxes. Around 80% of all known mammalian-caused pheasant mortality was due to foxes, therefore, a proportional allocation was made to include an additional 20% loss due to non-fox mammalian predators. Pheasant productivity used in the life equation was estimated by Gates and Hale (1975:64) to be 1.5 juvenile hens produced in the fall population (1 October) for every breeding hen or the spring population (1 April). The life equation assumes all other mortality factors occur at the same rate as found in Dumke and Pils (1973). Starting with 1000 hen pheasants on 1 January, by 31 December, the population would have increased to 1110 hen pheasants. While sampling limits and biases would allow a range of outcomes, it appears that the heavy raptor-fox predation would not inevitably decimate the population.

Cottontails. A reliable population index to WSA cottontails was not obtained, therefore, predation rates on them could not be estimated. From the raptor's standpoint, the cottontail was the most important and the most critical prey staple. A healthy, stable cottontail population was vital not only as a food source, but also served as an important buffer to other potential prey species as well.

Seasonal calculations of cottontails consumed provided the most realistic measures of the impacts of raptor predation on cottontails. Cottontails consumed by individual horned owl pairs were on the order of 12-15 animals during the winter and 2-8 animals during the spring. Corresponding values for individual redtail pairs were 6-11 rabbits during the winter and 7-13 rabbits during the spring (Table 27).

Live-trapping indicated winter cottontail densities on the sampled areas of woodlands and marsh/shrub-carr ranging from 3.1 to 9.5 cottontails per ha, with a mean of 5.8. Spring densities, obtained by a graphic extrapolation, ranged from 3.1 to 9.0 per ha (mean of 6.1). The impact of an individual raptor on the cottontails within its home range was also estimated, assuming: (1) that similar cottontails densities existed in all

Waterloo stands of woodlands and marsh/shrub-carr; and (2) that all cottontails preyed upon by raptors were taken only from these 2 cover types. Woodlands and marsh/shrub-carr vegetation in the average range of an adult, radio-tagged great horned owl comprised 91 ha in the winter and 82 ha in spring. Corresponding values were 53 ha and 29 ha, respectively, for redtails. An individual owl, therefore, removed 0.1 cottontails per ha during the 3 winters, or 1.7% of the winter rabbits. Spring removal was 0.1 animals per ha or 1.9% of the cottontails within the home range. A redtail removed 1.8% of the winter and 3.4% of the spring cottontail populations. It appears that Waterloo horned owls and redtails have little impact on cottontail densities in spite of heavy utilization of rabbits.

Microtines. Great horned owls and red-tailed hawks by themselves did not make a significant impact on microtine (mice and vole) populations at Waterloo. Winter consumption of microtines by both raptor species varied from 50.6 to 88.1 animals per km² (mean of 71.4); spring consumption ranged from 12.6 to 36.1 animals per km² (mean of 24.8) (Table 28). Getz (1970:226) determined the meadow vole density on unmowed sedge meadows in southern Wisconsin at 48 voles per ha in December and 9 voles per ha in May. Assuming there were similar vole densities in marshes at Waterloo, and that all voles were taken from these marshes, both raptors would have consumed only 1.7% of the winter population of voles and 4.4% of the spring population.

Craighead and Craighead (1956:304,307) stressed the importance of a *collective* raptor population with the continual application of predatory pressure in exerting a regulatory effect: "... tending to maintain an equilibrium among the varied elements of prey populations..." Collective raptor predation has been shown to limit meadow voles by exerting critical pressure during the early spring (Craighead and Craighead 1956:305-6). Keith (1974:18) believed predation on microtines tends to be inversely density-dependent and a dominant mortality depressant on declining and low populations. He



TABLE 28. Winter and spring consumption of mice and voles (microtines) by raptor pairs on the WSA.¹

Parameters	1972	1973		1974		1975	
	Spring	Winter	Spring	Winter	Spring	Winter	Spring
Number of Raptor Pairs Present							
Great Horned Owls	11	12	12	12	11	11	11
Red-tailed Hawks	19	20	21	21	21	20	20
Mean Number of Microtines Used by Each							
Great Horned Owl Pair	15	106	68	146	80	111	28
Red-tailed Hawk Pair	56	148	119	226	105	294	19
Total Number of Microtines Consumed ²	1 322	4 238	3 022	6 492	2 894	7 206	1 057
Microtines Consumed per Km ²	15.8	50.6	36.1	77.5	34.6	86.1	12.6

¹ Assume that biomass killed equals biomass consumed.

² Spring mean = 24.8 microtines per km²; winter mean = 71.4 microtines per km².

concluded that predation on microtines increases amplitudes of fluctuations, intervals between population peaks, and local and regional synchrony. A more indepth analysis of the impact of raptor predation on Waterloo microtines would have required examination of the food habits of the predator community over a longer period of time (5 to 10 yr) to include at least 2 complete cycles. On the WSA, horned owls and redtails alone apparently have little effect on microtine populations, but, together with other predators, are an integral part of a predatory community that is believed to have a dynamic influence on microtine numbers.

GREAT HORNED OWL BEHAVIOR

Background

The difficulty of gathering observations in a form lending itself to conventional statistical analyses, and the limited sample sizes obtainable precludes statistical evaluation of some of the following material, but tests were made where appropriate. Where not possible, such inferences as are drawn are presented for the readers' interest and hopefully with suitable restraint. Home ranges of great horned owls were examined each season, and owls categorized by sex and nesting status. Nesting females performed all the incubation and brooding, hence their home ranges in winter and spring are not comparable to those of successful males or unsuccessful owls. Indices ("V" values) to habitat preferences by owl

categories were obtained using the technique of Robel et al. (1970:293) in which percent cover used was divided by percent of the type existing within the home range; values over 1.0 indicated a preference.

Observations of owl behavior were made during monitoring of 15 radio-tagged owls—7 adults and 8 fledgling owls. Fledgling owls were radio-tagged while still in the nest or on tether platforms and monitored until death or dispersal. The 7 adult owls provided 1141 radio-days, with 1571 locations (1197 active or nocturnal, 374 roost or diurnal), and the 8 fledglings yielded 1416 radio-days, with 1483 locations (796 active, 687 roost) (Tables 29, 30). Adult owls were monitored during winters and springs of 1974 and 1975, but summer and fall behavior was monitored only in 1974. During the two monitored breeding seasons (the

winter-spring periods), both the male and female members of three breeding pairs were simultaneously radio equipped.

Winter

Home Range Size. Monthly home ranges offered descriptive insights obscured by the seasonal framework. The monthly home ranges of both members of a courting pair were nearly identical during the winter seasons until clutch initiation, or in the case of unsuccessful owls, until late spring. Home range size of both sexes during January varied from 71 ha to 266 ha, with a mean of 148 ha. At the start of laying in mid-February, successful males increased their home ranges

Great horned owls demonstrated a marked preference towards upland and lowland woodlots throughout the year.



TABLE 29. Seasonal summary of radio active or nocturnal locations, roost or diurnal locations, and radio-days for great horned owls at Waterloo.¹

Owls	Winter			Spring			Summer			Fall			Total		
	No. Locations		No. Radio-days												
	Active	Roost		Active	Roost		Active	Roost		Active	Roost		Active	Roost	
Fledglings	28	15	40	7	28	114	354	448	713	407	196	549	796	687	1 416
Adults															
Females	474	216	523	539	185	637	214	167	359	276	72	234	1 603	640	1 758
Males	479	139	357	402	113	416	91	70	184	225	52	184	1 197	374	1 141
Total	953	355	880	941	298	1 053	305	237	543	501	124	418	2 800	1,014	2 899

¹ For detailed table, see Appendix II.

TABLE 30. Temporal and spatial home ranges of individual adult great horned owls on the WSA.¹

Individual Owls	Winter				Spring				Summer				Fall			
	Jan	Feb	Mar	Total	Apr	May	Jun	Total	July	Aug	Sept	Total	Oct	Nov	Dec	Total
<i>Successful male owls</i>																
Semrau GHO (74)	NA	158	289	321	217	218	160	415	108	214	250	344	348	124	200	409
(75)	266	362	402	579	157	276	285	480								
Dunneison GHO (74) ²	71	149	182	281	83	40	NA	92								
Draeger GHO (74)	NA	110	132	164	46	126	81	233	36	241	200	343	218	115	122	253
<i>Unsuccessful male owls</i>																
Draeger GHO (75)	122	189	186	289	244	192	196	279								
<i>Successful female owls</i>																
Dunneison GHO (74)	40	1	1	42	1	13	55	58	58	83	168	168	459	325	450	653
Draeger GHO (74) ³	NA	97	1	97	9	15	123	175	115	262	200	427				
Fuchs GHO (74)	NA	55	1	58	34	26	72	106	109	70	438	477	262	171	102	557
<i>Unsuccessful female owls</i>																
Fuchs GHO (75)	94	78	89	146	93	30	300	380								
Jordan GHO (74)	NA	68	68	105	44	19	171	185	81	163	48	190	210	NA	NA	294
Jordan GHO (75)	148	261	219	278	145	114	133	280								
Dunneison GHO (75) ⁴	191	338	548	599	207	195	118	273								

¹ Area in hectares.

² Shed transmitter 22 May 1974.

³ Died 7 September 1974.

⁴ Deserted nest 26 February 1975 after 5-day incubation.

TABLE 31. Comparison of actual areas (hectares) of cover type means of successful male owls to unsuccessful owls of both sexes.

Cover Types	Successful Male Owls (4)		Unsuccessful Owls (5)		t Values
	\bar{x}	s_x	\bar{x}	s_x	
<i>Winter Season</i>					
Upland Hardwoods	18.3	3.67	20.5	7.90	ns
Lowland Hardwoods & Tamaracks	28.6	35.17	4.2	3.18	*
Marsh/Shrub-carr	59.3	42.30	54.4	76.22	ns
Upland Pastures & Grasslands	38.5	19.59	21.3	10.53	*
Lowland Pastures	39.7	22.75	55.8	31.47	ns
Cropland	135.3	99.30	117.5	97.64	ns
Strip Cover & Miscellaneous	16.8	8.79	9.9	11.47	ns
Total	336.4	175.08	283.6	193.41	ns
<i>Spring Season</i>					
Upland Hardwoods	15.1	1.75	18.9	3.65	ns
Lowland Hardwoods & Tamaracks	36.2	19.47	3.3	1.14	*
Marsh/Shrub-carr	39.5	13.34	53.6	23.28	ns
Upland Pastures & Grasslands	38.2	13.70	21.3	4.06	ns
Lowland Pastures	43.9	16.36	55.7	11.08	ns
Cropland	118.6	35.26	116.1	27.64	ns
Strip Cover & Miscellaneous	13.8	5.33	9.3	1.62	ns
Total	305.0	88.10	279.6	30.96	ns

*Significant at $P < 0.20$.

between 26% and 64%. Males also developed a scattered pattern of increased movements over a wide area, with activities concentrated in 8 to 12 locations, as opposed to only 4 to 6 locations prior to mid-February. Average home range size of successful males also enlarged in March, increasing from 195 ha to 251 ha. Locations, when combined for the 3 months, gave a winter season home range for successful male owls of 336 ha, compared to 66 ha for successful females.

Winter home range size in successful males is believed to have been at least partially dependent upon the availability of food within the home range during March (the peak in seasonal activity as expressed spatially). For example, the successful male owl of the Draeger pair had an extremely small March home range, and used relatively few perches (1 to 2 perches per hour) during most nights. The Draeger pair's site was located on a 6-ha knoll, surrounded by seasonally flooded pastures and cropland. During March and throughout early spring, water birds concentrated in these surrounding flooded pastures and were heavily utilized by the Draeger pair.

Average monthly home ranges of unsuccessful horned owls were smaller (approximately 140 ha) and exhibited little change from January through March. Mean size of winter home ranges was similar for unsuccessful owls of both sexes, at 289 ha for males and 282 ha for females.

TABLE 32. Winter habitat preference indices for great horned owls near Waterloo.¹

Cover Types	Successful Owls		Unsuccessful Owls	
	Males	Females	Males	Females
Upland Hardwoods	6.6	6.7	7.2	6.2
Lowland Hardwoods & Tamaracks	2.5	0.0	13.0	7.2
Marsh/Shrub-carr	0.5	0.2	0.3	0.6
Upland Pastures & Grasslands	0.2	0.0	0.0	0.4
Lowland Pastures	0.6	0.1	0.1	0.3
Cropland	0.3	0.0	0.4	0.2
Strip Cover	2.7	0.0	0.0	0.5
Miscellaneous Cover	1.7	0.0	1.0	0.8

¹Indices calculated after Robel et al. 1970:293; habitat preferences: ≥ 1.0 .

