History, nesting biology, and predation ecology of raptors in the Missouri Coteau of northwestern North Dakota
by Robert Kevin Murphy

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:

Although species composition of birds of prey (raptors) that nest in the northern Great Plains is being altered due to land use, detailed case histories of such change are lacking, few long-term data exist to help understand population dynamics of raptors in prairie areas, and implications of changes for other prairie wildlife on which raptors prey are poorly understood. I studied mechanisms and implications of land use impacts on raptors on the Missouri Coteau of northwestern North Dakota by (1) tracing change during the past century in raptor species composition and habitat on the 108-km2 Lostwood National Wildlife Refuge (LNWR), (2) assessing current (1981-90) population stability, annual reproductive success, and habitat relationships of raptors on LNWR and comparative species' nesting densities on an adjacent area of different land use, and (3) determining prey needs of common, large (>700 g) raptor species on LNWR and prey use in relation to habitat on an area of contemporary land use. Northern harriers (Circus cvaneus), Swainson's hawks (Buteo swainsoni), ferruginous hawks (B. recalls), and burrowing owls (Athene cunicularia) comprised the community of raptors that nested on LNWR before settlement in the early 1900s, great horned owls (Bubo virginianus) were rare but gradually increased over the last 40-50 years, red-tailed hawks (B. iamaicensis) pioneered about 30 years ago, and Cooper's hawks (Accipiter cooperii) pioneered in the past decade. Today, red-tailed hawks and great horned owls have replaced Swainson's and ferruginous hawks as dominant large raptors, coinciding with succession from mixed grass prairie to aspen parkland with brush-dominated uplands. Harrier abundance probably has changed little, but nesting burrowing owls have been absent >40 years. I suggest the most fundamental causes of change in the raptor community were altered susceptibility of prey to foraging behaviors of specific raptor species and decreased abundance of certain key prey species. During the 1980s red-tailed hawks and great horned owls exhibited high, stable nesting densities (mean, 0.23 and 0.13 occupied nests/km2) but erratic and low annual productivity (mean, 0.9 and 0.7 young/occupied nest); both species nested most in areas with highest densities of tree clumps, and the owl was associated with wetlands. Nearly all Swainson's hawk nests occurred on LNWR's boundary, and an adjacent area (93 km2) of different land use had twice as many occupied Swainson's hawk nests/km2 as LNWR. Great horned owl diets were studied during late spring and Swainson's hawk diets during summer, 1986-87 on areas of mixed land use; 2,900 and 1,284 prey items were recorded, respectively. Diet varied among families of both species. The owl relied heavily on avian prey from wetlands (total wetland prey: 57% of overall frequency and 76% biomass of diet) especially ducks and used less Leporid prey than reported elsewhere. Great horned owls depredated about 2-4 ducklings/km2 and 1.3-1.4 adult ducks/km2 during mid-May through June; adult females of several duck species were more vulnerable to owl predation than males. Swainson's hawks used many prey from wetlands (49% overall frequency, 42% biomass); mammals were the most important prey Class and overall diet was more diverse compared to study findings elsewhere. Variation in use of several important prey among Swainson's hawk families was mostly explained by nesting area habitat. A cursory survey of great horned owl and red-tailed hawk diets on LNWR suggested these raptors relied on prey from wetlands, especially ducks. Land use practices that favor nesting red-tailed hawks and great horned owls in prairies of the northern Great Plains are not

amenable to raptor species that nest mainly in the region and perhaps not to many other species of indigenous migratory birds.

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APPROVAL

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Robert Kevin Murphy

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Although species composition of birds of prey (raptors) that nest in the northern Great Plains is being altered due to land use, detailed case histories of such change are lacking, few long-term data exist to help understand population dynamics of raptors in prairie areas, and implications of changes for other prairie wildlife on which raptors prey are poorly understood. I studied mechanisms and implications of land use impacts on raptors on the Missouri Coteau of northwestern North Dakota by (1) tracing change during the past century in raptor species composition and habitat on the 108-km^2 Lostwood National Wildlife Refuge (LNWR), (2) assessing current (1981-90) population stability, annual reproductive success, and habitat relationships of raptors on LNWR and comparative species' nesting densities on an adjacent area of different land use, and (3) determining prey needs of common, large (>700 g) raptor species on LNWR and prey use in relation to habitat on an area of contemporary land use. Northern harriers (Circus cyaneus), Swainson's hawks (Buteo swainsoni), ferruginous hawks (B. regalis), and burrowing owls (Athene cunicularia) comprised the community of raptors that nested on LNWR before settlement in the early 1900s, great horned owls (Bubo virginianus) were rare but gradually increased over the last 40-50 years, red-tailed hawks (B. jamaicensis) pioneered about 30 years ago, and Cooper's hawks (Accipiter cooperii) pioneered in the past decade. Today, red-tailed hawks and great horned owls have replaced Swainson's and ferruginous hawks as dominant large raptors, coinciding with succession from mixed grass prairie to aspen parkland with brush-dominated uplands. Harrier abundance probably has changed little, but nesting burrowing owls have been absent >40 years. I suggest the most fundamental causes of change in the raptor community were altered susceptibility of prey to foraging behaviors of specific raptor species and decreased abundance of certain key prey species. During the 1980s red-tailed hawks and great horned owls exhibited high, stable nesting densities (mean, 0.23 and 0.13 occupied nests/km^2) but erratic and low annual productivity (mean, 0.9 and 0.7 young/occupied nest); both species nested most in areas with highest densities of tree clumps, and the owl was associated with wetlands. Nearly all Swainson's hawk nests occurred on LNWR's boundary, and an adjacent area (93 km^2) of different land use had twice as many occupied Swainson's hawk nests/km^2 as LNWR. Great horned owl diets were studied during late spring and Swainson's hawk diets during summer, 1986-87 on areas of mixed land use; 2,900 and 1,284 prey items were recorded, respectively. Diet varied among families of both species. The owl relied heavily on avian prey from wetlands (total wetland prey: 57% of overall frequency and 76% biomass of diet) especially ducks and used less Leporid prey than reported elsewhere. Great horned owls depredated about 2-4 ducklings/km^2 and 1.3-1.4 adult ducks/km^2 during mid-May through June; adult females of several duck species were more vulnerable to owl predation than males. Swainson's hawks used many prey from wetlands (49% overall frequency, 42% biomass); mammals were the most important prey Class and overall diet was more diverse compared to study findings elsewhere. Variation in use of several important prey among Swainson's hawk families was mostly explained by nesting area habitat. A cursory survey of great horned owl and red-tailed hawk diets on LNWR suggested these raptors relied on prey from wetlands, especially ducks. Land use practices that favor nesting red-tailed hawks and great horned owls in prairies of the northern Great Plains are not amenable to raptor species that nest mainly in the region and perhaps not to many other species of indigenous migratory birds.

THESIS INTRODUCTION

Raptors (Falconiformes, Strigiformes) are purported to be superb indicators of environmental quality and habitat change (Hickey 1969, Odum 1971, White 1974, Newton 1979). While cognizance of the role of raptors in ecosystem function grows, demands on natural resources including wildlife swell with increasing world population. These pressures stress need for appropriate baseline data on raptors as well as other indicator species or species groups to help safeguard wildlife as a whole. Resource personnel should have quantitative knowledge of annual variation and long-term change in population dynamics of indicator species, and should comprehend underlying causes of change and recognize variation due to man-caused impacts and perturbations. Ability to make such distinctions depends on many factors, the most vital including data quantity and quality and merit of wildlife indicator species to reveal change.

Altered reproductive status of several species of raptors such as the peregrine (Falco peregrinus) that relate to prevalence of pesticide residues (Hickey 1969, Cade et al. 1971) exemplify wildlife as biological indicators. Relationships of raptor populations to modifications in habitat structure, however, are less distinct. Declines of several raptor species in western North American prairies have been linked to habitat change. For example, decreased distribution of ferruginous (Buteo regalis) and Swainson's hawks (B. swainsoni) in prairie Canada has been associated with expanding cultivation and aspen (Populus spp.) trees (Houston and Bechard 1983, Schmutz 1984). More detailed case histories of change in raptor distribution and abundance could advance understanding and management of habitat of indigenous prairie wildlife communities to which raptors belong. Perceptions of what comprise natural patterns of biotic communities on contemporary landscapes need to be questioned and scrutinized if understanding of natural potential is to be appreciated (Botkin 1990). Craighead and Mindell (1981) alluded to this dilemma:

> "There is a tendency for each succeeding human generation to accept and be satisfied with existing conditions because they have no reference for comparing present conditions with those preceding or those that could exist with informed management."

Resource personnel in the northern Great Plains charged with managing breeding, migratory birds must be cognizant of their respective predator regimes, of which raptors are a part, because predators may affect reproductive success of species being managed (which may include some species of raptors)(Sargeant et al. 1993). Shifts in abundance of mammalian predators in the past century have important implications for recruitment of migratory birds but concurrent changes in avian predators are less well documented and implications for migratory bird management even less studied or understood. These topics need to be elucidated via study in representative areas of the northern Great Plains.

Thesis objectives were to explore the historical raptor-prairie habitat complex and assess raptors as models of habitat change, identify long-term demographic patterns and habitat relationships of a contemporary prairie raptor community, and document predation ecology of common large raptors.

Rationale of General Study Design and Thesis Organization

The scientific or hypothetico-deductive method is the ideal approach in wildlife research investigations (Romesberg 1981). The method depends on empirical facts to formulate hypotheses. While many questions exist regarding the ecology of birds of prey in the northern Great Plains, empirical information is inadequate to formulate precise and meaningful research hypotheses. Thus, observational study is the logical initial step to understanding raptor ecology in the region. Although an ambition of this study was to establish more solid grounds for research hypotheses and to formulate new predictions, I expected to be able to test some previously formed hypotheses where appropriate and supported by data collected.

There are several approaches to field investigation (Hall et al. 1978). Extensive studies that employ randomization are ideal because they generate valid variance estimates (Hurlbert 1984) that allow broad geographical inference, but they are costly and logistically difficult. These problems are compounded when studying widely dispersed organisms such as raptors (e.g., Allen 1987). Intensive investigation on single study area blocks are logistically much more feasible but have limited inferential value. Long-term study accounts for annual variation, particularly important in very dynamic environments; short-term (e.g., 2-3 years) study overlooks annual variation (Brown 1974, Wiens 1984) but is less costly.

I used the intensive study approach on single study areas mainly because of logistical constraints, but combined this with long-term study where feasible. Breeding biology of raptors was studied over many years on a national wildlife refuge because history, vegetation, wildlife, and land use records from the refuge and other sources could be assembled to retrospectively trace ecological change, but also because data from relatively inviolate areas tend to lack "noise" from short-term, local disturbances (Henny et al. 1973, Temple and Wiens 1989). Data were needed from a nearby area that was similar in all respects (e.g., soils, elevation, local climate, wetlands, trees) aside from land use to substantiate hypotheses about raptor abundance and distribution on the refuge. I arbitrarily chose a township (93 km^2) based on similarity to size of the refuge study area.

Nearly every aspect of raptor population ecology can be explained in terms of food (Newton 1979:290). What prey are used and where, when, and how they are obtained are basic questions of importance to management of raptors, as well as to species on which raptors prey (Craighead and Craighead 1956, Errington 1967). Study of raptor diets is difficult and costly (Marti 1987), so my priority was to record diets of only common, large (>700 g) species of raptors. Moreover, I expended most effort in an intensive approach on a study area under private ownership because diet study results from an area of typical land use would have wider application than from a refuge, while still bearing significance for management of public lands. Also, 1 species of interest was not present in adequate numbers on the wildlife refuge.

I optimally configured research procedures on private lands by using the same township study area to simultaneously yield predation ecology and nesting biology data. This approach is critical because implications of prey use are meaningful only in the context of net food demands of predators as influenced by their density and reproductive output (e.g., Craighead and Craighead 1956). Intensive study of diets of raptors on private lands was short-term (2 years) but I had sufficient, long-term data on potential causes of variation (e.g., climate, relative abundance of major prey) to judge representativeness of results. Also, I forfeited prey use study of 1 of 3 major raptor species on private lands to maximize quality and quantity of data collected on the other 2. The selection was influenced by priority of information need for each species and by differences in nesting chronology i.e., which species I could study thoroughly by virtue of minimal overlap with another.

Thus, this study focuses on implications and mechanisms of effects of land use change on certain northern prairie avifauna. Raptors served as a convenient vehicle to explore these topics. Part I of this thesis conveys the relevant information on historical ecology, Parts II and III on breeding ecology, and Parts IV, V, and VI on predation ecology. A summarizing discussion links conclusions and implications of the thesis components.

LITERATURE CITED

ALLEN, G. T. 1987. Estimating prairie falcon and golden eagle nesting populations in North Dakota. J. Wildl. Manage. 51:739-744.

BOTKIN, D. B. 1990. Discordant harmonies: a new ecology for the twenty-first century. Oxford Univ. Press, New York. 241pp.

BROWN, L. 1974. Data required for effective study of raptor populations. Raptor Res. Rep. 2:9-20.

CADE, T. J., J. L. LINCER, C. M. WHITE, D. G. ROSENEAU, and L. G. SWARTZ. 1971. DDE residues and eggshell changes in Alaskan falcons and hawks. Science 172:955-957.

CRAIGHEAD, F. C., Jr., and D. P. MINDELL. 1981. Nesting raptors in western Wyoming, 1947 and 1975. J. Wildl. Manage. 45:865-872.

CRAIGHEAD, J. J., and F. C. CRAIGHEAD. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania. 443pp.

ERRINGTON, P. L. 1967. Of predation and life, 1st ed. University of Iowa Press, Ames, Iowa. 277pp.

HALL, J. D., M. L. MURPHY, and R. S. AHO. 1978. An improved design for assessing impacts of watershed practices on small streams. Verh. Internat. Verein. Limnol. 20:1359-1365.

HENNY, C. J., F. C. SCHMID, E. M. MARTIN, and L. L. HOOD. 1973. Territorial behavior, pesticides and the population ecology of red-shouldered hawks in central Maryland, 1943-1971. Ecology 54:545-554.

HICKEY, J. J., ed. 1969. Peregrine falcon populations. Univ. Wisconsin Press, Madison. 596pp.

HOUSTON, C. S., and M. J. BECHARD. 1983. Trees and the red-tailed hawk in southern saskatchewan. Blue Jay 41:99-109.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187-211.

MARTI, C. D. 1987. Raptor food habits studies. Natl. Wildl. Fed. Sci. Tech. Ser. 10:67-80.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota. 399pp.

ODUM, E. P. 1971. Fundamentals of ecology. W.B. Saunders Co., Philadelphia, Pa. 574pp.

ROMESBERG, H. C. 1981. Wildlife science: gaining reliable knowledge. J. Wildl. Manage. 45:293-313.

SARGEANT, A. B., R. J. GREENWOOD, M. A. SOVADA, and T. L. SHAFFER. 1993. Distribution and abundance of predators that affect duck production - Prairie Pothole Region. U.S. Fish Wildl. Serv. Resour. Publ. 194. In Press.

SCHMUTZ, J. K. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. J. Wildl. Manage. 48:1180-1187.

TEMPLE, S. A., and J. A. WIENS. 1989. Bird populations and environmental changes: can birds be bio-indicators? Am. Birds 43:260-270.

WHITE, C. M. 1974. Current problems and techniques in raptor management and conservation. Trans. North Am. Wildl. Nat. Resour. Conf. 39:301-312.

WIENS, J. A. 1984. The place of long-term studies in ornithology. Auk 101:202-203.