Habitat Preferences. WSA horned owls utilized certain cover types with significantly greater frequencies than the relative occurrence of these types on the study area would suggest ($P < 0.01$; for unsuccessful males: $\chi^2 = 556$, $df = 5$; for successful males: $\chi^2 = 970$, $df = 8$; for unsuccessful females: $\chi^2 = 548$, $df = 4$; for successful females: $\chi^2 = 1525$, $df = 7$). Habitat use by owls was not random. Upland and lowland hardwoods received disproportionately high use in contrast to marsh/shrub-carr, cropland, and lowland pasture that were little used.

Differences between areas (in ha) of the various cover types used by successful male owls and the cor-

responding areas utilized by unsuccessful male and female owls could not be demonstrated except at $P < 0.10$, but small sample size ($n = 12$) severely limited the sensitivity of the statistical test (Table 31). Four phenotypically similar cover types were combined into two broader categories (lowland hardwoods and tamaracks as one group, and upland pastures and grassland as the second group) to enlarge sample sizes. Results were still only significant at $P < 0.20$. The apparent similarity of cover types between home ranges of successful and unsuccessful owls suggests that breeding success was not dependent upon the amount of any particular

TABLE 33. Spring habitat preference indices for great horned owls near Waterloo.¹

Cover Types	Successful Owls		Unsuccessful Owls	
	Males	Females	Males	Females
Upland Hardwoods	5.4	7.0	3.5	2.8
Lowland Hardwoods & Tamaracks	2.9	2.0	21.0	21.0
Marsh/Shrub-carr	1.2	1.1	1.1	1.3
Upland Pastures & Grasslands	0.3	0.3	0.6	0.4
Lowland Pastures	0.1	0.3	0.3	1.0
Cropland	0.2	0.1	0.2	0.1
Strip Cover	2.3	0.0	0.0	0.0
Miscellaneous Cover	3.0	0.6	3.0	1.8

¹ Indices calculated after Robel et al. 1970:293; habitat preferences: ≥ 1.0 .

TABLE 34. Temporal and spatial home ranges of fledged great horned owls on the WSA.¹

Individual Owls	Summer				Fall				Winter			Total
	Jul	Aug	Sept	Total	Oct	Nov	Dec	Total	Jan	Feb	Mar	
Dunneison (72)	2	24	23	46	40	8	216	221				
Dunneison (74)	28	138	109	246	212			212				
Fuch (74-75)	29	17	27	63	45	95	25	140	142			142
Island A (72)	14	6	60	67	23	19	495	498				
Island B (72)	17	21	80	88	77	71	1 549	1 549				
Draeger (72)	28	3	33	49	19	2	7	38				
Killian (73)	30	83	121	176	120	148	11	216				
Hwy 19 (73)	28	118	193	244	110			110				
Average	22	51	81	119	81	83	384	421				

¹ Area in hectares.

cover type within an owl's home range.

The quality of a breeding territory in terms of "included" cover types has been discussed by Southern (1949) and Lack (1966:144-45) when speculating about so-called "marginal" territories. Southern (1959) used food habits and adult mortality to measure quality of tawny owl territories; owls occupying low quality or marginal territories "relied heavily" on birds and suffered high adult mortality. Lack (1966:144) found that juvenile tawny owls were forced into marginal areas as a result of territorial behavior of the more dominant adults. Similarities in cover type composition of home ranges of successful and unsuccessful owls at Waterloo tend to discount the concept of marginal areas (assuming cover types were indices to food resources).

Different cohorts of owls at Waterloo defended territories containing similar percentages of the various cover types. These preferences are shown in Table 32. No conclusions

about successful females are drawn since activities associated with incubation and brooding greatly restricted their movements. A comparison of successful with unsuccessful males showed a highly significant difference in cover type utilization ($P < 0.01$, $X^2 = 23.2$, $df = 6$). Unsuccessful males used woodlands to a greater extent than their successful counterpart. I believe the responsibility of feeding a mate and nestlings forced the successful male to hunt more in lowland pastures and strip cover. Utilized cover types also differed significantly when unsuccessful males were compared to unsuccessful females ($P < 0.01$, $X^2 = 21.2$, $df = 6$). Unsuccessful males also utilized woodlands more heavily than did unsuccessful females. The latter cohort utilized marsh/shrub-carr and upland pastures more heavily than unsuccessful males. The high use of woodlands by unsuccessful males possibly reflects a greater interest in territorial defense and courting.

Baumgartner (1939:274) found evidence to suggest that male owls assumed a dominant territorial role by vigorously hooting over a 6-wk period, while females were heard for only 1 to 2 wk.

Activity Patterns. Roosting sites used during the winter were chiefly in upland white oaks that retained their leaves, or in large, densely branched black willows on lowland sites. Courting pairs used common roosting sites prior to nesting, and frequently hunted together. Vine-covered trees and evergreens, reported as common winter roosting sites by Baumgartner (1939:279) and Austing and Holt (1966:62,64), were seldom used at Waterloo. At the onset of laying, successful males began roosting within 75 m of the nesting sites, using a variety of roost sites when protective cover was scarce. Courting, unsuccessful pairs maintained common roosting sites and hunting areas throughout the winter.

TABLE 35. Summer and fall habitat preference indices of great horned owls near Waterloo.¹

Cover Type	Summer		Fall	
	Males	Females	Males	Females
Upland Hardwoods	5.2	3.7	5.5	3.9
Lowland Hardwoods & Tamaracks	2.4	19.5	3.5	21.3
Marsh/Shrub-carr	1.0	1.0	0.5	1.5
Upland Pasture & Grasslands	0.4	0.5	0.1	0.9
Lowland Pastures	0.2	0.6	0.3	0.5
Cropland	0.3	0.2	0.3	0.3
Strip Cover	0.3	1.2	2.3	0.4
Miscellaneous Cover	4.0	3.1	1.0	1.0

¹ Preference indices after Robel et al. 1970:293; habitat preference: ≥ 1.0 .

By mid-February, territorial hooting virtually ceased and hunting was believed to be the major occupation of males. Hunting was generally confined to woodlot edges or along streams overlooking permanent pastures with a good growth of grasses or marsh/shrub-carr vegetation (height > 15 cm). Heavily grazed pastures and croplands were seldom used by hunting owls. Perch hunting was the principal method of hunting used by adult owls. At no time during the study were owls observed or monitored "course" hunting (ranging or hunting by flying back and forth at low levels over vegetation).

Seven to 14 d prior to the laying of the first egg, nesting females restricted their nocturnal activity to the immediate vicinity of their selected nesting site. Roosting near the nest sites rarely occurred prior to laying. Errington (1932c:217) and Baumgartner (1938:275) believed that several months before the eggs were laid, great horned owls selected and roosted close to their future nesting site. Even though the locations of the better nesting structures were well known, it was not possible to predict the precise nesting sites of radio-tagged owls at Waterloo until just before laying began. Courting owls seemed to be aware of most suitable nesting structures within their home ranges, and, during the 4-wk period prior to egg laying, owls were known to inspect suitable nests. The Dunneison female, for example, was monitored to three known nesting sites during late January and early February, although laying did not begin until 20 February 1975. An inspection of 2 known nesting sites after her visits revealed track imprints in the snow on the nest and fresh whitewash. The Dunneison female's first recorded active telemetry fix at her 1975 nesting site was made on 28 January 1975, while

her first roosting fix was made on 20 February 1975 — the very day she began to lay eggs. Females performed all the incubation and brooding, whereas males supplied the food. Males were never found incubating at any time.

Spring

Home Range Size. The average home range size of successful males decreased from 251 ha in March to 126 ha in April, then increased to 206 ha in May (Table 30). In June, successful male home ranges declined to an average of 175 ha. The reduced April home range was unexpected, yet it was a consistent feature of each tagged male owl that was successful. During April, the successful female was still concentrating her activities around the nest, and, therefore, the food-gathering demands on the successful male must have been at or near the seasonal peak. The decreased home range of successful males in April must have been associated with increased prey availability and/or vulnerability — presumably the result of an influx of migrating birds, increased small mammal breeding activity, and/or the dispersion of wintering pheasants.

Mean home range size for all 3 spring months was 376 ha for successful males and 113 ha for successful females. The scattered movement pattern observed in late winter became less noticeable in May and June, and active locations tended to be concentrated to 4 to 6 locations per month.

Home range size for unsuccessful owls was 147 ha in April. During May, average size declined to 110 ha, then increased to 184 ha in June. The

spring home range for the single unsuccessful male monitored was 279 ha; spring home ranges for unsuccessful females averaged 280 ha. Spatially, the winter and spring home ranges for unsuccessful owls were nearly identical.

Habitat Preferences. Certain cover types were used disproportionately to their availability on the WSA ($P < 0.01$; for unsuccessful males: $\chi^2 = 262$, $df = 5$; for successful males: $\chi^2 = 682$, $df = 8$; for unsuccessful females: $\chi^2 = 896$, $df = 5$; for successful females: $\chi^2 = 706$, $df = 5$). Woodlots and marsh/shrub-carr were used more than expected, while cropland and pastures were utilized less than expected on the basis of occurrence.

Actual area of the various cover types within the home ranges of successful males again were not significantly different from the corresponding values for unsuccessful owls of either sex ($P < 0.10$) (Table 31). Highly significant differences were observed in cover type utilization (actual use within the territory) by successful and unsuccessful males ($P < 0.01$; $\chi^2 = 22.1$, $df = 6$), and unsuccessful female and male owls ($P < 0.01$; $\chi^2 = 89.3$, $df = 6$).

Nesting activities continued to restrict the movements of successful females which remained near their nestlings even after plumage growth of the young required little or no brooding (at around 4 wk). Successful females did not resume hunting until the young had fledged in mid-May, at which time hunting was concentrated in marsh/shrub-carr and lowland pastures (Table 33). Successful females did not simultaneously hunt the same area with their mates. However, common roosting sites, close to the fledged young, were noted.

Marsh/shrub-carr became a preferred spring cover type (not



Owls were also frequently found in marsh/shrub-carr cover during all seasons except winter. The presence of trees as elevated hunting perches was believed to be an important requirement for owl use.

preferred during the winter) of all owl cohorts, possibly due to an influx of prey associated with wetlands. Such prey were not available during the winter (Table 32). Successful males continued to prefer woodlots and strip and miscellaneous cover to a degree similar to winter usage, while the unsuccessful males still maintained a greater use of woodlots. Unsuccessful owls were nearly identical in terms of their habitat selection, although females also preferred pasture (Table 33).

Hunting Activity. Winter-to-spring changes in cover preferences were associated with corresponding seasonal changes in the owls' food habits. Dramatic increases in the spring utilization of passerines (changes in means from winter to spring were 2% and 9% biomass, respectively) and pheasants (6% compared to 23% biomass) were believed to be related to the increased owl use of marsh/shrub-carr and lowland pastures. Red-winged blackbirds and common grackles, commonly found in or migrating through wetland cover (Robbins, Bruun, and Zim 1966:280-82; Green and Janssen 1975:167,170) were by far the most common passerine prey species, representing half of all identified passerines. Dumke and Pils (in press) noted that radio-tagged pheasants at Waterloo established their initial nests in late April to early May in home ranges consisting primarily of wetland cover. A winter-to-spring decline in the consumption of cottontails (from 66% to 47% biomass) was possibly related to the decreased use of woodlots.

Summer

Home Range Size. Mean monthly home ranges for fledglings, initially 22 ha in July, increased to 51 ha in August and to 81 ha in September. The mean, 3-month summer home range of fledglings was 119 ha (Table 34).

Monthly mean home range sizes for adult owls of both sexes also expanded as the summer progressed. Average

sizes were 85 ha in July, 172 ha in August, and 217 ha in September (Table 30). Average adult male home range size during the 3 summer months was 343 ha, while that of females was similar, averaging 316 ha. Cover type utilization by females was not significantly different from that of males ($P < 0.05$, $X^2 = 12.3$, $df = 6$). Both sexes of horned owls continued to prefer woodlots, marsh/shrub-carr, and miscellaneous cover. Summer use of strip cover declined below 1.0 for male owls, although females now preferred this habitat (Table 35).

Habitat Preferences. Great horned owl movements during the summer season were not random ($P < 0.01$; for males: $X^2 = 143$, $df = 5$; for females: $X^2 = 591$, $df = 5$). Woodlots and miscellaneous cover were used more than expected solely on the basis of random movements. Marsh/shrub-carr was used in proportion to its presence on the landscape.

Spring and summer hunting habitats of adult owls were similar. Woodlot edges and marsh/shrub-carr cover were the primary cover types hunted. In spring, vegetation adjacent to woodlot edges or in wetlands was fairly short (generally 10 cm or less). However, as the growing season progressed, vegetation height increased substantially without a pronounced change in owl hunting habits. Dunstan (1970:102) observed a pronounced hunting use of areas with exposed ground; areas hunted were often cropped fields that were recently disced, cut, or harvested. At the WSA, increased usage was made of cropland



in summer, as the observed to expected summer ratio (1:4.6) was more balanced than in spring (1:7.4). Generally, vegetation less than 45 cm tall, adjacent to suitable hunting perches, received greater use than higher vegetation. However, WSA owls did not display any pronounced shift to areas with exposed ground or extremely low vegetation.

Activity Patterns. Fledged horned owls remained almost entirely dependent upon the adults for food and protection until early June when the number of activity locations in common with adult locations began to diminish. By early August, the fledglings were for the most part hunting on their own within the parental home range, although they still roosted near the adult female. An example of decreasing fledgling reliance on their parent could be seen with the Dunneison fledgling owl. In July, 76% of the Dunneison fledgling's roosting sites were with or near the female parent. Common sites declines to 56% in August, 53% in September, and 29% in October. Little fledgling movement outside the natal woodlot was observed during June and July. Generally, the type of cover surrounding the natal woodlots determined the movements, and, therefore, the home range size of fledglings during the summer. Fledglings in natal woodlots isolated from other wooded areas by open pasture or cropland moved less than fledglings in natal areas adjacent to marsh/shrub-carr or to adjoining woods.

Hunting was typically from an elevated perch. However, two fledglings were once observed hunting by walking about on the ground in a woodlot and a grazed pasture. Dunstan (1972:56) also reported ground hunting by fledgling horned owls feeding on grasshoppers and other insects in cattle pastures. Ground hunting appears to be used by fledgling owls while developing aerial or perch hunting skills. Although ground hunting by adult owls was not observed, crayfish and insect remains at tethering sites suggested that this activity occasionally occurred.

Paired owls began roosting and hunting separately in early June, and by the first of August pair-bonds seemed non-existent. Both members of a pair hunted and roosted independently, although considerable home range overlap was still noted. Baumgartner (1939:277) found nesting pairs of horned owls in New York apparently ceased their territorial behavior and led a solitary existence after the nesting season was over and the fledglings were essentially taking care of themselves. Territorial boundaries between adjacent pairs began to

break down in July and abnormal movements or range extensions were observed in some females. The Draeger female, for example, was monitored in several new locations in August that increased her monthly home range from 115 ha in July to 262 ha. However, the majority of telemetry locations were still within the home range mapped out in winter and spring. The known range overlap between adjacent adult females was not more than 15 ha, while adjacent male and female owls shared a common range of up to 50 ha.

Roosting patterns during the summer were variable. Adult owls found a wide variety of suitable sites

Female and male home ranges were 248 ha and 120 ha in November and 276 ha and 161 ha in December, respectively.

Habitat Preferences. Non-random movement characterized the fall season ($P < 0.01$; for males: $\chi^2 = 545$, $df = 6$; for females: $\chi^2 = 539$, $df = 5$). In addition, cover type utilization by adult owls differed between sexes ($P < 0.01$; $\chi^2 = 110.4$, $df = 6$). Adult males utilized, in order of descending preference, upland hardwoods, lowland hardwoods and tamaracks, strip vegetation, and miscellaneous cover. Females, however, preferred lowland hardwoods and tamaracks,

TABLE 36. *Dispersal timing and direction of great horned owl fledglings at Waterloo.*

Owlet	Dispersal Date	Direction of Dispersal
Dunneison	24 December 1972	Southwest
Fuchs	29 January 1975	Southwest
Island A	28 December 1972	North
Island B	27 December 1972	North
Draeger	22 December 1972	Northeast
Killian	5 December 1973	South
Hwy. 19	9 October 1973	Northwest

in hardwood stands, tamaracks, or open-grown trees in wetlands. For example, from a total of 13 monitored diurnal telemetry fixes for the Jordan female owl, 9 different roosting sites were observed in August. Ground roosting, as observed in South Dakota by Dunstan (1970:94) when the air temperature exceeded 19°C, was never known to occur at any time during the summer or fall months on the WSA.

Fall

Home Range Size. As the juvenile owls began to disperse, mean sizes of fledgling home ranges increased to 81 ha in October, 83 ha in November, and 384 ha in December. The mean, 3-month fall home range of fledglings was 421 ha. Monthly home range means for adults were 300 ha in October, 184 ha in November, and 219 ha in December. The mean for adults in fall was 433 ha. In October, both males and females occupied similar-sized home ranges, 283 ha and 310 ha, respectively. November and December home ranges of females were twice the size of those of males.

upland hardwoods, marsh/shrub-carr, and miscellaneous cover (Table 35). Although it is generally thought that the male initiates courtship and territorial defense activities (Baumgartner 1939:274; Karalus and Eckert 1974:250), fall habitat preferences of males, which remained essentially unchanged from the summer, provided little supportive evidence for the hypothesis.

Dispersal of Fledglings. Fledged owls remained within the parental home range until late December. An indication of the timing and direction of dispersal was obtained from 7 radio-tagged fledglings (Table 36). Dispersal dates ranged from 9 October to 29 January. The peak occurred during the last week in December when 4 owls left their natal areas. Timing of dispersal was believed to reflect renewed courtship and territorial activities by resident pairs. An example of forced fledgling dispersal was observed at the Fuchs site in the 1974-75 breeding season. The Fuchs fledgling failed to disperse in late December as anticipated, and was commonly located roosting with the female throughout December and January. Intentional flushes of the adult female once weekly in January failed to confirm the

TABLE 37. Comparisons of cover types comprising home ranges of adult great horned owls at Waterloo.¹

Cover Type	Winter ²	Spring ²	Summer	Fall	Average for All Seasons
Upland Hardwoods	19.5	17.2	20.9	22.0	19.9
Lowland Hardwoods & Tamaracks	15.1	17.9	13.6	16.2	15.7
Marsh/Shrub-carr	56.6	47.3	38.9	70.1	53.2
Upland Pasture & Grasslands	28.9	28.8	30.3	37.4	31.4
Lowland Pasture	48.6	50.5	53.8	63.3	54.1
Cropland	125.4	117.2	146.9	173.2	140.7
Strip & Miscellaneous Cover	13.0	11.3	14.0	17.3	13.9
Total	307.0	290.9	318.3	399.5	328.9

¹ Area means in hectares.

² Successful females not used.

TABLE 38. Home range overlap in the unsuccessful Jordan female - Draeger male pair.

Month	Common Home Range ¹	Percent of Monthly Area Range Shared with Mate	
		Jordan Female GHO	Draeger Male GHO
January	91.5	61.8	75.0
February	119.3	45.7	63.1
March ²	108.5	49.5	58.3
April	50.5	34.8	20.7
May	23.2	20.4	12.6
June ³	None		

¹ Area in hectares.

² Winter mean 60 %.

³ Spring mean 15 %.

presence of a second, untagged owl as its possible mate. The last monitored date of common fledgling-parent roosting was 29 January 1975. On 9 February 1975, the fledgling was found roosting to the south of all previously monitored locations, well outside the parental territory. Walking in on the adult female on 5 February 1975 revealed the presence of a second, untagged owl. This second owl was believed to be the newly acquired mate of the Fuchs female. However, the Fuchs adults failed to establish a nest in 1975, possibly because of this late pair-bond formation.

Stewart (1969:156,161) observed random fledgling dispersal during fall and winter months. Dispersal in a particular direction was also not evident at Waterloo (Table 36).

During the study, 49 great horned owl nestlings were banded within, or immediately adjacent to, the WSA. As of January 1978, only 3 recoveries (6%) have been received. Two banded fledglings were recovered during the hatching year. One owlet was illegally

shot 11 km north of the breeding location during the first week of November. The second bird was also found shot 8 km southeast of its nest site during the first week of January. A third owl was found dead near Kankakee, Illinois, 257 km south of the banding site, 2 yr and 3 months after banding. Stewart (1969:156) found that only 2 of 202 owls banded south of Latitude 50°N had travelled more than 160 km when recovered. Although young great horned owls were prone to move more than adults, the *B. v. virginianus* race (American Ornithologists' Union 1957:277-79) appears to be relatively sedentary or tends to return to its natal area to breed (Stewart 1969:156,158).

Other Activity Patterns. From early July to early December, adult owls led a virtually solitary existence except for juvenile-female adult contacts. Radio-equipped fledglings were never found with their male parent during the summer-fall. In early December common movements and

roosting locations of adult owls signaled the re-establishment of pair-bonds. This re-establishment was a matter of degree. The Draeger pair had a 75% home range overlap during the summer, and while the owls were never monitored together at the same location after early July, they used many of the same sites for nocturnal movements and roosting. The Draeger male apparently did not change his movement patterns or home range size, yet in October he had a 25% overlap with the immediately adjacent Jordan female. There was no range overlap between the Draeger male and the Jordan female in September, but the Jordan female greatly expanded her range from 48 ha in September to 210 ha in October. Although it appears that she initiated contact, this may have been in response to the Draeger male whose mate from the previous year died in September. By December 1974, the Draeger male and the Jordan female had evidently established a pair-bond as they were commonly monitored

together during the night and while roosting. The fate of the Jordan female's mate from the 1975 breeding season is unknown, although she was flushed with a second untagged owl, assumed to be her mate, in January-February 1973. The Jordan male may have left the area, died, or remained undetected in his former home range. The Jordan female shifted her fall-winter range substantially in 1974-75 to conform to the range of Draeger male. Her movement seemed to suggest that female owls were more flexible in shifting range patterns while the males apparently maintained fairly stationary home ranges.

Hunting activities of the WSA owls remained unchanged over the summer-fall period. Roosting patterns became less flexible during the fall as the loss of deciduous leaves greatly reduced potential roosting sites. Upland hardwoods received greater roosting use in the fall, in part because of availability of leafy oak roosting sites and also because of the resumption of courting which was concentrated in upland hardwoods.

Fledged owls hunted and roosted almost entirely on their own during the fall, although they still remained within the parental home ranges prior to dispersion. In the fall, fledglings made increased use of marsh/shrub-carr for hunting, although summer-fall roosting cover preferences remained virtually unchanged. The observed to expected ratio for nocturnal utilization of marsh/shrub-carr was 1:0.8 during the summer, compared to 1:1.2 in the fall.

Effective Hunting Range

Great horned owls were present in certain parts of the WSA throughout the study period, while other tracts of land consistently remained devoid of owls. Plotted home ranges of breeding pairs appeared to follow or were located near waterways. Spatial-temporal means for cover types used by WSA great horned owls were quite consistent between the various seasons (Table 37). There was no significant difference between the proportion of cover types in the home ranges of great horned owls ($P < 0.01$; $\chi^2 = 8.8$, $df = 18$). An indication of home range habitat typical of WSA horned owls was obtained by averaging the seasonal cover type means. The heavy utilization of woodlands and marsh/shrub-carr by radio-tagged owls strongly suggested that within the average 319-ha home range, the most essential cover was the 27% (89 ha) in woodlands and marsh/shrub-carr. The wide geographic range of

great horned owls indicates a very adaptable predator capable of using a variety of habitat types. However, great horned owls at Waterloo apparently did not course hunt or otherwise utilize certain tracts of land.

The amount of land actually utilized by an owl at Waterloo was actually far less than the calculated seasonal home range. The calculated home ranges represented "maximum" sizes, whereas the area actually used (the "utilized" home range) was somewhat less than the maximum boundaries. Odum and Kuenzler (1955:129) believed that a utilized home range was dependent upon the distribution of habitat features within the maximum home range, location of perches, feeding and nesting sites, and whether the male or pair actually made use of all of the defended area. Plotted activity locations of radio-tagged owls revealed that much of the land within home range boundaries probably was never used. Odum and Kuenzler (1955:120) conceded that the utilized home range would have more biological meaning; however, they did not establish any criteria for its determination. The approach examined at Waterloo for estimating utilized range was based on two assumptions: (1) the effective hunting distance of an owl from an elevated perch was 90 m (Fred Baumgartner, pers. comm.); and (2) all monitored activity locations were elevated perches from which the owls hunted. The area 90 m from each monitored, active location was measured, summed, and compared to the total range. The radio-tagged, adult owls had a utilized home range that encompassed about 40% of the maximum home range during the winter, spring, and fall, and 30% during the summer.

Home range overlap in paired owls also reduced the amount of land actually used. For example, the Jordan female - Draeger male unsuccessful pair had a 60% range overlap during the 1975 winter, and actually used only 430 ha of the expected combined home range of 614 ha (Table 38). During the spring, range overlap by the Jordan-Draeger pair declined to 15%, or a paired (combined) home range of 539 ha. Home range overlap in successful pairs was 80% during the winter (paired range of 368 ha), and 60% in the spring (407 ha).