PART I

A HISTORICAL SKETCH OF BREEDING RAPTORS AND THEIR PRAIRIE HABITAT ON LOSTWOOD NATIONAL WILDLIFE REFUGE, NORTH DAKOTA

INTRODUCTION

Native prairies and wetlands of North America's northern Great Plains have decreased in quality and extent since the region was settled by peoples of European descent about a century ago (Burgess 1964, Aus 1969, Coupland 1978, Kantrud et al. 1989, Dahl 1990). Thus the region's indigenous biodiversity has been diminished (Stewart 1975, Kirsch and Higgins 1976, Cowardin et al. 1983, Ryan et al. 1984, Anonymous 1986). For example, distribution or populations of some species of indigenous raptors have been reduced (Evans 1982, Houston and Bechard 1984, Schmutz 1984). Many refugia have been established, however, in an attempt to restore and maintain native biotic communities (Pittman 1937, Gabrielson 1943, Chapman 1947, Braun et al. 1978, U.S. Fish and Wildlife Service 1990). A crucial step in developing objectives for such areas is to determine composition of historically occurring wildlife communities and then discern habitat correlates requisite for management efforts (Botkin 1990). Raptor assemblages breeding on prairie areas may reflect habitat quality or quantity (Schmutz 1984, Gilmer and Stewart 1983); a reasonable expectation is that native raptors would model pristine conditions. This begs closer examination of factors associated with long-term change in prairie raptor communities, as well as of raptors currently nesting on refuges (U.S. Fish and Wildlife Service 1990).

Woody species seem to have proliferated on Lostwood National Wildlife Refuge (LNWR) and surrounding lands in northwestern North Dakota, apparently due to absence of fire (Vogl 1974, Wright and Bailey 1982). Change and impacts on indigenous wildlife are undocumented. Adequate historical information could be gathered to examine how well raptors serve to model long-term habitat change at LNWR. Composition of the raptor community that currently breeds on LNWR has been documented (Part II) for comparison.

The main objective was to describe nature and causes of historical change, if any, in the raptor assemblage at LNWR. I predicted a priori that composition of this raptor community deviated from what occurred historically depending on makeup and extent of increases in woody plants because broad distributional changes in certain breeding raptors of prairie Canada were linked to expanding distribution of trees (Houston and Bechard 1983, Schmutz 1984). A localized, detailed, and more recent case history would contribute a refined chronicle of change, test hypotheses proposed in previous studies, and potentially disclose other causative factors. A second objective was to see whether raptors revealed extra clues about presettlement habitat conditions on LNWR.

STUDY AREA

Location, Physiography, Geology, and Soils

LNWR is in southern Burke and northern Mountrail counties, North Dakota (48°37′N;102°27′W)(Fig. I-1). It is rolling to hilly (elevation 685-747 m) semi-arid grassland interspersed with many (n = 4,200) wetland basins and clumps (n = 518) of quaking aspen (*Populus tremuloides*) trees.

LNWR lies within the 20-30 km wide Missouri Coteau, a physiographic region chiefly of moderate relief (30-90 m), dead ice moraine deposited by the Wisconsin glacier over a previously occurring escarpment (Clayton 1967, Freers 1973, Bluemle 1977). Hummocky, knob-and-kettle topography typical of the Missouri Coteau consists almost entirely of non-integrated drainage; rainfall and snowmelt collect in wetland basins via surface runoff and subsurface seepage (LaBaugh 1986, Winter 1989). Presence of glacial till (Coleharbor formation) is evidenced by erratics and thin, gravelly, mostly loam soils. The far southern 12 km^2 of LNWR has numerous deep, brushy coulees that drain into a 1.9-km^2 saline lake.

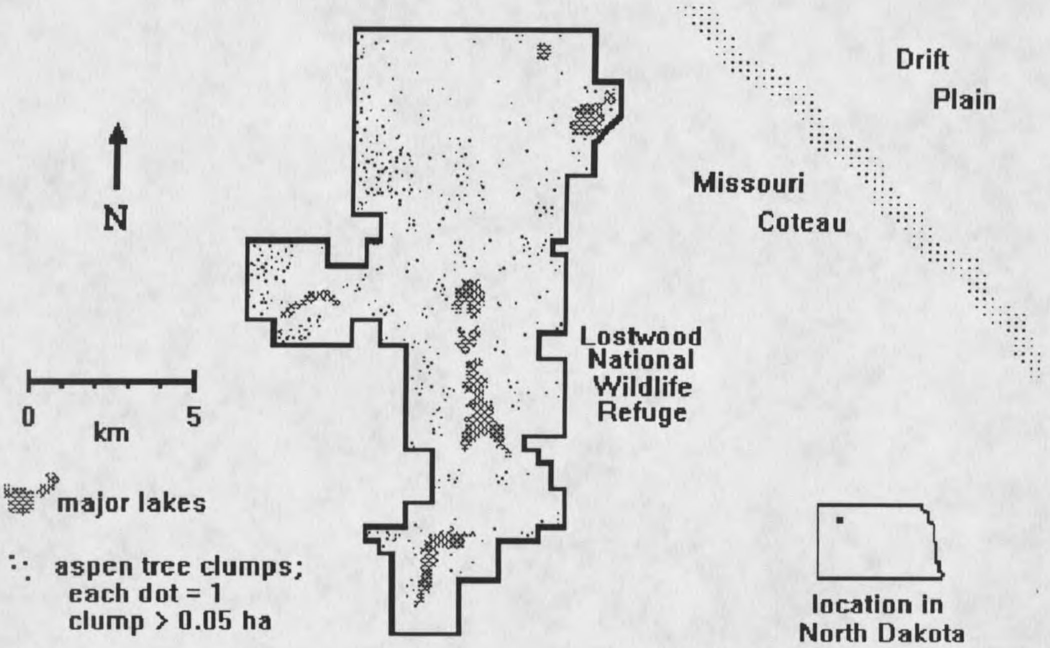

Figure I-1. Location, spatial configuration, and main physiographic features of Lostwood National Wildlife Refuge, northwestern North Dakota.

Habitat Composition

LNWR is in the Stipa-Agropyron association (Coupland 1950, 1974, Singh et al. 1983) in the mixed grass prairie of the Great Plains (Carpenter 1940, Whitman and Wali 1975, Barkley 1986). Native prairie comprises 55% of LNWR; dominant indigenous species are needlegrasses (*Stipa viridula*, *S. comata*) and wheatgrasses (*Agropyron* spp.), but Kentucky bluegrass (*Poa pratensis*) has invaded and become co-dominant. Dense stands of the low-growing shrub, western snowberry (*Symphoricarpos occidentalis*), currently dominate mesic sites and extend upslope toward xeric sites. Exotic grasses, mainly smooth brome (*Bromus inermis*), dominate mesic sites also (brome typically invades and spreads as a monotype from within decadent snowberry stands). Flora on xeric hilltops include blue grama (*Bouteloua gracilis*), prairie junegrass (*Koeleria pyramidata*), and threadleaf sedge (*Carex filifolia*) as codominants with native wheatgrasses and needlegrasses. Abundant native forbs are mainly of the Families Asteraceae and Fabaceae.

Twenty-one percent of the upland area on LNWR was broken and cropped for 5-40 years during 1910-55. Land cropped before the mid-1930s (about a third of all old cropland) has been partly reinvaded by native flora. Cropland farmed later was planted in the 1950s to smooth brome and other exotic grasses, which continue to dominate.

Trees (woody plants >6 m tall) comprise 2% of LNWR. Clumps of quaking aspen occur throughout the refuge (density of clumps, mean ± SD = 4.8 ± 4.1/km^2; clump size = 0.36 ± 0.37 ha)(Fig. I-1). Aspen typically pioneers and spreads along wetland borders (Maini 1960). Other trees include groups (n = 16) of 1-5 overmature or decadent eastern cottonwoods (*P. deltoides*), a 5-ha grove of American elm (*Ulmus americanus*) bordering a major lake, and small (0.1-0.5 ha) groves (n = 17) of stunted box elder (*Acer negundo*) or green ash (*Fraxinus pennsylvanicus*) at former farmsteads. Interspersed, tall shrubs (height 2-5 m) comprise another 2% of LNWR and include mainly round-leaved hawthorn (*Crataegus rotundifolia*), chokecherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*), willow (*Salix* spp.), and shrub-stage aspen.

Wetland basins make up 20% of LNWR and are diverse in size (0.01-224 ha), type (ephemeral or temporary to permanent [Stewart and Kantrud 1971]), and hydrologic features (fresh to saline, recharge or discharge regimes [LaBaugh 1986, Winter 1989]). Wetland attributes are detailed in Stewart and Kantrud (1971) and Kantrud et al. (1989). Percentage of total area and frequency of wetlands on LNWR by type is: temporary, 21 and 45%; seasonal, 25 and 44%; semi-permanent, 15 and 11%; permanent, 39 and <1%.

Road right-of-ways (25 km of gravelled road) and a headquarters facility comprise <0.3% of LNWR.

Climate and Weather

Area climate is "continental" (Jensen 1972:1) but highly variable resulting in periodic drought, severe winter blizzards (often as early as October or as late as April), low relative humidity, frequent cloudless days, brief but intense late afternoon thunderstorms (some with hail) in summer, early and late summer frosts, and frequent strong winds (>20-40 kph). There are huge annual, as well as daily, temperature fluctuations and precipitation is erratic (Kraenzel 1966, Jensen 1972). Average annual precipitation (1936-89) is 42 cm, >75% of which falls as rain during April-September (U.S. Fish and Wildlife Service [FWS], unpubl. refuge files). Average monthly temperatures range from 20°C in July to -15°C in January; record high and low temperatures are about 43°C and -48°C (Jensen 1972).

History and Land Use

LNWR was created in 1935 by Executive Order 7171 as a "...refuge and breeding ground for migratory birds and other wildlife" (Pittman 1937; FWS unpubl. refuge files). Homesteads were established on the area during 1904-1915 but either were abandoned by the early 1930s or were acquired by the federal government when LNWR was created; buildings and fences on homesteads subsequently were removed. In addition to a brief history of small grains farming, annual grazing by domestic livestock (at light stocking rates) on >75% of the area and harvesting of hay from wetland basins were sole economic uses after LNWR was established; livestock grazing was all but abolished in the 1970s, but limited cutting of hay continued in drought years. Fire suppression has been effectively practiced on the area since circa 1910.

METHODS

I relied on many sources to document historical (before 1980) changes in the raptor community and to glean relevant information on significant changes in prey populations. A major source was FWS unpublished refuge reports dating to 1938, mainly quarterly (through 1963) and annual narrative reports on file at LNWR, as in Littlefield et al. (1984). These included miscellaneous raptor observations as well as estimates of raptor abundance based on combinations of limited surveys and incidental observations. Quantitative value of these data was small but, collectively, levels of relative abundance were consistently suggested for major raptor species. Because negative attitudes prevailed towards predators during early decades of LNWR, the raptor community on this "migratory game bird refuge" was closely scrutinized and given regular attention in refuge reports. Other government documents were reviewed, especially original field notes of the U.S. Biological Survey (USBS) specific to the area (R. Kellogg and V. Bailey, unpubl., Smithsonian Inst., Washington, D.C.; F. Uhler, unpubl. refuge files). Bird lists (all unpublished or privately printed), published accounts such as records in Stewart (1975), and oologist's records (e.g., Kiff 1979, Bechard and Houston 1984) from surrounding areas provided additional perspective.

I could coarsely summarize abundance of individual raptor species in breeding seasons of the 1930s-1970s based on above records, but could only vaguely assess earlier abundances. For each decade I broadly characterized relative abundance during late spring through summer (May-August) as follows: (1) absent - no records found or reports explicitly conveying lack of occurrence, (2) rare - only 1 or 2 observations recorded every 3-10 years, (3) uncommon - reported most consistently among years as "uncommon," "infrequently observed," or "seldom seen this year," or refuge population guessed to be about 2-6 birds (i.e., 1-3 pairs), and (4) common - reported as "common," "abundant," "seen frequently in summer," "regularly observed," or population guessed to be about 5 or more pairs. Fortunately, narratives in each decade also included intermittent reports of more definitive data for common and uncommon species (e.g., lists of known nestings) that strengthened purported abundance. Precise nesting densities for the 1980s reported in Part II are summarized in Table I-1. I translated mean densities to relative abundance: rare, 0.001-0.009 occupied nesting areas/km²; uncommon, 0.01-0.08/km²; and common, >0.08/km².

Table I-1. Mean nesting densities of raptors on LNWR recorded during the 1980s.[a,b]

Species	Mean nesting density (occupied nesting areas/km²)
Red-tailed hawk (*Buteo jamaicensis*)	0.23
Swainson's hawk (*B. swainsoni*)	0.03
Ferruginous hawk (*B. regalis*)	<0.01
Cooper's hawk (*Accipiter cooperii*)	0.02
Northern harrier (*Circus cyaneus*)	0.70[c]
Great horned owl (*Bubo virginianus*)	0.13
Long-eared owl (*Asio otus*)	0.05
Short-eared owl (*Asio flammeus*)	0.19[c]

[a] From Table II-2 in Part II.
[b] Raptor breeding terminology follow Postupalsky (1974).
[c] Density of northern harriers and short-eared owls are estimates based on an average of estimated annual means from a sample survey.

I acknowledge drawbacks of my abundance summary: not all species could be similarly treated without bias, nor could relative abundance be uniformly defined among species without overlooking important differences in biology. Some species clearly were more inconspicuous or were of less interest than others (e.g., long-eared owl compared to ferruginous hawk). One species, the short-eared owl, tends to be abundant some nesting seasons but scarce or absent in intervening years (Part II) and therefore I do not attempt to categorize its average abundance during any decade. Above all, abundance of various raptor species during the breeding season relates directly to body size (Newton 1979); density of 0.05 pairs/km² conveys common abundance for large raptors (e.g., ferruginous hawk) but uncommon abundance for smaller raptors (e.g., Cooper's hawk, northern harrier), though I use similar bases to categorize abundance of all species.

To seek habitat correlates of change in raptor abundance, I reconstructed the area's pre- and post-settlement vegetation. LNWR was an ideal site for documenting successional change because the area was settled relatively recently (75 years before I began my study) and presettlement forb-grass composition was still qualitatively represented on large, relict land tracts. Main questions were: (1) historically, what was the general extent and nature of woody compared to non-woody vegetation?, and (2) what was the gross physiognomy (i.e., structural appearance or height and density) of the vegetation? To answer these questions I gathered evidence from: (1) surveyor's notes on general landscape features from the 1890s (U.S. General Land Office; Anonymous 1860) and 1930s (USBS contract; unpubl. files, FWS-Denver regional office)(Burgess 1964, Stearns 1974); (2) USBS notes (R. Kellogg and V. Bailey, unpubl., Smithsonian Inst., Washington, D.C.; F. Uhler, FWS unpubl. refuge files); (3) interviews of local residents that were present on the area during and just after settlement; (4) narratives from early naturalists, explorers, and military personnel from throughout the 1800's (for the northwestern part of the state in general (e.g., Clandening 1928); (5) landscape photographs of the area from circa 1905-1940; (6) aerial photographs (1:7920) of the area from 1938, 1954, 1969, and 1979 (FWS and U.S. Soil Conserv. Serv., unpubl.); and (7) a 1985 habitat compilation by FWS-National Wetland Inventory (FWS, unpubl. data).

I measured change in extent (area, ha) of western snowberry and snowberry-dominated types (snowberry >50% canopy cover) from 1938 and 1979 aerial photographs of a sample of 13 65-ha plots. The plots were randomly selected from the limited area of unbroken (native) prairie on LNWR that was lightly grazed or rested (i.e., left idle) from 1935 through 1990. I used this habitat type so that boundaries of snowberry patches or stands in current aerial photographs could be verified in the field (controlled burning was conducted on most of the rest of LNWR at least once in the 1980s).

I generated an age-growth regression for aspen trees from LNWR to test a hypothesis about the size and age of trees that supported raptor nests (Houston and Bechard 1983). Data were collected from sites similar (in slope, aspect, soils, and wetland proximity) to those of trees selected by raptors for nest placement. Growth annuli in aspen are difficult to count because of soft xylem (Maini 1960), but I was able to do so by selecting trees that had died recently (circa 3 years previous) and were dried and relatively hardened. Bole cross-sections were collected then machine-planed. Next, I dyed cross sections with commercial wood stains to distinguish growth rings. For all but some overmature or decadent trees, I could readily discern the annuli.

Where possible, I tested changes in raptor habitat by using linear regression (Sokal and Rohlf 1981, BMDP Statistical Software, Inc. 1985). Non-parametric tests were used when assumptions for parametric tests were not met (e.g., unequal variances, non-normally distributed data). I considered $\underline{P} < 0.1$ to be grounds for statistical significance.