The amount of land actually (effectively) hunted by great horned owls during the winter-spring, the most important seasons from a predation standpoint, would, therefore, be around 40% of the combined home range. The estimated actual home range of owl pairs during the winter was 172 ha for unsuccessful pairs and 147 ha for successful pairs. Corresponding spring values were 216 ha and 163

ha, respectively. Over the study, 34% of the paired owls were unsuccessful and 66% successful. Overall, the population of great horned owls actually used only an estimated 1791 ha or 21% of the 8373-ha study area in the winter. During the spring, the estimated actual range was 2087 ha or 25% of the WSA. Although actual range estimates are based only on tentative assumptions and a small amount of radio-telemetry data, I concluded that WSA great horned owls actually utilized only a small portion of the area they inhabited.

RED-TAILED HAWK BEHAVIOR

Background

This descriptive narrative of red-tailed hawk behavior is based primarily on observations and monitoring of radio-tagged hawks. The lack of information on unsuccessful redtails made a statistical comparison of successful and unsuccessful hawks impossible. My analysis was, therefore, based upon 2 hypotheses (with seasonal comparisons made between sexes), the first testing for random movement, and the second examining habitat utilization with preference indices after Robel et al. (1970:293).

The behavior of 9 radio-tagged adult and 4 fledgling redtails was studied. In addition, 8 adults were color-coded with fluorescent paints during the March-April period of 1971. Adults provided 1979 radio-days with 2782 locations (2518 active, 264 roosting). The 4 fledglings yielded 381 radio-days with 655 locations (593 active, 62 roosting) (Tables 39-40, Appendix III). During the spring of 1973, both members of a breeding pair, and their only fledgling, were simultaneously equipped with radios.

Winter

Home Range Size. The mean size of winter home range for both sexes was 164 ha. Size of the average male's range (157 ha) differed little from that of the female (167 ha). Monthly home range (means) were of similar sizes for January (110 ha), February (108 ha), and March (92 ha). Little difference in monthly means was noted between sexes.

Fitch, Swenson, and Tillotson (1946:207) found that redtails have circular or oval home ranges which

TABLE 39. Seasonal summary of active or diurnal locations, roost or nocturnal locations, and radio-days for adult and juvenile red-tailed hawks at Waterloo.¹

Hawks	Winter			Spring			Summer			Fall			Total		
	No. Locations		No. Radio-days												
	Active	Roost		Active	Roost		Active	Roost		Active	Roost		Active	Roost	
Fledglings				21	1	62	564	59	291	8	2	28	593	62	381
Adults															
Females	604	58	451	456	53	466	342	54	344	167	39	184	1 569	204	1 445
Males	375	23	163	189	9	182	224	8	97	161	20	92	949	60	534
Total	979	81	614	645	62	648	566	62	441	328	59	276	2 518	264	1 979

¹ For detailed table, see Appendix III.

TABLE 40. Monthly home range sizes of adult red-tailed hawks at Waterloo.¹

Individual Redtails	Winter				Spring				Summer				Fall			
	Jan	Feb	Mar	Total	Apr	May	Jun	Total	July	Aug	Sept	Total	Oct	Nov	Dec	Total
<i>Successful males</i>																
Daye RT (73)		126	117	160												
Baumann RT (73)	56	121	130	160	69	131		147								
Hensler RT (73)		138	89	150	103	143	7	179	90	79	32	117	108	103	71	390
<i>Successful females</i>																
Draeger Conifers RT (72) ²	25	91	86	132	83	46		91			44	44				
Knoll RT (72)		67	131	152	106	22		91	95	105		206				
Island RT (72)	253	213	153	344												
Lillie RT (74)		25	67	72	8	19	65	80	91	102	70	197	70	36	10	60
Lillie RT (75)	56	71	21	108	45	73	102	144								
Hensler RT (73)						26	11	31	59	58	36	71	111	75	44	185
Hensler RT (74)	42	120	32	136	28	43	27	72	53	43	23	65				
<i>Unsuccessful females</i>																
Daye RT (72)	225	104		225												

¹ Area in hectares.

² Deserted nest in early April.



Upland pastures with abundant grasses were highly preferred cover for red-tailed hawks. Pastures typically held high rodent populations.

TABLE 41. Winter and spring habitat preference indices for red-tailed hawks near Waterloo.¹

Cover Type	Winter		Spring	
	Males	Females	Males	Females
Upland Hardwoods	3.2	2.9	3.4	3.1
Lowland Hardwoods & Tamaracks	0.4	1.2	0.5	2.5
Marsh/Shrub-carr	1.0	0.9	0.4	1.2
Upland Pastures & Grasslands	2.5	2.1	3.4	2.1
Lowland Pastures	1.4	0.4	1.0	0.4
Cropland	0.3	0.6	0.4	0.4
Strip & Miscellaneous Cover	0.2	0.1	0.6	0.1

¹ Indices calculated after Robel et al. 1970:293; habitat preferences: ≥ 1.0 .

varied spatially according to the number and distribution of perch trees, food supply, territorial pressures, and physiographic features of the terrain. Home range boundaries of Waterloo redtails frequently appeared to follow public roads (which are modified by physiographic features) and woodlot edges containing selected trees which were used often as hunting perches. Redtail home ranges containing large amounts of unbroken lowlands hardwoods (> 15 ha) were larger than home ranges enclosing small, scattered woodlots (typical of upland areas). Redtails seldom utilized the internal portions of dense woodlots, and large blocks of closed-canopy lowland hardwoods were apparently of little value to the redtails. Austing (1964:35) found that redtail pairs occupying "fringe" habitat, primarily large blocks of lowland hardwoods, maintained larger home ranges in order to find sufficient prey. He suggested that the "fringe" area

redtails may be surplus breeding stock since stability of occupation and productivity were poor.

Habitat Preferences. Redtails utilized certain cover types with significantly greater frequency than the relative proportions of these cover types would suggest ($P < 0.01$; for males: $\chi^2 = 364$, $df = 6$; for females: $\chi^2 = 329$, $df = 6$). Non-random movements were generally confined to woodlots and upland pastures and grasslands.

During the winter, a highly significant difference was found between cover types used by male and female redtails ($P < 0.01$; $\chi^2 = 41.7$, $df = 6$). Habitat preferences of both sexes were oriented towards upland pastures and grasslands and upland hardwoods. Males also appeared to select march/shrub-carr and lowland pastures, whereas females also used lowland hardwoods (Table 41). In west-central Illinois, wintering redtails hunted idle grasslands (Froberg

1972:48), but in central Iowa, redtails seem to prefer open woods or stream bottoms (Weller 1964:58). In northern Illinois, Schnell (1968:375) observed that redtails in winter were frequently found in groups or groves of trees (as compared to open trees or poles), as well as corn stubble and grassland, and avoided plowed fields.

The greatest habitat use differences between sexes were found for lowland hardwoods and lowland pastures. It is not unusual, however, for conspecific raptors to demonstrate contrasting habitat preferences based on sex. Recent findings by Mills (1976:740-41) indicated different winter habitat utilization by male and female American kestrels. These differences may also reflect contrasting habitat preferences for prey species with the larger, normally more aggressive females pursuing larger prey (namely cottontails) commonly found along woodlot edges. The role of sex in prey selection of buteos has not been well documented. Woodford (1966:115-22)

acknowledged that falconers using accipiters preferred the female over males because: "...she is able to tackle any larger quarry that may present itself....", and Mueller and Berger (1970:456) found that male sharp-shinned hawks preferred smaller prey than did females. Snyder (1975:551) suggested that prey selection is related to past experience (successes), with a tendency for the birds to select the apparently more profitable prey item in terms of relative biomass. They also may be sex related.

Pair-bonds. Waterloo redtails maintained pair-bonds throughout the entire year. In winter, pairs were commonly observed from sunrise to 1000 h, perched next to each other on the same branch, on the leeward side of woodlots facing the rising sun. Use of the east edges of woodlots may have been related to sheltering from the prevailing northwesterly winter winds, and/or was an attempt at sunning. On overcast mornings, pairs were infrequently seen in these situations, suggesting that the redtails were seeking the more intense warmth of the sun on clear mornings.

The assertion that redtails mate for life in temperate regions (Austing 1964:11,41) and acquire new mates only after the death of one of the birds was not supported by my data. The tagged Daye male provided an example of pair-bond strength. The Daye male was monitored over a 2-month period, and was observed with his mate constructing a nest during late February and early March. On 7 March 1973, the bird was monitored near the southern edge of its home range at 1515 h. At 0800 h the following morning, no signal was received even though 2 redtails were observed on the breeding site, using the same favorite perches. A thorough ground check of the area with a hand-held antenna and receiver failed to locate any shed radio, and approaches of both resident birds failed to pick up the weak signal diagnostic of a broken antenna. Later the same day, the "lost" signal was received a considerable distance south of the previously occupied home range. After following the signal, I observed the Daye male soaring by himself at high altitude. This bird left the WSA shortly thereafter. Either the Daye female had acquired a new mate, or a new pair had taken over the Daye area. Judging from plumage characters, behavioral patterns, and perches used, the female was believed to be the original Daye bird. A new male apparently had replaced the original Daye male at a time when pair-bonds should have been, as the result of courtship, territorial defense, and nest building, at their annual high (Olen-dorff 1971:49). By comparison, other

redtail pairs maintained their pair-bonds throughout the study, suggesting that long-lived pair relationships also existed.

Other Activity Patterns. Froberg (1972:iii) observed that redtails in Illinois followed a daily pattern of perch-hunting from sunrise to 1000 h, soaring during mid-day, and perch-hunting from 1500 h to dusk. Winter hunting at Waterloo was primarily from lookout perches throughout the day without any pronounced soaring at mid-day, although hunting on the wing was occasionally observed. I observed the Island female harassing ("testing?") a flock of pheasants feeding in a picked cornfield at 0900 h. The tagged redtail appeared to be flying in an easy manner about 15 m above ground, when suddenly she made a shallow dive at the pheasants which flushed and flew off in different directions. The hawk pursued 1 pheasant a short distance before breaking contact, then quickly resumed her normal flight to her second perch.

In January, the Baumann redtail was observed making a more typical kill of a hen pheasant. The hawk was hunting from a perch in a 15-m white oak located in a dense, wide (approximately 4 m) fencerow of wild plum and grape vines. What seemed to be a dense overhead of canopy of vegetation for the pheasant was apparently no problem for the hawk to penetrate for the kill. Schnell (1968:375) found that redtails preferred sedentary hunting styles from relatively high (> 9 m) tree perches, allowing the raptor to strike down on ground-dwelling prey.

During early winter, Waterloo redtails spent only a small amount of their active time in actual flight; winter movements were primarily short, straight-line flights. The function of soaring in common buzzards was identified by Tubbs (1974:105) as either territorial advertisement, or searching for prey. Little intraspecific strife was observed among resident pairs during early winter; therefore, it appeared that there was little need of soaring for territorial advertisement. The abnormally mild winters also may have negated the need of soaring to locate prey.

Migrating redtails were first observed in late February, and numbers peaked in mid-March. A similar pattern was observed by Orians (1955:5) in Green County, Wisconsin. With the appearance of migrants, resident pairs at Waterloo started to soar more often, presumably in territorial defense. Tubbs (1974:105) observed three peaks in territorial activities of resident common buzzards in England: (1) during spring courtship; (2) during late nesting when feeding

large young; and (3) after the young dispersed, prior to winter. The "spring" peak in redtail courtship at Waterloo occurred during March, prior to clutch initiation.

Roosting patterns were rigidly maintained in terms of location, cover type, and mate association. While simultaneously monitoring the Hensler pair during 1973, I found that both birds consistently used only 3 roosting areas, all in upland hardwoods, and invariably roosted close together. Typically, the wintering birds moved independently to their roost about one-half hour before sunset. Shortly after sunrise, the pair normally moved a short distance to a common location on the east edge of their roosting woodlot, where they remained until mid-morning.

Spring

Home Range Size. Non-random movements also characterized redtails during the spring ($P < 0.01$; for males: $\chi^2 = 214$, $df = 6$; for females: $\chi^2 = 442$, $df = 6$). The mean size of the spring home ranges of both sexes was 106 ha, with males maintaining mean home ranges of 163 ha compared to 85 ha for females. The mean size of male home ranges remained roughly the same in both the winter and spring, but the female's mean home range size declined about 40% in spring. This decline therefore primarily reflected a functional change by the female.

The mean home ranges of both sexes combined remained were fairly consistent for April (72 ha), May (69 ha), and June (65 ha). However, males displayed a 60% increase in home range size between April and May, which coincided with hatching. I believe the increase in range of males was related to their increased hunting activity in order to provide food for newly hatched chicks. Fitch, Swenson, and Tillotson (1946:208) found a smaller spring territory because much of the hunting was done only in a limited part of the redtail's territory close to the nest, and the remainder of the area was used less than in other seasons. The spring home range at Waterloo was the smallest, although the proportion of cover types used was not significantly different between seasons ($P < 0.01$; $\chi^2 = 36.3$, $df = 21$) (Table 42). However, the smaller spring home range was largely due to the female's involvement with nesting, while the male hunted and continued to occupy large, winter-spring home ranges.

Habitat Preferences. Habitat preferences of both sexes in spring remained essentially unchanged from

TABLE 42. Spatial means of cover types used by adult red-tailed hawks at Waterloo.¹

Cover Type	Winter	Spring	Summer	Fall	Average for All Seasons
Upland Hardwoods	13.5	10.0	11.1	13.3	12.0
Lowland Hardwoods & Tamaracks	8.8	3.2	4.6	11.7	7.1
Marsh/Shrub-carr	30.5	15.3	9.1	80.1	33.8
Upland Pastures & Grasslands	17.4	11.3	15.1	16.1	15.0
Lowland Pastures	28.2	29.1	35.4	21.8	28.6
Cropland	57.9	34.8	37.3	61.0	47.8
Strip Cover	1.7	0.7	1.3	1.5	1.3
Miscellaneous Cover	5.7	1.8	2.8	6.1	4.1
Total	163.7	106.2	116.7	211.7	149.6

¹ Area means in hectares.

the winter (Table 41). Although males no longer preferred marsh/shrub-carr, they were still oriented to upland hardwoods, pastures and grasslands, and lowland pastures. Females showed a spring preference for upland and lowland hardwoods, marsh/shrub-carr, and upland pastures and grasslands. Cover types used by males differed significantly from those used by females ($P < 0.01$, $X^2 = 60.4$, $df = 6$). In terms of lowland habitat types, males continued to prefer lowland pastures, while the females selected lowland hardwoods. The females' strong orientation to the nest during late winter and early spring apparently accounted for a pair's preference for lowland hardwoods. In contrast, a hunting male would have been more successful in finding prey in lowland pastures. The high use of lowland pastures and marsh/shrub-carr by adults created the potential for frequent pheasant-redtail encounters, and was believed responsible for the high predation rate on pheasants in spring.

Nesting. Austing (1964:49) observed that both sexes assisted in nest construction, with the female performing all the incubation; the role of the male was mainly as a provider of food. Nest failures in Ohio (Austing 1964:35) were linked to the inability of the male to provide sufficient food, forcing the female off the nest to hunt for herself. In Massachusetts, Bent (1937:151,153) believed both sexes assisted in nest building, with the female again performing all the incubation, and her mate providing food and occasionally helping to feed the young. At Waterloo, 3 different nesting pairs were kept under close observation. Nest construction involved both sexes although the female spent the greater portion of her time forming the nest and bowl. Branches for nest construction were gathered by the birds flying to nearby trees, grasping a selected branch with their bills and pulling until it broke, or until it became evident that the branch was too strong, whereupon the bird would select another branch. Returning to

the nest, the redtail carried the branch in its bill, and landed on the nest edge to place the branch. The pair usually constructed a nest in 4 to 7 d. The choice of nesting material depending primarily on availability, and no preferences were noted. The bowl was usually lined with corn husks, (sometimes with cottonwood or aspen bark), and topped with fresh evergreen or newly emergent deciduous leaves. The birds continued to deposit "greens" in the nest until the nestlings were about 4 to 5 wk old.

Both sexes incubated at Waterloo. The female assumed the dominant role, while the male regularly sat on the eggs for periods of from 15 min to 5 h. In all cases, the female incubated during the night. The typical procedure was for the male to take over incubation at about 0900 h to 1030 h, when the female flew off to nearby hunting perches. The male also often incubated in the afternoon shift, usually for a shorter time, but sometime lasting up to 3 h. Although the male was observed bringing food to the incubating female, she usually hunted for herself. During the last week of incubation, the male's incubation time declined to 1.5 h or less per shift.

Once the eggs hatched, the male functioned solely as a provider of food, and the female performed all the brooding. The female remained strongly attached to the nest until the young were approximately 5 wk old (around the first week in June) although she would occasionally leave the nest for brief hunting-exercise trips. The frequency and duration of such trips increased as the young approached 5 wk of age.

The 5-wk old young were apparently sufficiently feathered to require little or no brooding. Without the need to brood, the female shifted her daily activities rather dramatically to hunting, and rarely even roosted near the

Lowland pastures with scattered trees were heavily used by hunting redtails. Cover types without trees for hunting perches were seldom used.



nest. Austing (1964:65) reported that the female began hunting when the young were about 3 wk old.

A curious interspecific relationship was observed. English sparrows commonly built their nests, woven mostly out of quack grass, within the much larger nest of the redtail. As many as 2 active sparrow nests were found within a redtail nest, and all 3 nests had nestlings at the same time. Barger (1941:65) also reported the occurrence of 3 English sparrow pairs nesting in 1 redtail nest near Ixonia, Wisconsin. It appears that the sparrows, true to their weaver ancestry and wide adaptability, were able to colonize the rather secure nesting site.

Other Activity Patterns. In southern Wisconsin, Orians (1955:5) determined that spring migration of redtails was usually completed by the end of April. At Waterloo, migrating redtails were rarely observed during the last half of April. Typically, migrating redtails evoked an immediate response from nesting redtails, resulting in soaring conflicts unless the migrant maintained a fairly high altitude. Tubbs (1974:109) found that the common buzzard in Britain defended a vertical breeding territory that varied from 122 m to 244 m, while Fitch, Swenson, and Tillotson (1946:208) noted a similar pattern in California redtails.

Spring roosting patterns of both sexes were modified by nesting; however, the female's choice of roosts was affected the most. Incubating and brooding kept the female strongly attached to the nest at night. In most cases, the male continued to use his winter roosts. Occasionally he roosted near the nest site, although this distance was believed to be related to availability of roosting sites. For example, the Knoll pair nested on a very small drumlin surrounded by a large area of treeless terrain (at least 0.4 km), and the male, therefore, invariably roosted on the drumlin near the nest site, which was 0.5 km from the winter roost. The Hensler pair, on the other hand, nested within 0.3 km of the primary winter roost, and the male made frequent use of the latter. Spring roosting sites were primarily in upland hardwoods.

Summer

Home Range Size. Summer home ranges for both sexes averaged 117 ha, with both the males and females maintaining a similar mean range (117 ha). However, the estimated summer home range size was based on only one tagged male, and considerable variations were noted in the sizes of summer home ranges of females (44 ha

to 206 ha). Two tagged redtails had large overall summer home ranges (> 150 ha) in spite of maintaining smaller monthly home ranges (< 105 ha). This would suggest some dramatic geographic changes between months. For example, a tagged female redtail at the Lillie site had an overall seasonal range of 197 ha, while monthly home ranges from July through September were 91 ha, 102 ha, and 70 ha, respectively.

July and August mean home ranges of breeding females were similar (75-78 ha), but declined in September (43 ha). During the latter month, adult females apparently became independent of their young as the fledglings were either fending on their own within the parental home range or had already dispersed. As independence of young hawks became more apparent, the adults shifted their daily activities to other segments of the home range, perhaps to reduce food competition.

Habitat Preferences. Movements of redtails during the summer again were not random, but were generally oriented to upland hardwoods, pastures, and grasslands ($P < 0.01$; for males: $X^2 = 160$, $df = 6$; for females: $X^2 = 184$, $df = 6$). Summer habitat use continued to center around upland hardwoods and cover types generally associated with grasses (marsh/shrub-carr, upland pastures and grasslands, and lowland pastures) (Table 43). As was typical of spring, only males were frequently found in lowland pastures and only the females appeared to prefer marsh/shrub-carr. Females no longer frequented lowland hardwoods, however, possibly resulting from their cessation of all nesting activities. Hunting was the prevalent summer activity, and habitat preferences, therefore, reflected hunting habitat preferences. While much of the home range was shared by each of the resident pairs,

direct competition for food may have brought about some noticeable differences in daily activities as indicated by the different habitat preferences. Except for early morning hours, adults rarely hunted within 100 m of each other over the same cover. A significant difference was observed between proportions of cover types used by males and females ($P < 0.01$; $X^2 = 17.3$, $df = 6$).

Activity of Fledglings. Redtails generally fledged during the first half of June at approximately 6.5 wk of age. During the first 18 d after fledging, the young birds confined their activities to within 150 m of the nest. Their behavior during this period was characterized by short flights, much wing exercise (flapping of wings in a stationary position), and persistent hunger cries. When the youngsters were about 9 wk old, they left the nesting woodlot and moved near the adults' center of activity (focal point of activity within the home range) or actually began following the hunting adults. At 10 wk, the 2 Knoll fledglings were observed to consistently perch near the hunting adults. Once the adults made a successful kill, the fledglings would immediately land next to the adult and beg for food. In contrast, the single Hensler fledglings in 1973 and 1974 were more sedentary, allowing the adults to bring the food to them (Table 44). A single fledgling would probably develop flying skills (and probably hunting skills as well) at a slower rate than fledglings forced to compete with their siblings. The small July home ranges of the Hensler fledglings (7 ha each), compared to the much larger ranges of the Knoll fledglings (58 ha and 76 ha), lend support to this contention. Redtail fledglings in Montana, where nesting chronology was similar to that in the WSA, remained in the immediate vicinity of the nest for 18 d to 25 d

TABLE 44. Summer and fall habitat preference indices for red-tailed hawks near Waterloo.¹

Cover Type	Summer		Fall	
	Males	Females	Males	Females
Upland Hardwoods	2.4	2.9	4.5	2.9
Lowland Hardwoods & Tamaracks	0.5	0.9	0.4	0.4
Marsh/Shrub-carr	0.3	1.2	0.4	0.6
Upland Pastures & Grasslands	2.5	1.3	3.4	3.4
Lowland Pastures	1.5	0.9	1.7	1.7
Cropland	0.4	0.5	0.7	0.2
Strip & Miscellaneous Cover	0.1	0.1	0.4	0.3

¹ Indices calculated after Robel et al. 1970:293; habitat preferences: ≥ 1.0 .

TABLE 43. *Spatial home ranges of red-tailed hawk fledglings on the WSA.*¹

Individual Fledglings	Summer			Total
	Jul	Aug	Sept	
Knoll Imm A ²	76	77	265	313
Knoll Imm B ³	58	61	124	143
Hensler Imm ⁴	7	44	44	53
Hensler Imm ⁵	7	43	25	44

¹ Area in hectares.

² Fledgling permanently left WSA (dispersed) 18 October 1972.

³ Suffered broken wing (humerus) during severe thunder storm 19 September 1972.

⁴ Lost radio-contact 1 September 1973, presumed dispersed.

⁵ Lost radio-contact 31 August 1974, presumed dispersed.

after fledging, with the adults supplying all the food during this time (Johnson 1973:44-45).

The first successful hunting attempt by a fledgling was observed in the first week of August when the fledgling in question was about 12 wk old. Prior to this time, the adults apparently supplied all of the fledgling's diet. Most of the prey items successfully taken by 12-wk-old fledglings were slow-moving frogs, toads, snakes, and some invertebrates. Food begging cries, however, were still heard well into August when the young were around 15 wk old. The mean home range in August of 56 ha reflected the increased movements and development of the juvenile.

Johnson (1973:46) found that juvenile Montana redtails remained associated with the adults (or at least remained within the parental home range) for 30 d to 70 d between fledging (estimated age of 10 wk to 16 wk, and dispersal by the young birds. Tagged WSA redtail fledglings dispersed 80 d to 123 d (at ages 17 wk to 33 wk) after fledging. The WSA fledglings were not capable of sustained, confident flights, until they were 9 wk old. Therefore, it seems unlikely that fledglings would be able to survive on their own at less than 15 wk old. At Waterloo, a fledgling, estimated 13 wk old, wandered into the Hensler territory on 26 July 1973, and began a series of very persistent hunger cries. This unmarked fledgling, which appeared quite hungry, was promptly driven from the territory by the Hensler adults.

By the first week in September, the fledglings apparently provided most of their own food, and their movements increased noticeably over a large part of the parental home range. The mean home range of fledglings in September was 115 ha, or double the size of their average August range. Neither of the

two Hensler fledglings made any effort to leave the home territory until they left permanently. Conversely, one of the Knoll fledglings made several short trips before leaving for good in late October. Similar findings were reported by Johnson (1973:46).