RESULTS: SURVEY OF HISTORICAL ACCOUNTS

Historical Raptor Habitat Base

Vegetation Reconstruction: Presettlement Flora

Two notable attributes were evident in the few descriptions of presettlement vegetation for the area encompassing LNWR (Fig. I-2): paucity or inconspicuousness of woody vegetation, and prairie grasses of short stature. Early, general descriptions were provided by M. Lewis and W. Clark. In April 1805, they described the country about 40 km south-southwest of present-day LNWR as "...destitute of timber" (Reid 1988:237) and a treeless plain "...generally covered with a short grass resembling very much the blue grass [likely blue grama]" (Cutright 1969:127).

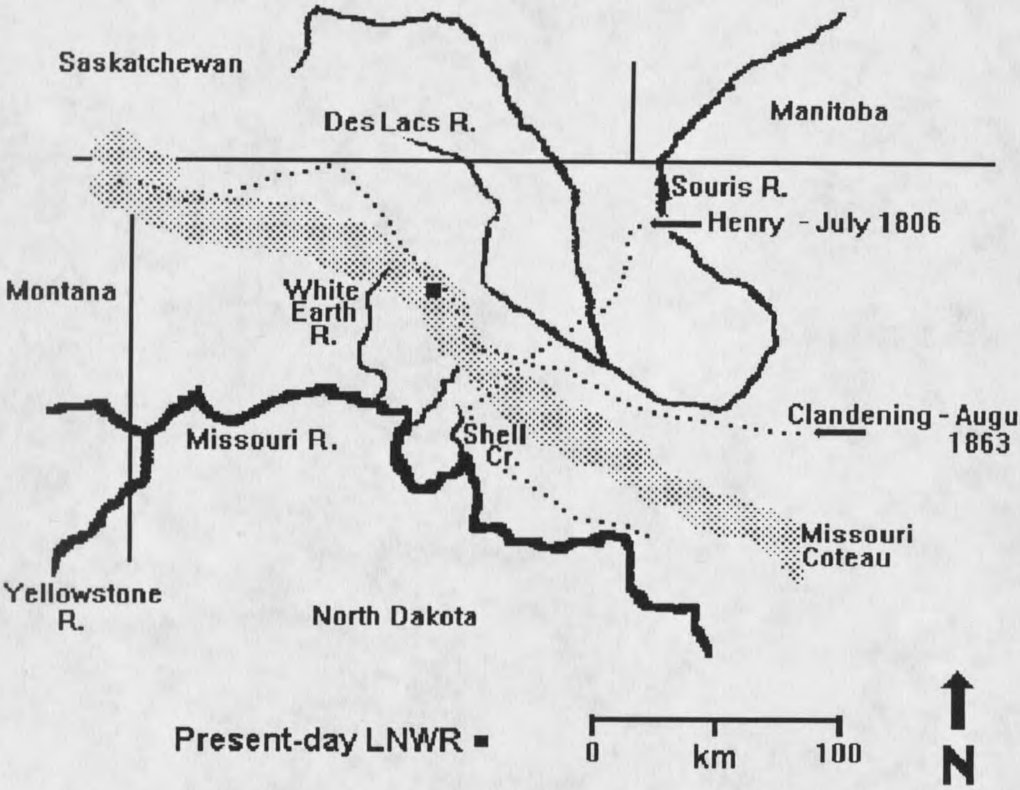

Figure I-2. Physiographic features of northwestern North Dakota and approximate routes travelled by 2 early explorers as reviewed in text.

A. Henry travelled in July 1806 through the Missouri Coteau probably to within 40 km southeast of LNWR (Fig. I-2)(*in* Coues 1897). He described the Coteau southwest of the Souris River as hills covered with large stones where "...there is no wood of any kind" (1897:315) and, from a vantage point on the Coteau (18 July): "To the N.W. ... the land appeared to rise into high hills... no wood was to be seen in any direction" (1897:318). Henry's journal entries at the time also were replete with observations of bison (*Bison bison*) in the same area, an animal prominent in evolution and maintenance of native prairie vegetation (Edwards 1978, Higgins 1986).

Denig (1961) described eastern Montana and western North Dakota north of the Missouri River in the mid-1850s: "...an ocean prairie many hundred miles in length and breadth... devoid of trees or even shrubs..." (1961:4) and "...immense tracts over which the traveler must pass for days in succession without meeting tree or brush" (1961:64). He alluded to grass composition: "...perennial prairie grass with which the level plains are covered, the fine blue grass that grows in the river valleys [perhaps fowl bluegrass, Poa palustris], and the short, very fine, curly buffalo grass [almost certainly blue grama] found everywhere..." (1961:65). He also referred to fire, fire frequency, and effects of fire: "The short summer season allows vegetation but little time to decay, and the firing of the prairies, which happens more or less every year in different parts, burns up all old grass..." (Denig 1961:67).

W. Clandening journeyed along the Missouri Coteau through the LNWR area in 1863 (Clandening 1928)(Fig. I-2). Following are typical of his accounts: when entering the Coteau about 65 km southeast of LNWR (2-3 August) "Camped at a small lake of poor water, with poor grass, it being eaten by the buffalo [bison]. The buffalo and wolves [Canis lupus] cover the plains" and "Buffalo are in clouds all over the country... the country is shorn of grass by them" and, on the Coteau very near present-day LNWR (4 August) "Some grass, getting more grass, buffalo more scarce" but, back on the Drift Plain, just north of LNWR (7 August) "The country is plain and barren... no grass nor water near... The fire has run over it this summer" (Clandening 1928:257-258).

Henry (in Coues 1897) and Clandening (1928) characterized the Coteau prairie in the early and mid-1800s as being covered with short grasses, or barren, wherever recent fire and especially bison occurred which apparently was most places in their respective summers of travel. This has been evident elsewhere in accounts of presettlement northern Great Plains (England and DeVos 1969, Nelson and England 1971, Higgins 1986), supporting a view that the region was, historically, in a more arid, short grass state (Visher 1916, Shantz 1923, Larson 1940, Bird

1971, Branson 1985). But, Henry and Clandening also implied periodic deferment or rest from heavy grazing and fire, during which grasses would recover (Larson 1940, England and DeVos 1969). Overall, Clandening was preoccupied by lack of grass forage for his party's horses due to bison in northwestern North Dakota, while Henry intimated anxiety over absence of wood fuel for roasting bison steaks. The only mention by these authors of shrubs or trees on the Missouri Coteau was a note by Clandening (1928:258) on 6 August of "small brushwood, cherry, etc." in drainages along the edge of the Coteau somewhere near LNWR.

Lands that comprise LNWR were surveyed originally by the U.S. Government Land Office in the 1890s. Descriptions of plant community structure recorded in surveyors' notes for the legal townships that comprise LNWR were consistent with those of early explorers. They indicated that presettlement LNWR was treeless prairie, though some tall shrub occurred (Table I-2).

Surveyor references to trees were confined to a single area covered with elm (that area still is covered with elm). Surveyors normally depended on trees, where available, to mark section corners and reference lines (Burgess 1964, Stearns 1974), but marking of elms in this clump was the only use of such "bearing trees" on the surveyed townships. The site occupied by elm is a steep (30°), north-facing slope above a lakeshore. Clearly, topography at this site made the area uniquely invulnerable to fire and allowed establishment of elm and, apparently, associated aspen (the surveyor's "poplar" in Table I-2)(Wells 1970). A west-facing slope above another lake was similarly protected from fire so that chokecherry and hawthorn occurred (section W 22 in Table I-2; these shrubs persist at the site today despite repeated prescribed burns in the 1980s that reduced shrub elsewhere). The survey notes (along with Clandening's relevant observation) suggest that tall shrubs such as hawthorn, chokecherry, and probably willow occurred

Table I-2. Summary of upland habitat features typically referenced in 1893-1898 Government Land Office survey of present-day LNWR.

Feature	Text reference	Date	Location[a]
Prairie grass			
	"The land in this township is all prairie"	5/98	U, E twps.
	"Land prairie, hilly and broken" or "...rolling"	throughout	
	"Tp. is covered with rich nutritious grasses"	5/98	E twp.
	"...dry grassy drain..." and "...grassy meadow..."	throughout	
Shrubs and trees			
	"There are numerous small grassy marshes or meadows on the margins of which poplar brush was frequently found, indicating that but for prairie fires, timber would abound"	5/95	L twp.
	"Brush on E. shore, cherry [chokecherry] and thorn [round-leaf hawthorn]"	6/95	W 22
	"Brush, poplar and elm" and "...bluffs to about 40 ft. high covered with brush" and "An elm tree, 7 ins. diam. bears S. ...marked" and "Thence ascend timbered bluff"	5/95	L 4/5
	"A little thorn bush [hawthorn] on S. shore"	6/95	W 9

[a] Townships and numbers of sections within townships as follows: W = T 160 N, R 91 W; U = 159 N, 91 W; L = 158 N, 91 W; E = 159 N, 92 W.

infrequently and in small patches where there was protection from fire on steep slopes, especially where slopes met permanent wetlands. Lack of reference to low brush such as snowberry reassert that such vegetation was scarce or inconspicuous.

Prevalence of aspen suckers or saplings around wetland borders in the 1890s was indicated by the surveyor's notes (Table I-2). Accompanying the observation was the notion that, at least through the 1800s, aspen never approached tree size because of recurrent fire, an idea with abundant support (Christy 1892, Stewart 1953, Bird 1971, Nelson and England 1971). Because aspen suckers become saplings in 3-5 years (DeByle and Winokur 1985), persistence of a grass prairie suggests fire had to occur at least every 5-10 years as Wright and Bailey

(1982:81) proposed. Aspen clones can persist for centuries as successive generations of suckers or ramets if periodically rejuvenated (Schier 1975).

Vegetation Reconstruction: 1900-1935

Settlement of LNWR by people of European descent occurred during 1904-1915. The major lake chain on the area (Fig. I-1), as well as a township and nearby town, were named Lostwood about 1906 because of incidents involving the scarcity of wood (Williams 1966). R. Kellogg, USBS biologist, examined the area 10-20 August 1910 (Smithsonian Inst. Archives, Record Unit 7176) and described it thusly:

> "This region is high prairie country... The only timber in this region was formerly on S.E. corner of Lostwood Lake but this was cut off by the homesteaders and now there is nothing left but small oak [sic; probably elm] and poplar brush, with a clump of willows here and there."

Kellogg (Smithsonian Inst. Archives, Record Unit 7176) also mentioned "...the shores of the Lostwood Lakes are strewn with the skulls and bones..." of bison, which had been extirpated from the area in the 1870s (Coues 1878, Hornaday 1889). Absence of this major grazing influence possibly had allowed prairie grasses to achieve greater density and height (Kirsch and Kruse 1973) but fire frequency and intensity likely then increased (Higgins 1986) and continued to check woody growth.

However, cessation of prairie fires coincided with the settlement era. Human population in 1885 over what today approximates Mountrail and Burke counties was "...40 white, 1 negro, 298 indian or half-breed..." (Anonymous 1909:340), but exceeded 25,000 persons by 1920 (Burke County and White Earth Valley Historical Society 1972, VanderBusch 1991). Last major conflagrations on LNWR occurred about 1905 and 1909 (Burke County and White Earth Valley Historical Society 1972:1013; pers. comm. with sons and daughters of original homesteaders), except for a 80-km^2 burn in 1943 almost entirely north of

LNWR (T. Stewart, pers. comm.; FWS unpubl. refuge narrative). Construction of roads, breaking of native sod, and fire fighting by homesteaders effectively worked in concert to halt prairie fires (Raby 1966, Nelson and England 1971).

F. Uhler surveyed the "Lostwood Chain of Lakes" for USBS in August 1929 (FWS, unpubl. refuge files) when it was being considered for acquisition as a Federal Migratory Bird Refuge. Uhler described uplands as "...rolling hills covered with grass and occasional patches of buck brush (Symphoricarpos sp.)[western snowberry], rose bushes, and silverberry (Eleagnus commutata) or a few clumps of stunted trees" (FWS, unpubl. refuge files). Novel in his descriptions were the mention of (1) trees (certainly aspen) other than the aforementioned elm clump and (2) low brush, especially snowberry. Uhler also stated that most upland prairie was being grazed by domestic livestock.

LNWR was resurveyed in spring and summer 1935. There were many references to disturbance from settlement such as tilled soils, wagon trails, and fences, but especially striking in this survey was that trees (aspen) and brush (presumably western snowberry or snowberry-dominated types) obstructed section lines where no mention of woody vegetation occurred in 1890s survey notes (e.g., "Enter... leave brush patch" or "On small ridge, in brush patch" and "Poplar grove 0.50 chains [10 m] wide..." [FWS-Denver Regional office, unpubl. files]). Still, very common throughout was the statement: "No bearing trees available."

Vegetation after 1935

First aerial photographs of LNWR taken in 1938 confirmed that marked change had occurred in the prevalence of quaking aspen. Tree clumps present only as brush in the early 1900s and noted (apparently) by Uhler as "stunted trees" in 1929, were clearly in evidence by 1938 when 158 aspen tree clumps covered about 21 ha (Table I-3). During the next 47 years the number and total area of clumps increased >3-fold and 20-fold, respectively. A majority of the total area currently occupied by aspen tree clumps was represented by small tree clumps in the 1930s (Table I-4); by the 1960s some 2.59-km^2 sections had >15 clumps/km^2. Prairie with at least 2-3 aspen tree clumps/section (about 1/km^2) is considered aspen parkland (Archibold and Wilson 1980). By this definition about 75% of LNWR was transformed from mixed grass prairie to aspen parkland in little more than a half-century.

Table I-3. Incidence of quaking aspen tree clumps on LNWR during the 1900s.

	circa 1910	1938	1953	1969	1985
Clumps					
N	0	158	316	474	518[a]
clumps/km^2		1.46	2.92	4.38	4.79
Area (ha)					
Total		21.1	80.0	153.1	184.2
Mean/clump		0.13	0.26	0.32	0.36
SD		0.09	0.22	0.30	0.36

[a] 1985 total excludes 17 clumps cut over by beaver (Castor canadensis) in the 1970s.

Table I-4. Contribution of quaking aspen of various age cohorts to aspen trees present on LNWR in the 1980s.

Approximate initial appearance[a] as trees	Contribution to aspen present in 1980s	
	% of clumps	% of area
1917-23	29.7	61
1933-38	28.4	25
1949-54	30.3	12
1965-70	11.6	2

[a] Based on an age-growth curve of aspen on the area (Fig. I-5), and initial detection of clumps as trees on aerial photographs taken in 1938, 1953, 1969, and 1985.

LNWR is 70-100 km southwest of the southern edge of the Aspen Parkland region of Canada (Bird 1961). The contemporary plant community at LNWR could be more precisely characterized as parkland rather than mixed prairie because LNWR is slightly higher relative to surrounding lands on the Missouri Coteau and therefore is slightly cooler and moister (Hegstad 1973). A consequence of these subtle differences is unique floristics that include growth sites potentially more conducive (i.e., less arid) for development of woody vegetation relative to prairie elsewhere along the Coteau (this phenomenon extends over about 900 km^2 of the Missouri Coteau, from about 25 km northwest of to 12 km southeast of LNWR; also see aspen distribution map in DeByle and Winokur [1985:9]). Thus, the area that encompasses LNWR could be considered an island or southern extension of parkland habitat.

Western snowberry is another conspicuous woody plant on LNWR. Lack of reference to low brush in historical accounts suggested the plant either was inconspicuous or occurred infrequently before settlement. An estimate of 5% composition (above-ground, dry weight biomass) comprised by snowberry and other low brush in pristine mixed grass prairie has been proffered based on relict sites (U.S. Soil Conservation Service 1975). This is close to snowberry cover composition on pristine sites reported by Coupland (1950, 1961). Like aspen, snowberry persistently resprouts under fire regimes and proliferates under fire suppression or infrequent fire (Pelton 1953, Anderson and Bailey 1979). Thus, it was unsurprising that initial reports of snowberry patches and aspen tree clumps coincided in the late 1920s (as per F. Uhler). Snowberry patches spread mainly by rhizomes, especially by trapping snow and hoarding soil moisture from surrounding grass and forbs (Pelton 1953). As snowberry continues to expand it can serve as successional precursor to aspen clone development (Bird 1961). Cattle grazing tends to hasten this trend because snowberry generally is unpalatable and competitively favored under most grazing systems (Pelton

1953).

Although it is impossible to ascertain precisely how widely snowberry occurred historically, it covered an average of 24% of upland native prairie on sample plots by the time the first aerial photographs were taken in 1938 (Table I-5). By 1985 extent of snowberry-dominated cover had doubled on the same plots (Wilcoxon signed rank test, P = 0.068). This trend parallels that of aspen proliferation on the area (Fig. I-3), and intimates that about 5% snowberry composition in the presettlement era is plausible.

Historical Raptor Community

Pre-1935 Observations: northwestern North Dakota and Peripheral Areas

There are few records of nesting raptors specific to LNWR before the 1930s although many exist for northwestern North Dakota and adjacent parts of Montana and Saskatchewan. For example, in April 1805, Lewis and Clark's party collected a great horned owl (*B. v. occidentalis*) in woody breaks along the Missouri River about 60 km southwest of present-day LNWR (Cutright 1969:129).

Coues (1874, 1878) surveyed birds as he travelled west from the Souris River through the Missouri Coteau near or south of LNWR in summer 1873. He noted that northern harriers were common: "...constantly saw marsh hawks throughout northern Dakota, they were the most abundant and universally distributed of all rapacious birds" (Coues 1874). Swainson's hawks also were "very abundant" and observed almost daily; they nested in shrubs on the prairie but in areas lacking these, ground nests were noted (Coues 1878). Of red-tailed hawks, Coues noted only 1 individual during the survey; it was shot on the Souris River where Swainson's hawks were the prevalent *Buteo* spp. (Coues 1878). He implied that distribution of ferruginous hawks was sparse and referred to the hawk as "occasional" (Coues 1874).

Table I-5. Extent of upland area dominated by western snowberry on selected 65-ha, quarter-section plots on LNWR in 1938 and 1985.[a]

Quarter section[b]	1938		1985	
	ha	% of upland	ha	% of upland
NE S. 9	46.6	36.6	95.3	74.8
NW S. 6	12.8	10.9	40.8	34.7
SE S. 6	35.9	30.1	64.0	53.6
NE S. 6	24.2	19.5	50.1	40.4
mean	29.9	24.3	62.6	50.9
SD	14.6	11.4	23.8	17.8

[a] Includes area where western snowberry and associated low brush species comprised >50% canopy cover. Some tall shrubs were included.
[b] Plots all from T 159 N, R 91 W. Plots were selected randomly; see Methods.

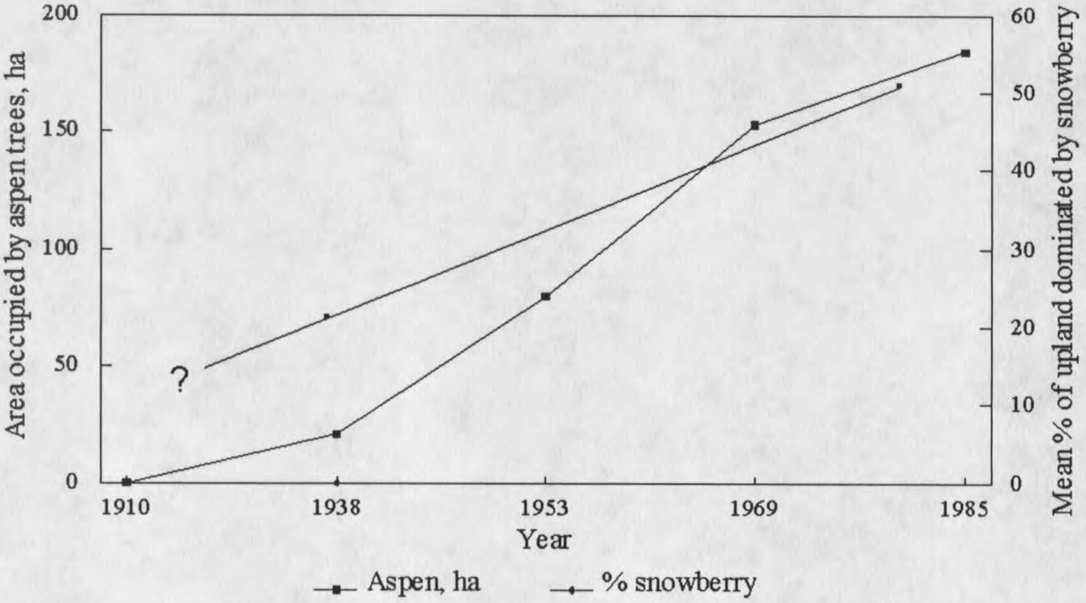

Figure I-3. Comparison of snowberry trends on plots with aspen expansion on LNWR.

Coues (1874) mentioned several species of owls. Short-eared owls were uncommon, but I believe Coues's impression of this owl's abundance likely depended on abundance of voles (Microtus spp.)(Clark 1975, Part II) during his survey. Burrowing owls (Athene cunicularia), however, were "...the only owl species inhabiting, in any numbers, the entirely treeless regions of the west... may be considered characteristic of the plains." Coues made little mention of great horned owls and implied they were restricted to wooded areas of the region.

Allen (1874) surveyed regional fauna including the Big Muddy Creek area about 120 km west-southwest of LNWR at the same time as Coues's more northeasterly survey. Similar to abundance implied by Coues, occurrence of great horned owls was occasional. But, Allen's impressions of raptor populations in this more arid area (mainly short grass-big sagebrush [Artemisia tridentata] shrubsteppe) differed in some respects e.g., short-eared owls were most common owls and burrowing owls were less common. Ferruginous hawks were the most common Buteo spp. observed; several ground nests with young were noted. Forty years later, however, Cameron noted that abundance of ferruginous hawks in eastern Montana had declined as had abundance of Swainson's hawks (Cameron 1913, 1914).

Bendire (1892) suggested that ferruginous hawks in North America during the late 1800s were most common on extensive prairies of the Dakotas. His quote of B. Goss (1892:260) reveals the most striking evidence of historic ferruginous hawk abundance (as well as other relevant notes on prairie ecology) on the Missouri Coteau of northwestern North Dakota:

> "The Ferruginous Rough-leg is not uncommon in the high broken prairie and lake regions of northwestern North Dakota. In May, 1880, I took four sets of their eggs, the nests being all placed on the ground, on rocky hillsides, generally near large bowlders [sic]. They were constructed of bones, turf, and dry grasses, usually quite bulky and rather poorly finished. Bleached buffalo skeletons were scattered all over the country in considerable numbers, and the ribs of these had principally been used by these hawks for the groundwork of their nests. While traveling over the country, I had several times seen circles of these ribs, lying on

> the ground, all pointing toward the center like the spokes of a wheel, and wondered at their regular arrangement. The finding of these nests solved the mystery; the annual prairie fires had burned the rest of the nest, and left the bones as placed by the bird. The buffalo ribs were used in lieu of sticks, there being no timber of any consequence in the Coteau Hills, where I found them breeding, within a distance of 15 miles."

Goss (in Bendire 1892:239) also described nests of Swainson's hawks in North Dakota as being in shrubs "...2 to 4 feet from the ground," and observed ground nests where prairie fires destroyed shrubs that had held previous years' nests!

Rolfe (1898) documented a decline in ferruginous hawks during the 1890s in an area about 250 km east of LNWR. The decline closely coincided with the coming of settlement, particularly cultivation. Ferruginous and Swainson's hawks were "quite common" and burrowing and short-eared owls "very common" in 1913 and 1918 on prairies and breaks along the Missouri River about 65 km southwest of LNWR (Gabrielson and Jewett 1924:300); harriers again were the most abundant hawk. Wood (1923) implied ferruginous and Swainson's hawks generally had declined in North Dakota by 1923, although ferruginous hawks still were quite common about 65 km northeast of LNWR in the late 1920s (Davy 1930). In southern Saskatchewan, ferruginous were "fairly common," Swainson's hawks "common and generally distributed" (Todd 1947:393), but burrowing owls "...now rare and local" (1947:405) in 1932.

Pre-1935 Observations: LNWR

R. Kellogg's records during 10-20 August 1910 comprise the first faunal documentation unique to LNWR (Smithsonian Inst. Archives, Record Unit 7176). Kellogg observed northern harriers as well as several short-eared owls (including a collected specimen). Of Swainson's hawks he noted: "...saw several of these hawks near Lostwood Lakes." Kellogg also recorded a great horned owl: "I saw one of these large pale horned owls" (apparently referring to the light-plumaged morph of B. v. occidentalis that today is the common subspecies breeding in the area [pers. obs.]; he referred to it as pallescens, now the recognized subspecies of the extreme southern Great Plains and desert southwest [Bent 1938:321, Johnsgard 1988]). But, sons and daughters of homesteaders from the area never heard nor saw the owl in the early 1900s (e.g., T. Stewart, pers. comm.).

V. Bailey surveyed the Drift Plain and Coteau east of LNWR on 11-20 July 1913 for USBS (Smithsonian Inst. Archives, Record Unit 7176). Although his observations occurred mostly along Des Lacs River (Fig. I-2), some on adjacent prairies were pertinent, e.g., harriers "...marsh hawks are common all over the prairie and marshes." And, ferruginous hawks were noted. Bailey also mentioned nesting of long-eared owls in the Des Lacs valley, records for northwestern North Dakota that would have predated those reported by Stewart (1975:159).

Notes on breeding birds of LNWR (also the Des Lacs River valley) during 1915-20 by Woodruff (1923) were mostly of waterfowl. Abundance of northern harriers impressed him, however: "A nest of the marsh hawk can be found every mile or so" (1923:6). He also provided details of 5 short-eared owl nests found.

Uhler's reconnaissance (FWS, unpubl. refuge files) of LNWR in August 1929 likewise focused on waterfowl, but mentioned occurrence of harriers and Swainson's hawks.

LNWR Raptors: 1935 through Present

Observations of raptors on LNWR by refuge managers and visiting biologists were recorded in narrative reports nearly every 3 months beginning in the late 1930s, except almost no notes were recorded during the mid-1970s. For example, the summer 1939 narrative complains of individuals shooting nesting ferruginous hawks, Swainson's hawks, and burrowing owls on LNWR from an adjoining highway and reports "...that persons invaded the refuge and intentionally destroyed nests of ferruginous rough-legged and Swainson's hawks." This narrative includes the first attempt to completely list nesting raptors at LNWR: harriers, Swainson's hawks, and ferruginous hawks, in decreasing order of abundance, were believed to be most common nesters. Burrowing owls, short- and long-eared owls, and great horned owls occurred but it was unknown whether they nested on LNWR.

In 1940 the first comprehensive list of birds of LNWR was assembled (FWS, unpubl. refuge narrative). It included Swainson's and ferruginous hawks, harrier, burrowing owl, and short-eared owl as nesting species; non-nesting raptor species included great horned owl and red-tailed hawk. A revised list in a 1942 narrative added long-eared owls as breeding birds, and noted great horned owls were occasional visitors.

Following is a summary of accounts, by species, of abundance of nesting raptors for the mid-1930s through 1980s. Relative abundance is summarized for species collectively in Fig. I-4.

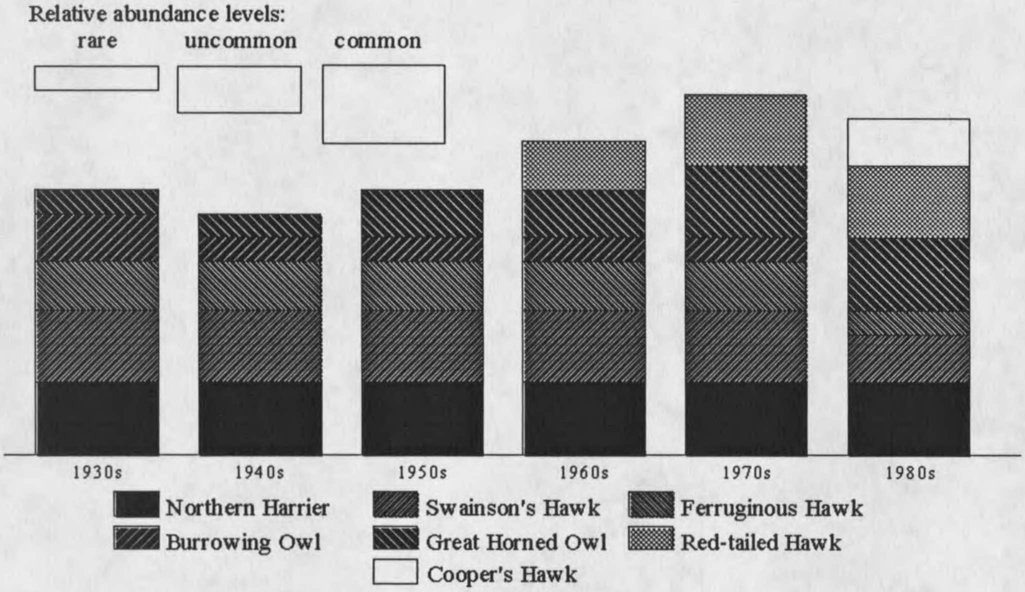

Figure I-4. Relative abundance and composition of raptors during breeding season on LNWR, generalized among decades of the mid-20th century. Excludes long- and short-eared owls which were hard to categorize.

Northern Harrier. Northern Harriers were consistently referred to as the most abundant nesting raptor at LNWR during the 50-year post-settlement period (Fig. I-4). Narratives referred to nesting harriers as "abundant" or "most abundant hawk" or "numerous." This was substantiated by quantitative study in the 1980s.

Ferruginous Hawk. Nesting ferruginous hawks were noted among narrative reports through the mid-1960s mostly as occurring uncommonly, e.g., "at least 3 pair nesting" (1942), "estimated" (i.e., speculated) refuge population 8 (i.e., 4 pairs)(1945), "observed regularly all summer" (1951) but "seen infrequently" in summer (1956). Except for few records before the 1940s, ferruginous hawks always were described as less prevalent than Swainson's hawks, but in the early to mid-1960s as being more prevalent than the newly-established red-tailed hawks (Fig. I-4). Estimates of refuge raptor populations in 1970 and 1972 narrative reports, however, did not include ferruginous hawks, and 10 years later the hawk was virtually absent as a breeding bird.

Swainson's Hawk. Next to northern harriers, Swainson's hawks were noted uniformly in refuge narrative reports as being the most abundant hawk, e.g., "...Swainson's and marsh hawks made up at least 90% of the summer hawk population... Swainson's are fairly common in summer" (1954). Narratives were replete with summer population estimates and notes of nests observed, e.g., "observed several nesting" (1939), "...5 nests located" (1959), and population estimates of 20 individuals (i.e., 10 pairs)(1945), 30 (1946), 12 (1955), 25 (1964), and 16 (1973). Specific details on nest sites were lacking other than some locations, e.g., "...returned to nest in grove near headquarters gate" (1940).

Red-tailed Hawk. Red-tailed hawks were not observed during the breeding season and rarely during the spring and fall migration period through the mid-1950s (except that inclusion of the hawk in a 1939 list of nesting raptors probably represented misidentified or errant individuals). For example, "...1 red-tailed hawk observed 12 April" (1950) and "...a few red-tailed hawks moved through the first week of April" (1955). The 1956 narrative noted "...more observations than a year ago" of migrating red-tailed hawks in spring, and cited an apparent krideri (light-plumaged subspecies [Lish and Voelker 1986]) individual as late as 3 May (this subspecies was not observed nesting during the 1980s [pers. obs.]). A red-tailed hawk was noted during summer 1958, but only mention of the species in 1959 was 1 observed 13 April; no red-tailed hawks were listed among migrant raptors observed in spring 1960 and 1961. Finally, 1962 and 1963 narratives included red-tailed hawks in respective lists of raptors observed throughout summer. In 3 following narratives the red-tailed hawk was considered a common summer resident, but less prevalent than Swainson's and ferruginous hawks. In 1971 several red-tailed hawk nests were noted in aspen tree clumps and the hawk was thought to be the most prevalent breeding Buteo spp. Narratives thereafter supported this observation and intensive study confirmed it quantitatively for the 1980s (Fig. I-4).