Dispersal direction was observed for only 1, radio-tagged fledgling, which appeared to drift off on a northward course. Six redtails banded as nestlings were recovered (Fig. 6). Five of the recoveries were reported within the hatching year. Four were recovered at least 100 km south of

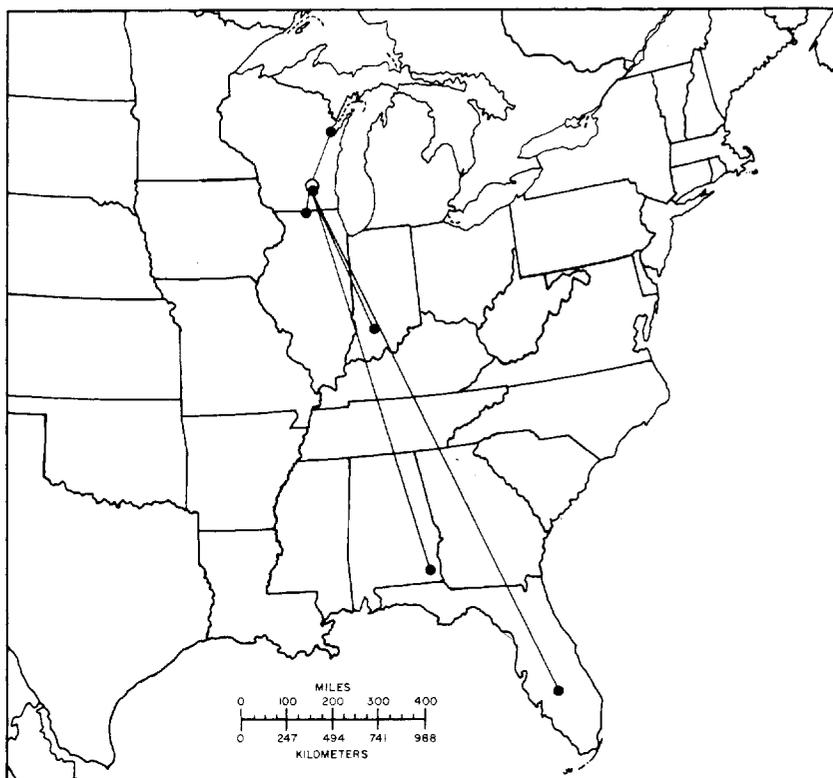
Waterloo. The fifth was reported 184 km to the northeast. Reported first year recovery dates were: 20 August, 24 September, 25 November, 5 December, and 10 December. The single recovery of an adult was reported only 10 km south of the WSA, 44 months after the hawk was banded as a nestling. This suggests that the bird may have returned to the vicinity of the natal area as a breeding adult. Orians (1955:5) observed a high percentage of juvenile redtails inhabiting urban areas in Wisconsin, and speculated that first-year birds found less competition from adults there and were able to tolerate the high human activity associated with urban areas. None of the juveniles banded at Waterloo were recovered in urban areas.

Other Activity Patterns.

Movements of adult redtails during warm summer days seemed to follow a definite pattern. From sunrise to 1000 h, the birds would perch hunt. During the mid-day, the birds would find a cool resting site—usually within the upper canopies of trees. Hunting resumed again around 1530 h in the late afternoon and continued until sunset. Little territorial soaring was observed, although dispersing juveniles were usually promptly driven from the territory.

Redtail pairs were frequently seen hunting within 100 m of each other during early morning hours, especially

Figure 6. *Dispersal of red-tailed hawks banded as nestlings on the WSA.*





when perching on utility poles adjacent to a highway. The birds continued their early morning perch hunting until increasing vehicular traffic forced them to less disturbed hunting sites.

Adults continued to use common, traditional roosting sites in upland hardwoods. Occasionally, fledglings joined the adults, but more frequently the young hawks roosted at different sites. While roosting at the traditional site, the fledgling generally perched closer to the female parent.

Orians (1955:5) found a rather prolonged fall migration, beginning in mid-August and lasting until the first of December. The peak fall migration of redtails appeared to occur from late September through early November. Migrating redtails generally drifted through the WSA without staying for any prolonged period. Some adult migrants did stay for periods of up to 4 months, generally utilizing the "fringe" areas around territories of resident redtails.

Fall

Home Range Size. The mean fall home range size for both sexes of 212 ha was the largest recorded for the 4 seasons. However, the fall mean was based only on 3 tagged birds, with only 2 of them providing extensive data. The October mean home range for both sexes of 96 ha was 4 times that recorded in September. This increase apparently resulted from: (1) territorial defense directed at migrants which peaked in number during October and November; and (2) increased movements caused by the influx of numerous pheasant hunters into the Waterloo area. The October home range size declined in November (71 ha), and again in December (42 ha). During December, migrant redtails were gone, and so were most hunters. The absence of snow cover during December made prey animals easily accessible, and although the adults were spending a greater part of their daily activities together, the period represented an activity lull before the breeding cycle resumed.

The single redtail male maintained a larger fall home range (390 ha) than

the 2 females (123 ha). A sexual difference in territorial defense was expected, with the male assuming the dominant role against the influx of fall migrants. The Hensler male was found throughout most of its territory in all 3 fall months, while the Hensler female, except for October, was generally more sedentary.

Habitat Preferences. In fall, certain cover types were utilized with significantly greater frequency than relative proportions of these types would suggest ($P < 0.01$; for males: $\chi^2 = 205$, $df = 6$; for females: $\chi^2 = 170$, $df = 6$). Fall cover types used by the male redtail were not significantly different from those used by the females ($P > 0.10$, $\chi^2 = 10.3$, $df = 6$). While the male moved about more than did the females, habitat preferences were similar. Upland hardwoods, upland pastures, and grasslands were highly used although some preference for lowland pastures was also noted. Again, hunting was believed to be the primary daily activity, and areas hunted predominantly involved those with grassy vegetation. Areas with grass less than 10 cm high were generally preferred, but adult hawks were occasionally observed hunting over much taller vegetation.

Roosting Activity. The pair of redtails followed the same roosting

pattern noted since early July, continuing to roost together in traditional, upland hardwood sites. A slight shift within the traditional roost was noted, with the birds moving a short distance to the southeast. This movement was believed to be a response to the cold, northwest winds prevalent during late fall and winter.

Color-coded Redtails

At Waterloo, eight redtails were live-trapped from 11 March to 4 April 1971, a time when migrant redtails were commonly observed. Birds were not radio-equipped during this period. Three of the eight redtails proved to be migrants and quickly disappeared from the study area. The remaining five birds were observed from 2 to 15 times each (mean of 8). The fluorescent paints were identifiable by a ground observer for up to 4 months. Green paints had the longest life time and blended in quite well with the natural background, while red paint was believed to be too visible and attracted undesirable (non-investigator) human interference. The spray paint dried within 15-20 s, and feather matting was not a serious problem. In general, spray paints were determined to be feasible only as a short-term marking technique.



INTERSPECIFIC COMPETITION

The great horned owls and red-tailed hawks at Waterloo are two avian predators that depend on 2 common factors: similar staple prey species and similar habitat. Direct competition is minimized through differences in activity cycles. Fitch, Swenson, and Tillotson (1946), Orian and Kuhlman (1956), Hagar (1957), and McInville and Keith (1974) have also examined the interspecific competition between horned owls and red-tails.

WSA horned owls maintained annual home ranges over twice the size (329 ha) of redtail home ranges (150 ha). However, the proportions of cover types within their home ranges were not significantly different ($P < 0.01$; $\chi^2 = 3.9$, $df = 5$) (Table 45). A comparison of cover type components of the home ranges suggests selection by both raptors for predominantly graminoid cover of pastures and grasslands. Hagar (1957:271) indicated horned owls in New York were generally restricted to large woodlots, yet no pronounced orientation to large woodlots could be demonstrated at Waterloo. While WSA horned owls did not seem to select home ranges containing the large blocks of woodlots, they did utilize wooded areas within their home ranges to a much greater extent than was noted for redtails.

Interspecific competition is general-

ly more intense, and therefore, more obvious, during the nesting season than at other times of the year (Olen-dorff 1971:20). The close proximity of active horned owl and redtail nests (Hagar 1957; Smith 1969) suggests that competitive exclusion does not exist. However, territorial spacing of active nests in Alberta (McInville and Keith 1974:7) and at Waterloo indicates some interspecific aggression and competition.

A comparison of home ranges of radio-tagged, successful horned owls and redtails occupying the same area at Waterloo indicated considerable range overlap. For example, over a 6-month period from January through June 1975, a mean of 89% of the Lillie redtail's home ranges were within the corresponding home ranges of the Draeger owls. In February and March, the owls commonly hunted near the redtail's nest. However, from April through June, the owls were never located within the woodlot occupied by the nesting redtails. The redtail, in turn, avoided the woodlots where the owls nested. Competitive exclusion, therefore, seems to occur only for a small area about the active nests.

The stable densities of horned owls and redtails over the Waterloo study suggests that some sort of "saturation" level was reached for resident raptors. A combination of intra- and interspecific territoriality, along with relative stability of total available prey, apparently brought about an optimum density of resident raptors within the available habitat.

TABLE 45. Comparisons of cover types comprising home ranges of great horned owls and red-tailed hawks on the WSA.

Cover Type	Waterloo Study Area	Great Horned Owls		Red-tailed Hawks	
	Percentage	Area ¹	Percentage	Area ¹	Percentage
Upland Hardwoods	4.5	19.9	6.1	12.0	8.8
Lowland Hardwoods & Tamaracks	3.2	15.7	4.8	7.1	5.2
Marsh/Shrub-carr	12.8	53.2	16.2	33.8	24.7
Upland & Lowland Pastures	14.6	85.5	26.0	43.6	31.8
Cropland	56.0	140.7	42.8	47.8	35.0
Strip & Miscellaneous Cover	5.8	13.9	4.2	5.4	4.0
Total ²		328.9		149.6	

¹ Area in hectares.

² Proportion of cover types between species not significantly different at $P < 0.01$; $\chi^2 = 3.9$; $df = 5$.

MANAGEMENT IMPLICATIONS

DIRECT PREDATOR MANAGEMENT

Predators play an important role in the normal functioning of ecosystems, and contribute to the aesthetic quality of our environment (Wis. Dep. Nat. Resour. 1977a; 1977c). Predator management by government agencies involves very complex philosophical, as well as biological, considerations. Policy decisions concerning predator management are not easily made. Among the more controversial decisions relating to predators is their control for the benefit of game populations.

Predator control or reduction has been justified as a tool of wildlife management (Berryman 1971; Broadbent 1971; Jantzen 1971). Predator reduction has been shown to increase game productivity (Balsler, Dill, and Nelson 1968; Chesness, Nelson, and Longley 1968) and survival (Bergerud 1971; Trautman, Fredrickson, and Carter 1974), while still being economically feasible (Beasom 1974). The question remains regarding how and under what circumstances such control, a direct form of predator management, is to be used or is justified.

A direct form of predator management does have some limitations. The federal Migratory Bird Treaty Act of 1972 effectively eliminated the legal "taking" of all raptors native to Wisconsin, taking being defined as "pursuing, hunting, shooting, wounding, killing, trapping, capturing, collecting raptors, or attempting to do so". The only provision which still allows the purposeful destruction of raptors is through a "Depredation Permit" issued by the U.S. Fish and Wildlife Service. These permits are of short duration (not more than one year), and are aimed specifically at birds doing significant damage to crops or other interests in a limited, designated geographic area. A "live-trap, transport, and release" technique as suggested by Berger and Hamerstrom (1962) is one direct method that would not end with the destruction of the raptor. However, resident horned owls and redtails would be difficult to remove effectively because of their homing ability, and furthermore, the vacant habitat would soon attract a replacement. For example, in May 1973, a chicken-depredating adult redtail was live-trapped on a farm north of the WSA.

The bird was color-coded, transported 80 km, and released. The bird was back at the farm in 7 d.

An experimental reduction of great horned owls and red-tailed hawks was planned as one of the original objectives of this study. Raptors were to be live-trapped, transported from the WSA, and released. A corresponding reduction of red foxes was also planned (Pils and Martin 1978:43-44). Fox reduction was scheduled to begin in the fall of 1973, and if such reduction failed to produce a reciprocal response in the WSA pheasant population, then a reduction program involving both foxes and raptors was to be initiated during the final year of both studies.

A re-evaluation of the predator studies in 1973 concluded that the experimental reduction of predators was neither feasible nor desirable. The decision to abandon the red fox reduction was due to: (1) a change in landowner attitudes towards foxes to one more protective in nature, (2) sharply rising pelt prices, (3) establishment of the red fox as a game species in October 1972, (4) the observed ability of foxes to rapidly replace lost resident foxes because of their great mobility, and (5) interference anticipated from other animals (dogs, raccoons, skunks, etc.) in trapping foxes for their removal (Pils 1977:87). The removal of raptors without a corresponding reduction in foxes was not considered a logical alternative.