Great Horned Owl. Great horned owls were scarce through the 1940s (Fig. I-4). Early narratives referred to the owl as only a rare visitor or scarce resident, e.g., several observations in winter 1942 were more than usual "...4 observed [during winter], were only occasional visitors in past" (1942), but more typical descriptions were "...1 observed all winter" (1943), "...not present in winter" (1944), and "...not heard or seen all fall" and "...rarely observed on refuge" (1951). Two nests were observed in 1952 and again in 1954; a 1952 nest had 2 eggs on 11 April and eggs hatched in both 1954 nests. By the mid-1950s the owl clearly was no longer rare or scarce, e.g., "...frequently seen" (late winter 1953), "...are more in evidence now... some limited control may be desirable" (summer 1955, although somewhat contradictory for the previous quarter "...few and seldom seen"), and "...present but not numerous" (1958). An apparent upward trend in abundance, however, continued through the 1960s, e.g., "...commonly flushed from tree groves" (1964), "...commonly observed, population stable" (1965), "...common year round" (1966). Ten to 15 resident horned owls were guessed to occur on the refuge during this time. The 1972 narrative reported "...great horned owls regularly observed." Refuge managers' suspicions that nesting great horned owls had become common by the 1970s were substantiated in the 1980s.

Burrowing Owl. Records of burrowing owls were scant and reports of their nesting status generally lacking. Based on early refuge narratives, burrowing owls apparently were uncommon breeding birds through the 1930s. Local landowners recalled nesting burrowing owls in the vicinity of LNWR in the early 1900s to 1930s and wondered why the "ground owls" had disappeared (C. Helde, pers. comm., A. Mortenson, pers. comm.). After the 1930s presence of breeding burrowing owls at LNWR were implied by refuge narratives only in 1940 and 1942 and an observation of a pair "...one and one-half miles south of [LNWR] headquarters" in 1940. Thereafter, the owl was only occasionally seen through the mid-1950s and once each in 1967 and 1979.

Short-eared Owl. Occurrence of short-eared owls was hard to characterize. Besides their inclusion in the 1940 list of breeding raptors (FWS, unpubl. refuge narrative), the species was reported every few years in refuge narratives as being present in summer, undoubtedly reflecting its cyclic nature (Clark 1975). For example, short-eared owls were very common or "greatly increased" in 1963, 1966, 1969, 1972, and 1978, and occurred at high densities in 1981-82 (Part II). But, for intervening years short-eared owl abundance typically was described as "...nowhere near as numerous" to "...rarely observed" or "...observed only in spring and fall." In the 1969 narrative, a guess of 1 short-eared owl nest/section (2.59 km^2) was reported.

Long-eared Owl. Few records of long-eared owls exist through the 1970s. Inclusion of this species as a breeding bird in the 1942 bird list was about the only hint of its occurrence on LNWR before the 1980s, except for a 1953 report "...observed from time to time but not present in great numbers" (FWS, unpubl. refuge narrative). I suspect the owl occurred on LNWR after the 1930s but was overlooked because of its secretive behavior (Bent 1938). The only other records for this owl on LNWR through the 1970s occurred in 1973 when an investigator searching for crow nests found almost no crows nesting but discovered long-eared owls setting in several crows' nests (FWS, unpubl. refuge narrative).

Cooper's Hawk. Cooper's hawks were noted occasionally on migration but not as nesting birds on LNWR through the 1970s (FWS, unpubl. refuge narratives). But, this hawk apparently pioneered in 1982 when it was discovered nesting in 1 of the largest (2-3 ha) aspen tree clumps in the most heavily wooded tract on LNWR (composition 13% aspen trees, 15 tree clumps/km^2). One nesting pair occurred each year in the same tree clump during 1982-85 then an average increment of 1 pair/year occurred during the next 4 nesting seasons, at widely scattered locations on LNWR (FWS, unpubl. refuge files; Part II). Relative nesting abundance of the hawk approached common (density was 0.05 pairs/km^2 by 1989-90 [Part II]) less than a decade after it apparently first nested on LNWR (Fig. I-4).

Historical Raptor Prey

Richardson's ground squirrels (Spermophilus richardsoni) occur north and east of the Missouri River (Jones et al. 1983:137), in prairie of shortest grass height especially closely grazed areas (Bailey 1926, Jones et al. 1983). They are key prey of ferruginous and Swainson's hawks in the northern Great Plains (Bailey 1926, Lokemoen and Duebbert 1976, Schmutz et al. 1980, Gilmer and Stewart 1983, Houston 1990). Historically, astonishing numbers of Richardson's ground squirrels were present in a nearly continuous distribution (Jones et al. 1983:138). In 1875 E. Coues said they occurred "by hundreds of thousands over as many square miles of territory... millions of acres of ground are honeycombed with its burrows..." (unreferenced citation in Jones et al. 1983:138).

On LNWR, Richardson's ground squirrels were common in 1910 according to R. Kellogg, and V. Bailey said the ground squirrel was

"...abundant all over the country" encompassing LNWR in 1913 (Smithsonian Inst. Archives, Record Unit 7176). Richardson's ground squirrels still were common on LNWR as late as 1939 and 1940 but by the mid-1940s the population was so small it was considered an exception to see 1 (FWS, unpubl. refuge narratives). Thereafter, Richardson's ground squirrels were not mentioned in refuge narratives or other reports even though thirteen-lined (_S. tridecemlineatus_) and Franklin's (_S. franklinii_) ground squirrels were occasionally noted. In the 1980s, Richardson's ground squirrels were scarce on LNWR and distributed sparsely on the refuge periphery but were common on adjacent, heavily grazed prairie (pers. obs.).

DISCUSSION: INTERPRETATION AND IMPLICATIONS OF HISTORICAL CHANGE

Change in Raptor Composition

Nine species of Strigiform or Falconiform raptors nested on LNWR during the past 100 years. Only 5 of these are considered true grassland species (Johnsgard 1978, Andersen 1991): Swainson's hawk, ferruginous hawk, northern harrier, short-eared owl, and burrowing owl. To broadly summarize change in true grassland raptors, I generated a simple index of grassland raptor diversity (abundance x variety) by summing relative abundance levels for these 5 species at 3 approximate junctures in history: presettlement (circa 1895), LNWR establishment (1935), and current (1985)(Table I-6). This index changed little from presettlement to when LNWR was established but has changed significantly since. The status of Swainson's and ferruginous hawks, which were common and uncommon in the late 1800s, approached rare and absent during the 1980s. Thus, the overall index value could be halved by the end of the present century, compared to its beginning. Total number of nesting species of raptors has increased, however, from 6 in 1935 (assuming long-eared owls nested then) to 8 currently. Abundance of harriers and short-eared owls probably changed little from presettlement to the

1980s, but total abundance of other nesting raptors almost certainly was greater in the 1980s than before settlement and was dominated by generalist species (red-tailed hawks and great horned owls).

Table I-6. Summary of relative diversity[a] of breeding grassland raptors on LNWR, 1895-1985.

Species	1895	1935	1985
Burrowing owl	2	2	0
Ferruginous hawk	2	2	1
Swainson's hawk	3	3	2
Short-eared owl[b]	2	2	2
Harrier	3	3	3
Diversity index (total)	12	12	8

[a] Diversity index based sum of relative abundance of species: 0 = absent, 1 = rare, 2 = uncommon, 3 = common. See methods for characterization of relative abundance levels.

[b] Short-eared owl abundance based on average year for this strongly cyclic species.

Mechanism of Change in the Raptor Community

Transition in composition and relative abundance of nesting raptor species on LNWR since the late 1800s ultimately was due to mainly disclimax (i.e., postclimax) successional trends in mixed grass prairie vegetation. These trends were manifested by woody plant proliferation and increased height and density of vegetation. Marked expansion in quaking aspen and western snowberry were overt symptoms of modern anthropogenic impact to an ecosystem that evolved under frequent, severe disturbance (Gleason 1922, Weaver 1968, Heady 1975). Suppression of fire was the key factor. Loss of periodic, intense grazing by vast herds of bison, however, likely also favored brush and tree increase. Historically, fire and bison impact were not independent of each other (Higgins 1986), nor were they sole determinants of pristine, northern mixed grass prairie (Shantz 1923, Coupland 1950).

Food ultimately explains most aspects of raptor population ecology (Newton 1979:290). Nest sites also are important. The following were likely major mechanisms of change in the raptor community at LNWR.

Predator-prey Relationships

Effects of coincident increases in vegetation height, litter accumulation, and proliferation of low brush, especially snowberry, resulted in cover so dense that most prey were either undetectable or invulnerable to foraging burrowing owls, Swainson's hawks, and ferruginous hawks. These birds mostly hunt aerially or from low perches and are not morphologically and behaviorally adapted to foraging in dense, rank cover (Zarn 1974, Wakeley 1978, Jasikoff 1982, Marks and Ball 1983, Janes 1985). Prey in denser cover could be exploited by red-tailed hawks and great horned owls, however, because these 2 raptors are versatile, perch-and-wait hunters that rely on elevated hunting perches (Rudolph 1978, Petersen 1979, Janes 1984, 1985, Preston 1990). Elevated perches that became available on LNWR in the form of well-dispersed aspen tree clumps were relatively neutral or negative habitat attributes for nesting Swainson's and ferruginous hawks (Schmutz et al. 1980, Houston and Bechard 1983, Janes 1985, Part II). Short-eared owls and northern harriers would not have been as negatively affected by successional changes that occurred because these birds can forage in denser vegetation than Swainson's and ferruginous hawks and their main prey, voles, tend to inhabit rank plant cover (Eadie 1953, Getz 1961, Steele 1977). Increased vegetation height and density also was an unfavorable habitat change for Richardson's ground squirrels that were key prey for Swainson's and ferruginous hawks.

Nest Site Habitat

Change in the makeup of raptors nesting at LNWR also could be influenced by nest site limitations. Short-eared owls and northern harriers nest on the ground in dense vegetation (Duebbert and Lokemoen 1977, Hamerstrom and Kopeny 1981). Therefore, nest site availability did not limit these species as successional change occurred at LNWR. In contrast, nest sites became less available for burrowing owls as brush and overall vegetation height and density increased because the owl requires unobstructed views around nesting burrows, usually in the form of heavily grazed prairie (Zarn 1974, Marks and Ball 1983). Burrowing owl nest site availability also may have declined due to fewer potential burrow nest sites associated with decreased abundance of Richardson's ground squirrels. This rodent provides nest site burrows for the owl in areas of the northern Great Plains where prairie dogs (Cynomys spp.) do not occur (Zarn 1974, Marks and Ball 1983), such as northwestern North Dakota (Jones et al. 1983). But, badger (Taxidea taxus) holes and dens of other mammals sometimes were available and could have been used (Coues 1874).

Establishment of aspen tree clumps was the most obvious change in raptor nest site availability at LNWR during the 1900s. Aspen trees provided sites needed by red-tailed hawks to place their large, bulky nests. Houston and Bechard (1983) suggested that coinciding increases in distribution of aspen and nesting red-tailed hawks in Saskatchewan corresponded to when nest sites became available for the hawk. I tested this straightforward hypothesis with my data: pioneering by red-tailed hawks about 1960 should have coincided with initial appearance of mature (>25 cm dbh) aspen trees that red-tailed hawks prefer for nest sites on LNWR (Part II). Fires were effectively suppressed on LNWR by 1905-10, at which time aspen growth was released. Aspen on LNWR reaches maturity (25 cm dbh) in about 40+ years (Fig. I-5). Therefore, pioneering by red-tailed hawks on LNWR in about 1960 did not occur precisely as predicted by the above nest-site hypothesis but lagged only by about 10 years. In Saskatchewan red-tailed hawks pioneered into new areas when aspen height reached about 10 m (Houston and Bechard 1983). On LNWR, this height would coincide with dbh of about 20 cm (from Part II, Table II-4) and an age of about 30 years (Fig. I-5), precisely the interval suggested by Houston and Bechard (1983). Aspen this size would have been available on LNWR in the late 1930s, about 20 years before nesting by red-tailed hawks was first noticed. This suggests that (1) some other factor was limiting when trees first were available that would support red-tailed hawk nests, (2) red-tailed hawks did not begin to nest until very optimal (i.e., large) dbh nest trees were available, or (3) pioneering of red-tailed hawks lagged behind that in nearby aspen parklands of Canada because LNWR was isolated (70-100 km from) from the relatively contiguous parkland habitat.

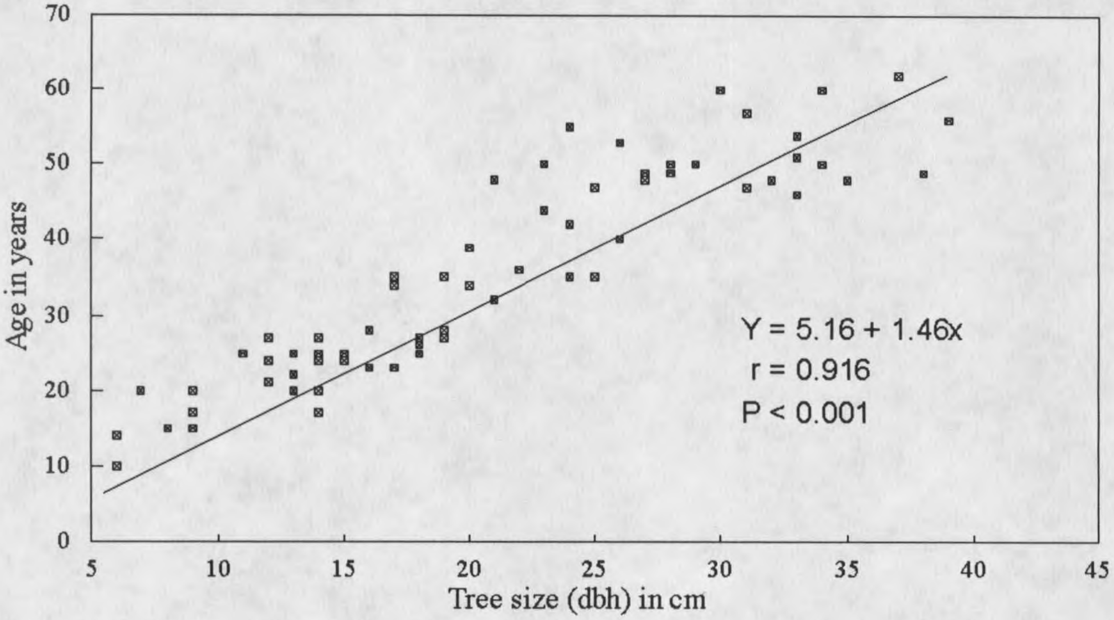

Figure I-5. Relationship of quaking aspen size to age on LNWR ($\underline{n}$ = 72 trees measured).

Enhanced availability of elevated perches probably is at least equally important as nest sites in establishment of breeding red-tailed hawks (Janes 1987). Lack of nesting by red-tailed hawks in areas on LNWR with few tree clumps, even though clumps present may have had suitable nesting sites (Part II), implied that availability of large nest trees in the late 1950s coincided with some minimal threshold of hunting perch dispersion or height that also was reached.

A suggested increase in abundance of great horned owls on LNWR in the 1960s-70s coincided with establishment of breeding red-tailed hawks (Fig. I-4) that provided the owl with more suitable nest sites than were previously available (reviewed in Sargeant et al. 1992). But the coincident and comparatively gradual increase in abundance of great horned owls can likely also be attributed to better prey access via enhanced dispersion of hunting perches (Rudolph 1978, Peterson 1979).

Other interspecific interactions among nesting raptor species may have contributed to historical change observed. Interspecific territoriality, aggressive interaction, and reduced productivity under close interspecific nesting can occur among _Buteo_ spp. (Rothfels and Lein 1983, Janes 1987) and between _Buteo_ spp. and great horned owls (Houston 1975, Dunkle 1977, Bosakowski et al. 1988). Increased abundance of great horned owls and competition with red-tailed hawks were partly implicated in declines of Swainson's hawks in Oregon (Littlefield et al. 1984, Janes 1987). But in general, intraspecific behavior and habitat, especially food supply, more significantly determine spacing and abundance of these and most other raptors (Newton 1979). Because habitat change on LNWR was a precursor to effects of interspecific interactions on abundance and composition of raptor species, interactions among species were of secondary importance as mechanisms underlying changes in makeup of the raptor community.

Changes in composition and abundance of mammalian predators in the northern Great Plains (Sargeant et al. 1992) may have influenced transition in raptor species composition observed, directly by predation on adult raptors, their eggs or young, or indirectly by competing for prey. Red fox (_Vulpes vulpes_), coyotes (_Canis latrans_), and badger could depredate raptor nests on the ground or in low shrubs. Harriers, however, nest exclusively on the ground, and their density and success on LNWR remains high with these mammals present (Part II) but burrowing owls could be vulnerable to these mammalian predators. Raccoon (_Procyon_ lotor) first occurred on LNWR in the 1950s and have been uncommon since (FWS, unpubl. refuge files). Their affinity for climbing trees potentially makes small populations of raccoons important predators of eggs or young in stick nests in such sites (Johnson et al. 1989). Also, striped skunk (Mephitis mephitis) occur on LNWR and may depredate nests of ground-nesting raptors but to my knowledge this has not been documented in the northern Great Plains. Overall, I suspect mammalian predators were relatively unimportant causes of change in the raptor community.

Effects of long-term rest or nondisturbance of mixed grass prairie vegetation on raptors have been discussed. Loss of immediate or short-term effects of disturbance to vegetation could have been another potential though perhaps minor mechanism of change in raptor composition on LNWR. Swainson's hawks forage in close association with prairie fires and modern-day agricultural operations (Palmer 1988). This behavior evolved presumably because Swainson's hawks historically exploited catastrophic habitat disturbances such as wildfires and high intensity grazing by bison that would have made prey vulnerable (e.g., Baird et al. 1874:270). Idle prairie as a static upland environment would not be conducive to this. Burrowing owls and ferruginous hawks also likely obtained benefits from these kinds of immediate changes in vegetative cover. Historically, Swainson's hawks apparently were able to nest in areas recently (≤1 year) burned (B. Goss, in Bendire 1892:239). Burrowing owls occupy prairie areas a few days after burning occurs (Higgins and Kirsch, in Marks and Ball 1983).

Extent of cultivation (total, about 21% of LNWR during 1910-55) probably had negligible or slightly positive impact on raptors (e.g., Schmutz 1984, 1989). But, a marked influx of humans during settlement may have negatively affected abundance of nesting raptors, especially ferruginous hawks, before LNWR was established. Some evidence suggests ferruginous hawks are more sensitive than other raptors to presence of humans during courtship and early nesting stages (Evans 1982, Roth and Marzluff 1989). Any such impacts, however, would have been short-term because the area was depopulated by the 1930s.

Raptors as Models of Habitat Conditions

Although evidence suggests historical change in species composition of the raptor community on LNWR is attributable ultimately to vegetation succession in absence of recurrent, catastrophic fire and grazing, an alternate perspective has merit. Resource personnel interested in restoring native wildlife diversity on public lands in mixed grass prairie may ask what the historic raptor community communicates about historic habitat conditions, a question that addresses use of raptors as biological indicators.

Cognizance of great horned owl and red-tailed hawk abundance is not needed to appreciate increasing prevalence of quaking aspen at LNWR. Less obvious, however, were implications of the diversity of historically nesting raptors for comprehending the northern mixed grass prairie environment before settlement. Swainson's hawks, ferruginous hawks, and burrowing owls indicated prevalence of short-stature, presettlement prairie vegetation. Historical accounts conveyed common abundance of Richardson's ground squirrels that also suggested this condition. Widespread occurrence of northern harriers in the late 1800s, however, seemed to contradict the notion of a short physiognomy by suggesting relatively tall, dense cover also occurred. I've provided evidence (e.g., Clandening 1928) that idle prairie areas occurred near tracts of heavily grazed or burned, sparsely vegetated prairie. Thus, contrasting plant physiognomy between adjacent areas could explain local sympatry of breeding harriers and burrowing owls.

Furthermore, local sympatry of raptor species associated with disparate vegetation height and density could have occurred because habitat within areas was diverse. On LNWR, the knob-and-kettle topography and occurrence between short grass, tall grass, and fescue prairies and aspen parkland potentially support a wide range of vegetation types over small areas. Based on relict sites currently under burning and grazing treatments that simulate the same historic disturbances, plant cover that likely dominated this range of sites is summarized in Table I-7. Hypothetically, it ranged from dense, moderately tall (canopy height 25-40 cm), mostly grass cover in mesic sites such as low prairie edges and lower slopes of hillsides, to short (<10 cm) herbaceous cover on xeric knolls. Plants of intermediate height especially wheatgrasses and needlegrasses, also fescues (_Festuca_ spp.) and several species of forbs (Asteraceae, Fabaceae) dominated sites in between. It is conceivable that, in an average moisture year between fire or major grazing episodes, the mosaic of vegetation types present was amenable to species of raptors affiliated with sparse as well as robust prairie.

Table I-7. Hypothetical list, by site type, of plants dominant (>10% canopy cover) before settlement on LNWR.

Mesic sites
- fowl bluegrass
- prairie cordgrass (_Spartina pectinata_)
- northern reedgrass (_Calamagrostis inexpansa_)
- big bluestem (_Andropogon gerardii_)
- mat muhly (_Muhlenbergia richardsonis_)

Intermediate sites
- green needlegrass (_Stipa viridula_)
- western wheatgrass (_Agropyron smithii_)
- goldenrod (_Solidago_ spp.)

Xeric sites
- blue grama
- prairie junegrass (_Koeleria cristata_)
- plains muhly (_Muhlenbergia cuspidata_)
- needle-and-thread (_Stipa comata_)
- threadleaf sedge (_Carex filifolia_)
- fringed sage (_Artemisia frigida_)

Furthermore, historic vegetation height-density clearly was temporally dynamic. Drought, fire, and grazing by bison, Richardson's ground squirrels, and other herbivores severely reduced vegetation height some years, but lack of these factors produced an opposite physiognomy in other years. Thus, a community of short-grass consociates would have been favored during drought or in the year after a burn, but species associated with taller vegetation would have benefited in wet years or during periods of rest from fire and heavy grazing. Grazing and burning of northern mixed grass prairie tend to promote relatively arid conditions that favor the more xerophytic range of plants capable of growing on a given site type, while idle treatment or rest tends to create conditions conducive to potentially occurring mesophytes (Coupland 1950, 1974, Bird 1971, Singh et al. 1983). Implications for wildlife correspond directly. For example, widespread declines in Richardson's ground squirrels occurred during a series of high moisture years in Saskatchewan, and contributed to decreases in nesting ferruginous hawks (Houston and Bechard 1984).

SUMMARY AND CONCLUSIONS

Northern harriers, Swainson's hawks, ferruginous hawks, and burrowing owls comprised the community of raptors that nested on LNWR before settlement occurred in the early 1900s; short-eared owls probably also were common, albeit irregularly. Great horned owls were rare but gradually increased over the last 40-50 years, red-tailed hawks pioneered about 30 years ago, and Cooper's hawks pioneered in the past decade. Today, red-tailed hawks and great horned owls have replaced Swainson's and ferruginous hawks as dominant large (>700 g) raptors, coinciding with succession from mixed grass prairie to aspen parkland with snowberry-dominated uplands. Harrier abundance probably has changed little, but nesting burrowing owls have been absent >40 years. These changes, viewed in concert with effects of plant succession on habitat and prey, imply many causal mechanisms. Except perhaps for pioneering by Cooper's hawks, I suggest that the most fundamental causes of change in the raptor community were altered susceptibility of prey to foraging behaviors of specific raptor species and decreased abundance of certain key prey species, and that changes in nest site availability were secondary causes.

Presettlement species composition and abundance of nesting raptors posed contradicting implications for comprehending historic wildlife habitat at LNWR. Occurrence of ferruginous hawks, Swainson's hawks, and burrowing owls suggested prairie vegetation in the late 1800s was shorter and sparser than currently exists, a notion supported by historical accounts of vegetation physiognomy. However, a taller vegetation component also occurred to provide habitat for nesting harriers and short-eared owls and for their vole prey. In the Missouri Coteau of northwestern North Dakota, short, sparse cover and tall, dense cover could have coexisted in some years because of high heterogeneity of plant growth sites, or could have been alternately favored among series of years depending on prevailing disturbance (bison grazing, fire, or rest) or moisture regime (e.g., drought years). This supports the concept that native, mixed grass prairie is composed of a continuum of vegetation types (McMillan 1959, Ryan 1986, 1990), fundamental to holistic or ecosystem-oriented wildlife management.

I conclude that Swainson's hawks, ferruginous hawks, northern harriers, burrowing owls, and short-eared owls were characteristic breeding raptor species on LNWR before settlement in the early 1900s. Habitat that supported these species and associated native fauna was mixed grass prairie that was almost entirely treeless but had occasional tall shrubs at interfaces of steep slopes and permanent wetlands. Mesic and xeric sites of presettlement prairie were dominated by herbaceous vegetation shorter and sparser than what exists currently, and the prairie was temporally dynamic due to periodic, severe fire and grazing impacts absent through most of the twentieth century.

LITERATURE CITED

ALLEN, J. A. 1874. Notes on the natural history of portions of Dakota and Montana territories. Proc. Boston Soc. Nat. Hist. 17:33-86.

ANDERSEN, D. E. 1991. Management of North American grasslands for raptors. Natl. Wildl. Fed. Sci. Tech. Ser. 15:203-210.

ANDERSON, M. L., and A. W. BAILEY. 1979. Effect of fire on a _Symphoricarpos occidentalis_ shrub community in central Alberta. Can. J. Bot. 57:2819-2823.

ANONYMOUS. 1986. List of North Dakota's threatened and endangered biota. North Dakota Outdoors 49:28-32.

---. 1860-1900. U.S. Public land survey in North Dakota. N.D. Water Commission. Bismarck. Unpubl. files.

---. 1909. The Dakota territorial census of 1885. North Dakota Hist. Soc. Collections 4:338-348.

ARCHIBOLD, O. W., and M. R. WILSON. 1980. The natural vegetation of Saskatachewan prior to agricultural settlement. Can. J. Bot. 58:2031-2042.

AUS, P. B. 1969. Land use and environmental deterioration in North Dakota. North Dakota Q. 37:19-28.

BAILEY, V. 1926. A biological survey of North Dakota. U.S. Dep. Agric. North Am. Fauna 49. 226pp.

BAIRD, S. F., T. M. BREWER, and R. RIDGWAY. 1874. North American land birds. Little and Brown, Boston, Mass. 560pp.

BARKLEY, T. M., ed. 1986. Flora of the Great Plains. Univ. Press of Kansas, Lawrence, Kansas. 1392pp.

BECHARD, M. J., and C. S. HOUSTON. 1984. North Dakota oologists. Blue Jay 42:176-183.

BENDIRE, C. 1892. Life histories of North American birds. Smithsonian Inst. U.S. Natl. Mus. Spec. Bull. No. 1, Washington D.C. 446pp.

BENT, A. C. 1938. Life histories of North American birds of prey, part 2. Smithsonian Inst., U.S. Natl. Mus. Bull. 170, Washington, D.C. 465pp.

BIRD, R. D. 1961. Ecology of aspen parkland of western Canada. Can. Dept. Agric., Res. Branch. Publ. 1066. 155pp.

---. 1971. Ecology of the aspen parkland of western Canada in relation to land use. Can. Dep. Agric. Contrib. 27. 155pp.

BLUEMLE, J. P. 1977. The face of North Dakota: the geologic story. North Dakota Geol. Surv. Educ. Ser. 11. 73pp.

BMDP STATISTICAL SOFTWARE, Inc. 1985. SOLO user's guide. Univ. California Press, Berkeley. 286pp.

BOSAKOWSKI, T., R. SPEISER, and D. G. SMITH. 1988. Nesting ecology of forest-dwelling great horned owls, _Bubo virginianus_, in the eastern deciduous forest biome. Can. Field-Nat. 103:65-69.

BOTKIN, D. B. 1990. Discordant harmonies: a new ecology for the twenty-first century. Oxford Univ. Press, New York. 241pp.

BRANSON, F. A. 1985. Vegetation changes on western rangelands. Soc. Range Manage. Range Monogr. 2. 76pp.

BRAUN, C. E., K. W. HARMON, J. A. JACKSON, and C. D. LITTLEFIELD. 1978. Management of National Wildlife Refuges in the U.S.: its impacts on birds. Wilson Bull. 90:309-321.

BURGESS, R. L. 1964. Ninety years of vegetational change in a township in southeastern North Dakota. Proc. North Dakota Acad. Sci. 18:84-94.

BURKE COUNTY AND WHITE EARTH VALLEY HISTORICAL SOCIETY. 1972. Pioneers and progress. Bismarck Tribune, Bismarck, North Dakota. 1288pp.

CAMERON, E. S. 1913. Notes on the Swainson's hawk (Buteo swainsoni) in Montana. Auk 30:381-394.

---. 1914. The ferruginous rough-leg, Archibuteo ferruginous in Montana. Auk 31:159-167.

CARPENTER, J. R. 1940. The grassland biome. Ecol. Monogr. 10:617-684.

CHAPMAN, H. H. 1947. Natural areas. Ecology 28:193-194.

CHRISTY, R. M. 1892. Why are the prairies treeless? Proc. Royal Geogr. Soc. 14:78-100.

CLANDENING, W. H. 1928. Across the plains in 1863-1865. North Dakota Hist. Q. 2:247-272.

CLARK, R. J. 1975. A field study of the short-eared owl, Asio flammeus (Pontoppidan), in North America. Wildl. Monogr. 47. 67pp.

CLAYTON, L. 1967. Stagnant-glacier features of the Missouri Coteau in North Dakota. North Dakota Geol. Surv. Misc. Ser. 30:24-46.

COUES, E. 1874. Birds of the northwest. U.S. Gov. Printing Office, Washington, D.C. 791pp.

---. 1878. Field notes on birds observed in Dakota and Montana along the forty-ninth parallel during the seasons of 1873 and 1874. Bull. U.S. Geol. Geog. Surv. Territories 4:545-661.

---, ed. 1897. New light on the early history of the great northwest: the manuscript journals of Alexander Henry and of David Thompson 1799-1814, Vol. 1, the Red River of the North. F.P. Harper, New York. 446pp.

COUPLAND, R. T. 1950. Ecology of mixed prairie in Canada. Ecol. Monogr. 20:271-315.

---. 1961. A reconsideration of grassland classification in the northern Great Plains of North America. J. Ecol. 49:135-167.

---. 1974. Fluctuations in North American grassland vegetation. Pages 233-241 in R. Knapp, ed. Handbook of vegetation science. Part VIII. Vegetation dynamics. Dr. W. Junk, b. v. Publisher, The Hague, Netherlands.

---. 1978. Future land use on the prairies. Pages 175-178 in W. A. Davies, ed. Nature and change on the Canadian plains. Canadian Plains Res. Center, Regina.

COWARDIN, L. M., A. B. SARGEANT, and H. F. DUEBBERT. 1983. Problems and potentials for prairie ducks. Naturalist 34:4-10.

CUTRIGHT, P. R. 1969. Lewis and Clark: pioneering naturalists. Univ. Nebraska Press, Lincoln. 506pp.

DAHL, T. E. 1990. Wetlands losses in the United States 1780's to 1980's. U.S. Fish Wildl. Serv., Washington, D.C. 13pp.

DAVY, G. L. 1930. Nesting of the ferruginous roughleg hawk in northern North Dakota. Oologist 47:14-18.