Furthermore, the removal of great horned owls and red-tailed hawks was believed to be of little value as a realistic pheasant management tool. Raptor removal would require high manpower (an estimated minimum of 20 manhours per trapped raptor) over an extended period of time. I estimate that to achieve a 50% reduction of horned owls and redtails on a 4000-ha wildlife area similar to Waterloo, it would require the full-time use of an experienced trapper for a 6- to 8-wk period (from the end of the fall migration of redtails in late November to late January). This technique is simply not economically feasible on a large scale. Also anticipated with raptor reduction was the adverse public relation problems associated with the removal of raptors solely to achieve a higher pheasant density. It was therefore decided that the time scheduled for the reduction of WSA predators would be better served, from both a research and management standpoint, by the continued collection of predator life history data.

INDIRECT PREDATOR MANAGEMENT

One of the major objectives of this study was to formulate management practices that could conceivably reduce predation on pheasants by raptors. It becomes evident that any management recommendations designed to reduce this predatory pressure must involve indirect methods. Such methods revolve around "habitat manipulation" designed to reduce raptor-pheasant encounters primarily during winter and spring.

Factors such as weather and land use, while having a major influence on pheasant densities, cannot be effectively controlled by management. Only management considerations relating to factors that can be controlled are discussed. For the most part, the following considerations have not been tested, but remain hypotheses, mostly based on my study findings and circumstantial evidence. A lack of study time and manpower restraints prevented a thorough evaluation of the suggested management considerations.

The Waterloo Study Area is by no means atypical to many other large, state-owned wildlife areas in southern Wisconsin. However, the management considerations discussed will only apply to areas where substantial land is state-owned for wildlife purposes.

The Wisconsin Department of Natural Resources recognized two forms of wild life management involving pheasants on state-owned land: (1) an Extensive Wildlife Habitat Program based upon small scattered holdings (up to 32 ha) of primarily wetland vegetation, with less than 10% of the total area within the established projects designated for purchase; and (2) an Intensive Wildlife Habitat Program based upon large projects (up to 4200 ha) covering a variety of habitats (although still emphasizing wetlands) with a minimum purchase goal of 50% of the lands within established boundaries (J. A. Beale, pers. comm.).

Extensive Management

The Extensive Wildlife Habitat Program is primarily designed to preserve and restore critical wildlife habitat for game production. Gates



Winter food patches for pheasants can be potential death-traps for pheasants when planted adjacent to elevated perches (trees). The relative openness of corn-only food patches also contributes to higher pheasant losses.



Predator-resistant dense nesting cover, used primarily in waterfowl management, has the potential to be secure nesting cover for pheasants as well. The measuring board in photo is marked in decimeters.

(1970) outlined guidelines for an extensive program where pheasant nesting and winter cover units are designated and acquired to sustain existing pheasant populations under limited land-buying (economic) capabilities. His goal was 16 ha of winter cover and 105 ha of nesting cover in each 23-km² management block. While labelled "extensive", management of these small parcels is, by necessity, intensive. Recommendations for indirect, intensive management on the smaller parcels aimed at reducing horned owl and red-tail predation on pheasants are:

1) The removal of all trees that could be used as elevated hunting perches. Tree removal on a small scale (only 5% of the total area in each completed 23-km² management block) would have little, if any, effect on regional raptor populations, but would discourage raptors from hunting managed pheasant habitat. Management of acquired blocks of pheasant nesting cover (separate blocks would vary in size from 8 ha to 32 ha) would necessitate thorough tree removal. Tamarack swamps were highly rated by Gates (1970:18) as winter pheasant cover. However, tamarack stands at Waterloo also functioned as preferred raptor habitat in winter and spring, and the trees were commonly used as hunting perches. Pheasants become quite vulnerable when forced to move from tamarack stands to find food. Therefore, the acquisition of tamarack as pheasant winter cover should be discouraged in favor of a greater selection for, and the maintenance of, con-

tiguous blocks of *closed-canopy* shrub-carr (8-12 ha in size) for every 23 km² of land.

2) Emphasis on nesting cover which provides concealment for pheasants. Cover establishment on available upland sites should emphasize tall, dense, rank cool-season grasses and legumes (dense nesting cover or DNC) that has been shown to function as a barrier to ground predator ingress (Duebbert 1969:229; Duebbert and Kantrud 1974:257; Duebbert and Lokemoen 1976:47-48). Ideally, these blocks of cool-season grasses and legumes should vary in size from 15 ha to 54 ha. However, smaller fields may have to be utilized because of a lack of larger parcels. Although this approach is specifically aimed at mammalian predators, I believe DNC can function as an effective barrier to course- or perch-hunting avian predators. Excessive public hunting in DNC may create numerous trails, thus reducing its value as a predator barrier. Low-lying, state-owned land outside the shrub-carr units should also be in nesting cover. Herbaceous vegetation of asters-goldenrods on drained, formerly cultivated wetlands should be encouraged as the cover species, with canary-timothy grass cover as a second choice (Frank and Woehler 1969:806; Gates 1970:4-6). Mixtures or monotypic stands of warm-season grasses also deserve consideration.

3) Emphasis on concealment cover adjacent to winter food patches. A reliable source is essential to winter pheasants. The most

dependable food source should be the food patches planted according to Frank and Woehler (1969:807-8). The cornsorghum mixture should be planted as close to the winter roosting cover as possible, because pheasants that are forced to travel to a food source, especially over open terrain, are more vulnerable to predation. Since corn-only food patches tend to be too open, the addition of sorghum provides overhead protection as well as alternate food. A border of shrubs around the open sides of food patches provides loafing and escape cover. No trees which could be used as perches by hunting raptors should be located within 90 m of the food patch.

4) Priority should be given to acquisition of parcels that can be managed as either high-grade winter cover or reliable nesting cover. The best way to safeguard pheasants from avian predation is to have cover available so that they are not forced into vulnerable situations. Sedge meadows, monotypic canary stands, predominantly cattail wetlands, and floodplain wetlands are not recommended for pheasant nesting cover. Gates (1970:20) stated that the densest and driest wetland cover during April will be of the greatest value to nesting pheasants.

5) Avoiding stocking of pheasants. An active program of stocking pen-raised pheasants on wildlife areas may directly affect raptor predation on wild pheasants. Pen-raised pheasants traditionally stocked on Wisconsin's wildlife areas suffer high mortal-



Ideally, winter food patches for pheasants should be planted adjacent to suitable escape-roosting cover, and at least 90 m from trees that may act as elevated hunting perches for raptors.

ity from the gun and from predation (Woehler, unpubl.). Hessler et al. (1970:267) found a 74% predation mortality of game-farm pheasants stocked in August and September. Horned owls and redtails may become "conditioned" to preying upon the highly vulnerable stocked birds, and, over a period of years, may develop a "specific search image" (Tinbergen 1951) to selectively hunt for pheasants or to frequent habitats known to contain pheasants. The findings of Snyder (1975:551) relating redtail prey selection with past successes supports this conclusion. Therefore, any stocking of pheasants on lands under the Extensive Wildlife Habitat Program should be strongly discouraged.

Intensive Management

The purpose of the Intensive Wildlife Habitat Program is to provide "... areas in which any citizen may hunt, trap or fish..." (Wis. Dept. Nat. Resour. 1977b;1977c), with wildlife production a secondary, but important concern. Recommendations for indirect predator management on large-scale, state-owned parcels managed under the Intensive Wildlife Habitat Program are:

1) Selective tree removal and emphasis on cover types lacking suitable hunting perches for raptors. Extensive tree removal on large, state-owned projects is neither feasible nor

desirable. However, selective tree removal near areas of high pheasant concentrations may be a realistic approach. Traditional shrub-carr wintering sites can be improved by selective tree removal. Again, 8- to 12-ha areas of closed-canopy shrub-carr should be maintained. Additional wintering sites are to be encouraged to maximize pheasant distribution. Concentrations of pheasants during the winter or spring seasons invariably bring about increased mortality from predation. To avoid this, a number of heavy stands of aster-goldenrod and/or cattail in lowland areas, and small groves of pine and spruce (30 m by 90 m) on open, upland sites should be developed.

Dumke (pers. comm.) found that some flocks of wintering pheasants at Waterloo heavily utilized small conifer plantations. Conifer-oriented pheasants experienced a lower predation mortality than did birds associated with shrub-carr or herbaceous winter cover. The flexible outer branches of young conifers were not used as hunting perches by horned owls and redtails. Only a 15- to 35-y conifer cycle is recommended since older conifers develop stouter branches suitable as raptor perches. Deciduous trees that over-top the conifers should be removed from the plantation. Pheasant travel lanes constructed from various evergreen and deciduous shrubs should be useful for connecting the various pheasant winter habitat units. Pheasant travel lanes should be a minimum of 6 m wide to help minimize mammal predation characteristic of narrow hedgerows.

2) Development of tall, dense, rank cover as quality nesting vegetation for pheasants. To minimize predator access via hunter-created trails, DNC units should be established in large contiguous blocks (minimum size of 16 ha). DNC units up to 160 ha may be necessary to maintain quality, predator-resistant nesting cover.

3) Emphasis on concealment cover adjacent to winter food patches. Traditional and potential wintering sites should have at least one food patch (0.4 ha to 1.2 ha) associated with, and preferably, immediately adjacent to, the winter cover. Winter food patches not associated with quality winter cover promote pheasant vulnerability to raptors.

4) Intentional management of buffer species to shift predation away from target game populations. The high utilization of cottontails and small mammals by horned owls and redtails at Waterloo suggests that their population levels and management have the potential to affect rates of pheasant predation. The basic premise is to increase small mammal and cottontail numbers in areas where they are vulnerable to raptors or to increase their vulnerability (Byer 1974:228).

Findings at Waterloo suggest that a cover composition of weedy annual plants, and/or early cropland successional stages associated with graminoid cover, will encourage small mammal abundance. The desired small mammal cover can be established and maintained by periodic prescribed burns or soil manipulation with farm equipment. Weedy corn patches (planted adjacent to raptor hunting perches) are especially desirable for both small mammals and cottontails, and can be effective for up to 3 y. Snow deeper than 10 cm tends to protect small mammals from raptors, therefore, a buffer management plan must also include cottontails as an alternate prey.

Cottontail numbers can be increased by providing briars and open shrubs along the edges of woodlots, and a system of trails (3-6 m wide) throughout the woodlot. Corn-sorghum food patches, in woodlot clearings or adjacent to woodlots, will also attract and hold cottontails (and raptors). Periodic inspections of the buffer management areas are essential during the winter to determine if, indeed, small mammals and cottontails are present in abundance, and pheasants avoid the areas. Management plans for pheasant habitat manipulation should be considered separately from plans directed at cottontails and other buffer species.

Areas adjacent to woodlots and

associated raptor hunting perches should receive high priority as management sites for buffer species. The south and east exposures of woodlots are preferred because they are protected from the winter winds, receive more solar energy, and thus are more resistant to snow accumulation. The establishment of hedgerows perpendicular to the south and east edges of woodlots could also act as natural snow fences. Tree-lined ditches or fencerows require greater development inputs, and, therefore, would be secondary to woodlots in importance.

Buffer species management during the spring becomes less important due to the return of migrating birds and the emergence of hibernating animals. Avian predation on pheasants can be reduced if pheasants can be induced to avoid poor nesting cover, i.e., floodplain wetlands and private hayfields. A good juxtaposition of high quality pheasant nesting (bait) cover within 0.32 km of traditional winter sites should attract pheasants which would otherwise nest in poorer areas, and thus should receive high priority.



Small conifer plantations can offer raptor-secure winter roosting sites for pheasants. The planting of conifer cover is recommended where natural cover is lacking.

CONCLUDING STATEMENTS

The Waterloo raptor study examines the role of great horned owls and red-tailed hawks as living organisms within a biotic community, and as pheasant predators. Relatively dense, resident populations of horned owls and redtails inhabited the Waterloo Study Area; by extrapolation, high densities of raptors probably inhabit most of the better pheasant range in southern Wisconsin. Both raptors are reproducing at levels adequate to maintain their populations at current rates of raptor mortality. This ability to maintain a stable population was primarily a function of territoriality. Both redtails and great horned owls actually utilized only a small portion of their territory, while other areas were defended but not frequented. Because of such territory size and occupancy, raptors are able to adapt to changes in the prey base. If prey populations decline, the raptors will move about to use other portions of their territory. Likewise, if prey populations increase (e.g., as a result of buffer species management), raptor numbers will be limited by the larger perimeters of their territories.