DEBYLE, N. V., and R. P. WINOKUR. 1985. Aspen: ecology and management in the western United States. U.S. For. Serv. Gen. Tech. Rep. RM-119. 283pp.

DENIG, E. T. 1961. Five Indian tribes of the upper Missouri. J. C. Ewers, ed. Univ. Oklahoma Press, Norman. 217pp.

DUEBBERT, H. F., and J. T. LOKEMOEN. 1977. Upland nesting of American bitterns, marsh hawks, and short-eared owls. Prairie Nat. 9:33-40.

DUNKLE, S. W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. Auk 94:65-71.

EADIE, W. R. 1953. Response of Microtus to vegetative cover. J. Mammal. 34:263-264.

EDWARDS, T. 1978. Buffalo and prairie ecology. Proc. Midwest Prairie Conf. 5:110-112.

ENGLAND, R. E., and A. DEVOS. 1969. Influence of animals on pristine conditions on the Canadian grasslands. J. Range Manage. 22:87-94.

EVANS, D. L. 1982. Status reports on twelve raptors. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Wildl. 238. 68pp.

FREERS, T. F. 1973. Geology of Burke County, North Dakota. North Dakota Geol. Surv. Bull. 55. 32pp.

GABRIELSON, I. N. 1943. Wildlife refuges. MacMillan, New York. 257pp.

---, and S. G. JEWETT. 1924. Notes on the birds of western North Dakota. Auk 41:296-303.

GETZ, L. L. 1961. Factors influencing the local distribution of Microtus and Synaptomys in southern Michigan. Ecology 42:110-119.

GILMER, D. S., and R. E. STEWART. 1983. Ferruginous hawk populations and habitat use in North Dakota. J. Wildl. Manage. 47:146-157.

GLEASON, H. A. 1922. The vegetational history of the Middle West. Ann. Asso. Am. Geogr. 12:39-85.

HAMERSTROM, F., and M. KOPENY. 1981. Harrier nest-site vegetation. Raptor Res. 15:86-88.

HEADY, H. F. 1975. Rangeland management. McGraw-Hill, New York. 460pp.

HEGSTAD, G. D. 1973. Vascular flora of Burke, Divide, Mountrail, and Williams counties in northwest North Dakota. Ph.D. Thesis, North Dakota State Univ., Fargo. 253pp.

HIGGINS, K. F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. U.S. Fish Wildl. Serv. Resour. Publ. 161. 39pp.

HORNADAY, W. T. 1889. The extermination of the American bison, Vol. 2. Annu. Rep. Smithsonian Inst. (1887), Washington, D.C. part 2, pages 367-548.

HOUSTON, C. S. 1975. Close proximity of red-tailed hawk and great horned owl nests. Auk 92:612-614.

---. 1990. Saskatchewan Swainson's hawks. Am. Birds 44:215-220.

---, and M. J. BECHARD. 1983. Trees and the red-tailed hawk in southern saskatchewan. Blue Jay 41:99-109.

---, and ---. 1984. Decline of the ferruginous hawk in Saskatchewan. Am. Birds 38:166-170.

JANES, S. W. 1984. Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. Ecology 65:862-870.

---. 1985. Habitat selection in raptorial birds. Pages 159-188 _in_ M. L. Cody, ed. Habitat selection in birds. Academic Press, Orlando, Fla.

---. 1987. Status and decline of Swainson's hawks in Oregon: the role of habitat and interspecific competition. Oregon Birds 13:165-179.

JASIKOFF, T. M. 1982. Habitat suitability index models: ferruginous hawk. U.S. Fish Wildl. Serv. Biol. Rep. FWS/OBS-82/10.10. 18pp.

JENSEN, R. E. 1972. Climate of North Dakota. Natl. Weather Serv., North Dakota State Univ., Fargo. 48pp.

JOHNSGARD, P. A. 1978. The ornithogeography of the Great Plains states. Prairie Nat. 10:97-112.

---. 1988. North American owls: biology and natural history. Smithsonian Inst. Press, Washington, D.C. 295pp.

JOHNSON, D. H., A. B. SARGEANT, and R. J. GREENWOOD. 1989. Importance of individual species of predators on nesting success of ducks in the Canadian Prairie Pothole Region. Can. J. Zool. 67:291-297.

JONES, J. K., Jr., D. M. ARMSTRONG, R. S. HOFFMAN, and C. JONES. 1983. Mammals of the Northern Great Plains. Univ. Nebraska Press, Lincoln, Nebraska. 379pp.

KANTRUD, H. A., G. L. KRAPU, and G. A. SWANSON. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85. 111pp.

KIFF, L. F. 1979. Bird egg collections in North America. Auk 96:746-755.

KIRSCH, L. M., and K. F. HIGGINS. 1976. Upland sandpiper nesting and management in North Dakota. Wildl. Soc. Bull. 4:16-20.

---, and A. D. KRUSE. 1973. Prairie fires and wildlife. Proc. Tall Timbers Fire Ecol. Conf. 12:289-303.

KRAENZEL, C. F. 1966. The Great Plains in transition. Univ. Oklahoma Press, Norman. 428pp.

LABAUGH, J. W. 1986. Wetland ecosystem studies from a hydrologic perspective. Am. Water Resour. Asso. Bull. 22. 10pp.

LARSON, F. 1940. The role of bison in maintaining the short grass plains. Ecology 21:113-121.

LISH, J. W., and W. G. VOELKER. 1986. Field identification aspects of some red-tailed hawk subspecies. Am. Birds 40:197-202.

LITTLEFIELD, C. D., S. P. THOMPSON, and B. D. EHLERS. 1984. History and present status of Swainson's hawks in southeastern Oregon. Raptor Res. 18:1-5.

LOKEMOEN, J. T., and H. F. DUEBBERT. 1976. Ferruginous hawk nesting ecology and raptor populations in northern South Dakota. Condor 78:464-470.

MAINI, J. S. 1960. Invasion of grassland by Populus tremuloides in the northern Great Plains. Ph.D. Thesis, Univ. Saskatachewan, Saskatoon. 231pp.

MARKS, J. S., and I. J. BALL. 1983. Burrowing owl (Athene cunicularia). Pages 227-242 in J. S. Armbruster, ed. Impacts of coal surface mining on 25 migratory bird species of high federal interest. U.S. Fish. Wildl. Serv. FWS/OBS-83/35.

MCMILLAN, C. 1959. The role of ecotypic variation in the distribution of the central grassland of North America. Ecol. Monogr. 29:285-308.

NELSON, J. G., and R. E. ENGLAND. 1971. Some comments on the causes and effects of fire in the northern grasslands area of Canada and the nearby United States, ca. 1750-1900. Can. Geog. 15:295-306.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota. 399pp.

PALMER, R. S., ed. 1988. Handbook of North American birds, Vol. 4 and 5. Yale Univ. Press, New Haven, Conn. 433 and 465pp.

PELTON, J. 1953. Studies on the life history of Symphoricarpos occidentalis Hook. in Minnesota. Ecol. Monogr. 23:17-39.

PETERSEN, L. 1979. Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. 111. 63pp.

PITTMAN, K. 1937. Wildlife and the land: a story of regeneration. Comm. Report 75th U.S. Congress, U.S. Gov. Printing Off. 79pp.

POSTUPALSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Raptor Res. Rep. 2:21-31.

PRESTON, C. R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. Condor 92:107-112.

RABY, S. 1966. Prairie fires in the north-west. Saskatchewan Hist. 19:81-99.

REID, R., ed. 1988. Lewis and Clark in North Dakota. State Hist. Soc. North Dakota, Bismarck. 374pp.

ROLFE, E. S. 1898. Notes from the Devil's Lake region. Osprey 2:125-128.

ROTH, S. D., Jr., and J. M. MARZLUFF. 1989. Nest placement and productivity of ferruginous hawks in western Kansas. Trans. Kans. Acad. Sci. 92:132-148.

ROTHFELS, M., and M. R. LEIN. 1983. Territoriality in sympatric populations of red-tailed and Swainson's hawks. Can. J. Zool. 61:60-64.

RUDOLPH, S. G. 1978. Predation ecology of coexisting great horned and barn owls. Wilson Bull. 90:134-137.

RYAN, M. R. 1986. Nongame management in grassland and agricultural ecosystems. Pages 117-139 <u>in</u> J. B. Hale, L. B. Best and R. L. Clawson, eds. Non-game management in the Midwest: a developing art. Northcent. Sec., The Wildl. Soc., Grand Rapids, Michigan.

---. 1990. A dynamic approach to the consevation of the prairie ecosystem in the Midwest. Pages 91-106 <u>in</u> J. M. Sweeney, ed. Management of dynamic ecosystems. North Cent. Sect., The Wildl. Soc., West Lafayette, Indiana.

---, R. B. RENKEN, and J. J. DINSMORE. 1984. Marbled godwit habitat selection in the northern prairie region. J. Wildl. Manage. 48:1206-1218.

SARGEANT, A. B., R. J. GREENWOOD, M. A. SOVADA, and T. L. SHAFFER. 1993. Distribution and abundance of predators that affect duck production - Prairie Pothole Region. U.S. Fish Wildl. Serv. Resour. Publ. 194: In Press.

SCHIER, G. A. 1975. Deterioration of aspen clones in the middle Rocky Mountains. U.S. For. Serv. Res. Pap. INT-170. 14pp.

SCHMUTZ, J. K. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. J. Wildl. Manage. 48:1180-1187.

---. 1989. Hawk occupancy of disturbed grasslands in relation to models of habitat selection. Condor 91:362-371.

---, S. M. SCHMUTZ, and D. A. BOAG. 1980. Coexistence of three species of hawks (<u>Buteo</u> spp.) in the prairie-parkland ecotone. Can. J. Zool. 58:1075-1079.

SHANTZ, H. L. 1923. The natural vegetation of the Great Plain region. Ann. Asso. Am. Geogr. 13:81-107.

SINGH, J. S., W. K. LAUENROTH, R. K. HEITSCHMIDT, and J. L. DODD. 1983. Structural and functional attributes of the vegetation of northern mixed prairie of North America. Bot. Rev. 49:117-149.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. W.H. Freeman Co., New York, NY. 859pp.

STEARNS, F. 1974. The use of the American General Land Office Survey in syndynamical vegetation analysis. Pages 73-80 in R. Knapp, ed. Handbook of vegetation science. Part VIII. Vegetation dynamics. Dr. W. Junk, b. v. - Publishers, The Hague, Netherlands.

STEELE, R. W. 1977. A demographic study of Microtus pennsylvanicus in relation to habitat structure. M.S. Thesis, Univ. Guelph, Guelph, Ont. 123pp.

STEWART, O. C. 1953. Why the Great Plains are treeless. Colorado Q., Colorado Univ. 2:40-50.

STEWART, R. E. 1975. Breeding birds of North Dakota. Tri-college Center for Environmental Studies, Fargo, North Dakota. 295pp.

---, and H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Dep. Inter. Bur. Sport Fish. Wildl. Res. Publ. 92. 57pp.

TODD, W. E. C. 1947. Notes on birds of southern Saskatchewan. Ann. Carnegie Mus. 30:383-421.

U.S. FISH AND WILDLIFE SERVICE. 1990. Conservation of avian diversity in North America. U.S. Fish Wildl. Serv. Off. Migr. Bird Manage. 22pp.

U.S. SOIL CONSERVATION SERVICE. 1975. Field technical guide: Coteau vegetation zone. U.S. Dep. Agric., Soil Conserv. Serv., North Dakota. 14pp.

VANDERBUSCH, D. 1991. Soil Survey of Mountrail County, North Dakota. U.S. Dep. Agric., Soil Conserv. Serv. 187pp.

VISHER, S. S. 1916. The biogeography of the Northern Great Plains. Geogr. Rev. 2:89-115.

VOGL, R. J. 1974. Effects of fire on grasslands. Pages 139-194 in T. T. Kozlowski and C. E. Ahlgren, eds. Fire and ecosystems. Academic Press, New York.

WAKELEY, J. S. 1978. Factors affecting the use of hunting sites by ferruginous hawks. Condor 80:316-326.

WEAVER, J. E. 1968. Prairie Plants and their environment - a fifty year study in the midwest. Univ. of Nebraska Press, Lincoln. 276pp.

WELLS, P. V. 1970. Postglacial vegetational history of the Great Plains. Science 167:1574-1582.

WHITMAN, W. C., and M. K. WALI. 1975. Grasslands of North Dakota. Pages 53-75 in M. K. Wail, ed. Prairie: a multiple view. Univ. North Dakota Press, Grand Forks.

WILLIAMS, M. A. B. 1966. Origins of North Dakota place names. Bismarck Tribune, Bismarck, North Dakota. 356pp.

WINTER, T. C. 1989. Hydrologic studies of wetlands in the northern prairie. Pages 16-54 _in_ A. G. van der Valk, ed. Northern prairie wetlands. Iowa State Univ. Press, Ames, Iowa.

WOOD, N. A. 1923. A preliminary survey of the bird life of North Dakota. Univ. Mich. Mus. Zool. Misc. Publ. 10:1-85.

WOODRUFF, F. M. 1923. Conditions of the breeding game birds in North Dakota, expedition of the Chicago Academy of Sciences. Wilson Bull. 35:4-20.

WRIGHT, H. A., and A. W. BAILEY. 1982. Fire ecology. J. Wiley and Sons, New York. 501pp.

ZARN, M. 1974. Habitat management series for unique or endangered species: burrowing owl. U.S. Bur. Land Manage. Tech. Note 11. 25pp.

PART II

COMPOSITION, NESTING BIOLOGY, AND HABITAT OF BREEDING RAPTORS ON LOSTWOOD NATIONAL WILDLIFE REFUGE, NORTH DAKOTA

INTRODUCTION

Basic ecological data on raptors (Falconiformes and Strigiformes) of the northern Great Plains are needed by resource managers for many reasons. Nesting and productivity trends convey the health of raptor breeding populations (Hamerstrom 1969, Hickey 1969, Fox 1971, Odum 1971, Newton 1979) and this knowledge helps protect against or mitigate negative land use impacts (Kennedy 1980, Craighead and Mindell 1981, Armbruster 1983, Steenhof 1987, Postovit and Postovit 1989, Woffinden and Murphy 1989, Phillips and Beske 1990). Major population changes are suspected for some raptor species and need verification (Evans 1982, Anonymous 1986, U.S. Fish and Wildlife Service 1991). Also, nest site and foraging habitat characteristics that affect raptor distribution and reproduction are documented in few areas of the northern Great Plains (Schmutz et al. 1980, Gilmer et al. 1983, Schmutz 1984, 1989), and need to be explored to substantiate paradigms for land management decisions. Last, potential impacts, if any, of different raptor species on survival and recruitment of other migratory birds for which managers are responsible relate directly to raptor distribution and demography (Craighead and Craighead 1956, Rusch et al. 1972, Petersen 1979, Sargeant et al. 1992).

Lostwood National Wildlife Refuge (LNWR) was established in 1935 in northwestern North Dakota as part of the National Wildlife Refuge System under the U.S. Fish and Wildlife Service (FWS)(Gabrielson 1943). A primary goal of LNWR is to restore and maintain native biodiversity (FWS-Denver regional office, unpubl. refuge operating statement). Inventory of composition and demographic features of wildlife currently on the refuge is a logical initial step toward reaching this goal, and federal laws mandate this approach (U.S. Fish and Wildlife Service 1990). For raptors, inventory data that do not account for interaction with environmental influences such as climate and prey population changes are not very meaningful and make it difficult to separate true raptor population changes from regional shifts in distribution (Kochert 1986). Because of wide annual fluctuation in climate and prey abundance in the northern Great Plains (Kraenzel 1966, Jensen 1972, Duebbert and Frank 1984, Higgins et al. 1992), long-term (>5 years) studies are needed to adequately assess effects of such variation on raptor demographic parameters (Brown 1974, Johnson et al. 1984, Wiens 1984, Brown and Amadon 1989).

Objectives of this study were to determine (1) composition and population stability, (2) reproductive performance and factors that influence annual raptor reproductive output, and (3) nesting habitat of raptors on LNWR.