Year-to-year differences in prey vulnerability at Waterloo noticeably affected raptor food habits and productivity. The number of horned owls pairs actively breeding, for example, was found to influence cottontail abundance, whereas owl productivity seemed to be affected by the combined staple prey index. Red-tail brood size was related to vulnerability of small mammals, as determined by snow depth. Both raptors are highly adaptable predators. Their food habits, although tempered by past successes, are opportunistic in nature. Some prey escape this predatory pressure seasonally by migrating or by hibernation — the ring-necked pheasant cannot.

The level of raptor predation upon pheasants at Waterloo was regulated by weather conditions, particularly snow cover and spring rainfall, and by the vulnerability of buffer species such as cottontails and small mammals. At Waterloo, under certain conditions, great horned owls and red-tailed hawks took full advantage of a highly vulnerable pheasant population. It

appears that a community of predators hold the Waterloo pheasant population below carrying capacity of the habitat. One way to field test this conclusion involves multi-species predator reduction. Although I am convinced that such an approach would yield higher pheasant numbers, it would be costly and inconsistent with multiple use management on state-owned lands. For these reasons, it does not appear to be a feasible alternative at this time.

Raptor predation on pheasants can be reduced through habitat management techniques. Such tools would involve habitat manipulation designed to reduce pheasant-predator encounters. While adverse weather cannot be controlled, management can, however, discourage pheasants from using, high-risk vegetation. For example, the acquisition and development of pheasant nesting cover on river flood plains would be unsound. Proper management will require great initial commitments of money and planning, but the finished product should be long-lived.

My finding that pheasant predation mortality is additive rather than com-

pensatory requires some defense. The "Erringtonian philosophy" regarding predator-prey relationships has generally held that predation does not determine population levels of prey animals; predation is merely a compensatory form of mortality for any population in excess ("surplus") of its carrying capacity (Errington 1967:219-36). Surplus prey populations are doomed to die, if not from predation, then from disease, starvation, exposure, or a host of other forms of natural mortality. Errington (1946:227-35) held that social intolerance, i.e., territorial behavior, in effect acts as a self-limiting (self-regulating) agent in determining how many animals can exist in a natural environment. His philosophy has dominated our thinking on predation for the past two decades.

The work of Gates (1971) and Dumke and Pils (1973) implicated predation as the key additive mortality factor of ring-necked pheasants in Wisconsin. They concluded that predation primarily by red foxes, great horned owls, and red-tailed hawks held pheasant densities below the carrying capacity of the habitat.

Frank and Woehler (1969:802) sought to increase pheasant densities by improving habitat quality; it was believed that the better pheasant habitat would hold more birds because living requirements could be achieved within a smaller home range. In spite of an intensive program of pheasant habitat manipulation on the WSA, pheasant populations failed to increase significantly (Frank and Woehler 1969:809). Recent findings by other researchers have likewise refined the understanding of the vital role that predation plays in the population dynamics of game species (Balsler, Dill, and Nelson 1969; Chesness, Nelson and Longley 1968; Bergerud 1971; McInville and Keith 1974; Trautman, Fredrickson, and Carter 1974; Pils and Martin 1978).

Criticisms of Errington's thinking rests upon two factors: (1) Errington primarily worked with bobwhite quail and muskrats, 2 highly social animals. Keith (1974:24) felt that had Errington worked on ungulates or lagomorphs instead, his conceptual model might have been substantially altered. (2) There is an element of cir-

cularity in Errington's argument concerning the notion of a "surplus" cohort linked to that of "carrying capacity". Errington defined carrying capacity mainly in terms of predation's impact and then determined carrying capacity by after-the-fact observation (Watson 1970; Keith 1974:25).

Keith (1974:19) stressed the importance of long-term field studies in his efforts to quantify and appraise mortality, and to better understand the functioning of ecosystems. In order to understand more clearly the population dynamics of ring-necked pheasants and their responses to changes in mortality, a long-term study, using the ecosystem approach, may also be necessary. There is a need for a team approach to long-term studies, not only to describe the characteristics of individual populations (such as population size; sex and age composition; rates of birth, death, ingress, and egress; disease; behavior; physiology; and genetics), but also to gain cohesive knowledge on the way the various populations in an ecosystem interact.

APPENDIXES

APPENDIX I. Scientific names of plants and animals cited.

- Plants¹**
Alfalfa (*Medicago sativa*)
Ash, white (*Fraxinus americana*)
Aspen (*Populus* spp.)
Aster (*Aster* spp.)
Basswood (*Tilia americana*)
Canary grass (*Phalaris arundinacea*)
Catalpa (*Catalpa speciosa*)
Cattail (*Typha* spp.)
Cherry, black (*Prunus serotina*)
Corn (*Zea mays*)
Dogwood (*Cornus* spp.)
Elm, American (*Ulmus americana*)
Grape (*Vitis* spp.)
Goldenrod (*Solidago* spp.)
Hickory, shagbark (*Carya ovata*)
Maple, silver (*Acer saccharinum*)
Maple, sugar (*A. saccharum*)
Mint (*Mentha* spp.)
Oak, red (*Quercus borealis*)
Oak, white (*Q. alba*)
Oats (*Avena sativa*)
Pine (*Pinus* spp.)
Plum (*Prunus* spp.)
Quack grass (*Agropyron repens*)
Sedges (*Carex* spp.)
Sorghum (*Sorghum* spp.)
Spruce (*Picea* spp.)
Tamarack (*Larix laricina*)
Timothy (*Phleum pratense*)
Willow, black (*Salix nigra*)
- Birds²**
Blackbird, red-winged (*Agelaius phoeniceus*)
Bobwhite quail (*Colinus virginianus*)
Buzzard, common (*Buteo buteo*)
Chicken, domestic (*Gallus* spp.)
Crow (*Corvus brachyrhynchos*)
Duck, domestic (*Anas* spp.)
Grackle, common (*Quiscalus quiscula*)
Grouse, ruffed (*Bonasa umbellus*)
Hawk, red-shouldered (*Buteo lineatus*)
Hawk, red-tailed (*B. jamaicensis*)
Jay, blue (*Cyanocitta cristata*)
Kestrel, American (*Falco sparverius*)
Owl, great horned (*Bubo virginianus*)
Owl, tawny (*Strix aluco*)
Pheasant, ring-necked (*Phasianus colchicus*)
Sparrow, English (*Passer domesticus*)
- Mammals³**
Chipmunk, eastern (*Tamias striatus*)
Ground squirrel, Franklin's (*Citellus franklinii*)
Ground squirrel, Richardson's (*Spermophilus richardsonii*)
Ground squirrel, Striped (*Citellus tridecemlineatus*)
Hare, snowshoe (*Lepus americanus*)
Mouse, Hanson's harvest (*Reithrodontomys megalotis*)
Mouse, house (*Mus musculus*)
Mouse, Hudsonian meadow jumping (*Zapus hudsonius*)
Mouse, northern white-footed (*Peromyscus leucopus*)
Mouse, prairie deer (*P. maniculatus*)
Muskrat (*Ondatra zibethicus*)
Rabbit, cottontail (*Sylvilagus floridanus*)
Rat, Norway (*Rattus norvegicus*)
Shrew, cinereous (*Sorex cinereus*)
Shrew, giant mole (*Blarina brevicauda*)
Shrew, southern saddle-backed (*S. arcticus*)
Squirrel (*Sciurus* spp.)
Voles, meadow (*Microtus pennsylvanicus*)

¹ Plant reference: Fernald, M. L. (1950).

² Bird reference: American Ornithologist's Union (1957).

³ Mammal reference: Jackson, H. H. T. (1961).

APPENDIX II. Seasonal summary of radio-locations for great horned owls.

Individual Owls	Winter			Spring			Summer			Fall			Total		
	No. Locations		No. Radio-days	No. Locations		No. Radio-days									
	Active	Roost		Active	Roost		Active	Roost		Active	Roost		Active	Roost	
FLEDGLINGS															
Dunneison Imm (72)							39	70	75	22	30	81	61	100	156
Dunneison Imm (74)				3	7	13	52	50	92	65	14	29	120	71	134
Fuchs Imm (74-75)	28	15	40				50	45	92	130	28	92	208	88	224
Island Imm A (72)				2	10	43	59	53	92	79	37	92	140	100	227
Island Imm B (72)				2	10	43	62	53	92	67	29	92	131	92	227
Draeger Imm (72)							40	75	92	12	17	83	52	92	175
Killian Imm (73)							20	48	86	32	33	66	52	81	152
Hwy. 19 Imm (73)				0	1	15	32	54	92	0	8	14	32	63	121
Total	28	15	40	7	28	114	354	448	713	407	196	549	796	687	1 416
ADULTS															
<i>Adult females</i>															
Dunneison (74 & 75)	162	72	164	196	58	182	55	47	92	124	29	92	537	206	530
Fuchs (74 & 75)	144	59	150	87	38	182	51	42	92	109	27	92	391	166	516
Draeger (74)	86	23	46	67	36	91	44	40	83				197	99	220
Jordan (74 & 75)	182	62	163	189	53	182	64	38	92	43	16	50	478	169	487
Subtotal	474	216	523	539	185	637	214	167	359	276	72	234	1 603	640	1 758
<i>Adult males</i>															
Dunneison (74)	99	37	73	42	9	52							141	46	125
Semrau (74 & 75)	179	44	148	178	40	182	47	27	92	116	23	92	520	134	514
Draeger (74 & 75)	201	58	136	182	64	182	44	43	92	109	29	92	536	194	502
Subtotal	479	139	357	402	113	416	91	70	184	225	52	184	1 197	374	1 141
Total adults	1,053	355	880	941	298	1,053	305	237	543	501	124	418	2 800	1 014	2 894

APPENDIX III. Seasonal summary of radio-locations for red-tailed hawks.

Individual Hawks	Winter			Spring			Summer			Fall			Total		
	No. Locations		No. Radio-days												
	Active	Roost		Active	Roost		Active	Roost		Active	Roost		Active	Roost	
FLEDGLINGS															
Hensler Imm (73)			13	0	33	155	5	62				168	5	95	
Hensler Imm (74)			8	1	7	92	14	54				100	15	61	
Knoll Imm A (72)			0	0	11	164	33	92	8	2	28	172	35	131	
Knoll Imm B (72)			0	0	11	153	7	83				153	7	94	
Total			21	1	62	564	59	291	8	2	28	593	62	381	
ADULTS															
<i>Adult females</i>															
Daye (72)	82	0	37									82	0	37	
Draeger Conifers (72)	126	4	66	86	0	91	18	5	80			230	9	237	
Knoll (72)	52	4	39	118	1	54						170	5	93	
Island (72)	149	0	74									149	0	74	
Lillie (74 & 75)	138	43	145	156	40	182	30	11	92	5	19	92	329	113	511
Hensler (73 & 74)	57	7	90	96	12	139	294	38	172	162	20	92	609	77	493
Subtotal	604	58	451	456	53	466	342	54	344	167	39	184	1569	204	1445
<i>Adult males</i>															
Daye (73)	47	4	17										47	4	17
Baumann (73)	127	12	83	65	1	91	3	0	5				195	13	179
Hensler (73)	201	7	63	124	8	91	221	8	92	161	20	92	707	43	338
Subtotal	375	23	163	189	9	182	224	8	97	161	20	92	949	60	534
Total adults	979	81	614	645	62	648	566	62	441	328	59	276	2518	264	1979

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ACKNOWLEDGMENTS

It is not possible to carry out a study of this magnitude without the vital assistance of a great number of people. Credit for the original idea of a study on predators at Waterloo must be given to the late Farm Wildlife Group Leader, J. M. Gates. J. B. Hale provided valuable assistance in defining the study's objectives, and providing guidance. Recognition must be given to the field assistants who shared the long hours of monitoring, the hazardous climbs, and the very routine field work that prevailed: R. W. Zeller, A. E. Beske, and L. E. Vine. Credit is given to those individuals who also provided field assistance and provoked countless discussions on predator-prey relationships: C. M. Pils and M. A. Martin. Acknowledgment is given to the technical reviewers of the manuscript: J. R. March, S. Postupalsky, S. A. Temple, and R. K. Anderson. D. R. Thompson, Chief of the DNR's Technical Services Section and John Cary, Staff Specialist for the University of Wisconsin-Madison, provided extensive assistance in statistical analysis. Thanks is given to J. R. March, Farm Wildlife Group leader, for his strong encouragement and support during the writing stages of this report. Throughout the study, there were 4 people who provided the encouragement, support, technical assistance, as well as constructive criticism to keep this study on an even, stable, and, hopefully, productive course: R. W. Zeller, field assistant and good friend; Frances and F. N. Hamerstrom, Jr., *personae gratae* and unofficial study advisors; and Ursula C. Petersen, confidante and intellectual stimulator.

This study was supported in part by funds from the Federal Aid in Wildlife Restoration Act under Pittman-Robertson Project W-141-R. This report represents a Final Report for Study 104.

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