STUDY AREA

Geology, physiography, soils, habitat composition, climate, and history and land use of LNWR are detailed in Part I and are briefly summarized here. LNWR encompasses 108 km² in southern Burke and northern Mountrail counties, North Dakota (48°37'N;102°27'W). It is rolling to hilly (elev. 685-747 m), semi-arid grassland interspersed with numerous (n = 4,200) wetland basins and clumps (n = 518) of quaking aspen (Populus tremuloides) trees. Habitat composition is 55% native, mixed grass (Stipa and Agropyron spp.) prairie; 21% old cropland reinvaded with native flora or dominated by tame grasses; 20% ephemeral or temporary to permanent wetlands (wetland classification according to Stewart and Kantrud [1971]); 2% trees (defined as woody plants >6 m high), mainly quaking aspen; and 2% tall shrubs (2-5 m high).

Before settlement of the area in the early 1900s, LNWR was almost entirely treeless prairie with uplands dominated by grasses and forbs (Part I). Elimination of catastrophic fire and grazing events during the late 1800s to early 1900s resulted in increased vegetation height and density and spread of woody species, mainly quaking aspen and western snowberry (Symphoricarpos occidentalis), a rhizomatous, low-growing (0.5-1 m high) shrub. LNWR was changed from mixed grass prairie to mostly aspen parkland by the 1980s, with a concurrent increase from 5-10% (estimated) to about 50% of native uplands composed of snowberry-dominated vegetation. During the 1980s, mean density and mean clump size of quaking aspen trees on LNWR were 4.8/km^2 (SD = 4.1) and 0.36 ha (SD = 0.37).

Annual land management practices during 1981-90 included: (1) prescribed burning in May-August of an average of about 9% (SD = 9) of LNWR, to restore and maintain native flora; (2) livestock grazing on about 5% of LNWR, mostly rest-rotation grazing during summer at stocking rates of 0.8 Animal Units/month/ha; (3) harvest of hay from seasonal wetlands and old cropland areas on 5-15% of LNWR; (4) restoration of old cropland areas (20-40 ha annually) by disc-harrowing and herbicide treatments of tame grasses, followed by seeding of native grasses; and (5) control of noxious weeds especially leafy spurge (Euphorbia esula) on scattered locations totalling 20 ha.

Average monthly temperatures for LNWR range from 20°C in July to -15°C in January (Jensen 1972). Average annual precipitation (1936-89) is 42 cm, most (>75%) of which falls as rain during April-September (FWS, unpubl. refuge files). Annual water levels in wetland basins of the northern Great Plains vary markedly which influences abundance of wetland-dependent prey of raptors (Kantrud et al. 1989, Higgins et al. 1992). My study occurred during years of slightly above average (1981-86), average (1987), and far below average (1988-90) water conditions on LNWR, based on records of wetlands in mid-May (FWS, unpubl. refuge files).

Vertebrate wildlife that were common on LNWR and potentially important to nesting raptors as prey included: (1) birds - grebes (Podicipediformes), ducks (Anserinae), sharp-tailed grouse (Tympanuchus phasianellus), rails and coots (Rallidae), shorebirds (Charadriidae), and abundant passeriform birds especially sparrows (Emberizinae) and blackbirds (Icterinae); (2) mammals - masked shrew (Sorex cinereus), meadow vole (Microtus pennsylvanicus), deer mouse (Peromyscus maniculatus), jumping mouse (Zapus spp.), ground squirrel (Spermophilus spp.); (3) amphibians and reptiles - tiger salamander (Ambystoma tigrinum), leopard frog (Rana pipiens), and plains garter snake (Thamnophis radix)(Murphy 1990). Leporids either were widespread and scarce (white-tailed jackrabbit [Lepus townsendii]) or narrowly distributed and unavailable to nearly all raptors (snowshoe hare [L. americanus] and eastern cottontail [Sylvilagus floridanus]).

Raptors that nested on LNWR were migratory except great horned owls (Bubo virginianus), which occurred year-round and likely were sedentary as elsewhere in North America (Johnsgard 1988).

METHODS

Terminology

Raptor breeding terminology I used closely followed Postupalsky (1974). An occupied nest was a nest at which any of the following were observed: (1) an adult in an incubating position, (2) eggs, (3) young, (4) occurrence of a raptor pair at least through the time when incubation normally occurred, or (5) a newly constructed or refurbished stick nest within 0.2 km of where territorial behavior by a raptor pair had been observed in spring. I refer to the occurrence of a nest being occupied as a nest occupancy and the plural, nest occupancies, to include all such occurrences over time regardless of whether the same or different specific nest structures (e.g., a stick nest) were used.

An occupied nesting area (synonymous with Postupalsky's [1974] occupied breeding territory) was the area ≤1 km of occupied Buteo spp. and great horned owl nests and ≤0.5 km of Cooper's hawk (Accipiter cooperii) nests. For great horned owls, I also considered >5 records of observations and vocalizations of owls within 1 km of each other during January-June to indicate an occupied nesting area. If a stick nest occurred near the center of these observations, I assumed it to be the owl pair's occupied nest and nesting area center. Otherwise an owl nesting area was considered to be centered among visual or observational records because great horned owl pairs sometimes defended areas in which stick nests were unavailable or were destroyed just before spring (great horned owls do not construct their own stick nests [Craighead and Craighead 1956:197, Petersen 1979]). I did not address nesting area for other species.

I defined nest site as the precise location of an occupied nest including the supporting substrate (e.g., a tree, a grass clump).

A meaningful indicator of raptor productivity is the average number of large or fledged young produced per occupied nest (Craighead and Craighead 1956:237, Brown 1974, Postupalsky 1974, Steenhof 1987). I considered an occupied nest successful if it produced $\geq$1 large (>3 weeks old) nestling and unsuccessful or failed if it did not. Nest success was the proportion of occupied nests that was successful. Mean annual nest success and productivity were determined for species with $\geq$10 nests occupied every year, otherwise data were pooled from all years. Although I did not endeavor to determine clutch size or whether eggs were laid in occupied nests, I found need to use the term active nest and defined it as an occupied nest in which eggs were laid (Postupalsky 1974).

The annual breeding population of a raptor species was the total number of paired or mated birds that occupied nests on LNWR during a breeding season. It may have included pairs of raptors that did not lay eggs in a given year but excluded raptors that were non-territorial (hereafter referred to as floaters) or unpaired. Similarly, I referred to any mated raptors that occupied a nest as nesting (e.g., nesting pairs, nesting red-tailed hawks), regardless of whether eggs were produced, and I expressed nesting density as the number of occupied nests/km^2. I considered a nesting species common if its mean annual nesting density was >0.08 occupied nests/km^2, and considered a species' breeding population to be stable across years if the standard deviation of the mean annual density comprised <10% of the respective mean. The raptor breeding season was composed of spring (March-May) and summer (June-August).

Geographic origins of comparative data published from other areas in North America were summarized in tables by abbreviating location within states or provinces as (e.g.) c (central), sc (southcentral), or nw (northwestern). No abbreviation was used if data originated from throughout a given state or province.

Assessment of Raptor Breeding Populations

I used 2 distinctly different methods to monitor raptor breeding populations: (1) a census of nesting raptors except northern harriers (*Circus cyaneus*) and short-eared owls (*Asio flammeus*) was conducted during 1983-90 by systematically searching all potential nesting habitat on LNWR, and (2) a survey of northern harriers and short-eared owls was conducted on sample plots during 1981-89 to yield estimates of their total breeding populations on LNWR.

Raptor Census

In January-March of each year, I systematically recorded approximate locations of hooting (territorial) great horned owls by using techniques in Rusch (1983). Next, I searched all wooded habitats on horseback and on foot for owls and owl nests during late March to early April when great horned owls were in mid- to late incubation. During this search I also checked and noted condition of all large (>20 cm diameter) stick nests that had been present at the end of the previous nesting season. This helped furnish clues in identifying locations of occupied nests of later-nesting species that might refurbish old nests. Adult red-tailed (*Buteo jamaicensis*) and ferruginous (B. regalis) hawks returned to nest at this time so their initial nesting area affinities were noted.

In late May after foliage had emerged on trees and shrubs, a second search of all potential nesting habitat of raptors was made on foot. Timing of this search coincided with late incubation or hatching of red-tailed and ferruginous hawks, but early incubation of Swainson's (B. swainsoni) and Cooper's hawks. Snag tree cavities (excavated by northern flickers [Colaptes auratus]) also were checked for occupancy by cavity-nesting raptors.

I took precautions to minimize disturbance of nesting raptors during searches (Fyfe and Olendorff 1976, Grier and Fyfe 1987). Most occupied nests initially were observed from >300-400 m away and were not approached closer during potentially sensitive courtship and incubation stages of nesting.

Locations of nests and sighted raptors were marked on aerial photographs (1:19,500) in the field and later summarized on a master map (Craighead and Craighead 1956:6). Cumulative records helped confirm locations of several territorial, apparently non-laying pairs (especially of owls) that were not clearly attached to a specific nest site. The database was greatly augmented by records of raptor sightings by myself and other biologists during work on concurrent research on LNWR. Because of the thorough and repeated coverage of the area, I assume I accounted for nearly all raptor pairs on LNWR (besides northern harriers and short-eared owls which were not covered by the census), except in 1983 and 1984 when spring surveys for great horned owls were incomplete.

I visited and climbed to nests after I presumed eggs had hatched to assess nest fate, count young, and measure nest site characteristics. Nestling age was estimated based on primary remige measurement (Petersen and Thompson 1977, Schmutz 1977, Bechard et al. 1985) and overall plumage development (Moritsch 1983), and was used to project approximate hatching date by backdating.

Northern Harrier and Short-eared Owl Survey

Breeding populations of harriers and short-eared owls on LNWR were estimated from counts of nests found on sample plots in concurrent studies (Kruse and Piehl 1986; A. Kruse and B. Bowen, unpubl. ms.; FWS, unpubl. refuge files). During late April-early July, 1981-89, 12-14 plots (size mean = 73 ha, SD = 77; _n_ = 18 plots) of native habitat were searched every 3 weeks by using 2 vehicles and a 50-m cable-chain drag (Higgins et al. 1977) to locate nests of ground-nesting birds except Passeriforms. Plots were not randomly located on native prairie on LNWR (Fig. II-1) mostly because motorized vehicles used for nest searches were prohibited on a 23-km^2 block (22% of LNWR) classified as National Wilderness Area, and blocks of native prairie on western and southern parts of LNWR were smaller and too fragmented by old cropland. Therefore, sample plots of native prairie used for estimating breeding populations of northern harriers and short-eared owls were in the central and northeastern parts of LNWR (Fig. II-1).

Although non-random sample selection invalidates estimates of population parameters in the strict sense (Scheaffer et al. 1990), I contend estimates of northern harrier and short-eared owl populations were acceptable approximations. I base this contention on the following: (1) I projected point and interval estimates of numbers of northern harriers and short-eared owls on sample plots to only the 77 km^2 of LNWR that excluded lakes (permanent and saline wetlands, total 8 km^2) and old cropland (23 km^2), but then based population estimates on the total area (108 km^2) without any increment in estimated raptor numbers for 31 km^2 of lakes and old cropland; (2) the survey technique ignored possible occurrence of non-laying pairs; (3) wide confidence intervals surrounded estimates of population means; and (4) an assumption that sample plots were representative of native prairie on LNWR was reasonable. Because of this conservative approach, I assume the probability that reported interval estimates contained the respective population parameters was >90% (i.e., $P < 0.1$). Also, because only active nests were detected by the survey technique, density of northern harriers and short-eared owls was reported as active nests/km^2.

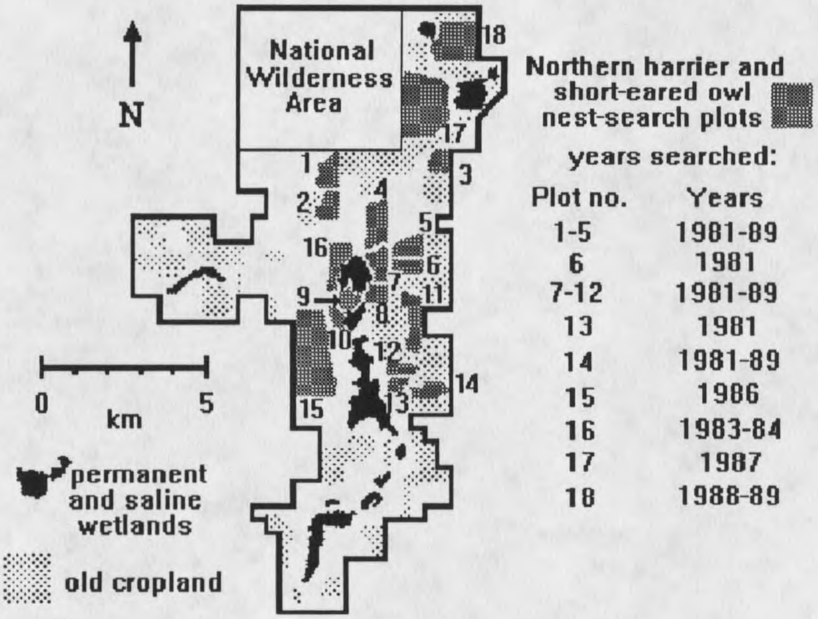

Figure II-1. Location of northern harrier and short-eared owl nest-searching plots on LNWR during 1981-89 and years when respective plots were searched. Areas not eligible for nest-searching are indicated: a National Wilderness Area, permanent and saline wetlands, and uplands with histories of cropping during 1910-55.

Nest success and productivity of northern harriers and short-eared owls were estimated based on data from sample plots. Because searches of plots relied solely on a cable-chain drag (Higgins et al. 1977) to discover nests and disregarded other observations to detect nesting adults, nest success and productivity determined from these plots likely overestimated true parameters. Some failed nest attempts may have gone undetected in the 3-week interval between nest searches (Mayfield 1961, 1975, Klett et al. 1986). Therefore, I applied the correction described by Mayfield (1961, 1975) to generate unbiased estimates of northern harrier and short-eared owl nest success and productivity. Results were presented as Mayfield nest success and Mayfield productivity.

Raptor Habitat Assessment

Measurements at Nests Recorded in Raptor Census

Attributes recorded at nest sites of censused raptors were nest tree (or shrub) species, tree bole diameter at breast height (dbh), nest height above ground (to nest rim), tree height, and distance from nest tree to nearest tree clump edge. I also constructed an imaginary cylinder of 1 m radius with the nest centered in its base and classified the approximate percentage of areal canopy coverage (i.e., shading and shelter) afforded the nest by the nest tree or surrounding trees after foliage had emerged in early to mid-May. Classes of percentage cover were none (0-10%), low (11-30%), moderate (31-60%), and high (>60%). Nest canopy cover data were not reported for great horned owls because their young already were half grown in early May.

For each major raptor censused, I defined cumulative nest occupancies as the number of occurrences of occupied nests in each 2.59-km^2 section on LNWR during 1983-90. Except, 1983 and 1984 data for great horned owls were excluded due to incomplete censuses those years. In each section, cumulative nest occupancies were compared to (1) density of aspen tree clumps, and (2) a wetland abundance index equal to the product of total area and number of wetlands (seasonal to permanent types).

Measurements at Nests Recorded in Raptor Survey

An index of vegetation height and density was recorded at nests of northern harriers and short-eared owls by using a 100% visual obstruction method (Robel et al. 1970, Kirsch et al. 1978). These Robel height-density readings were recorded at north edges of nests and were rounded to the nearest 0.5 dm. Vegetation type within 0.5 m of nests also was recorded as either brush dominant (>95% of canopy cover), grass dominant, grass with brush understory, brush with grass understory, or wetland. Brush was defined as shrub <1 m high.

Prey Populations

Annual change in density estimates or abundance indices of several common, potential vertebrate prey of raptors were related to raptor population or productivity trends. Adult ducks were surveyed each May on a stratified random survey of 0.65-km^2 plots on LNWR (Hammond 1969) and 90% confidence interval estimates of abundance were generated. Censuses of male sharp-tailed grouse displaying on leks on LNWR each April (FWS, unpubl. refuge files) served as an index of spring grouse abundance. I operated snap-trap transects during June-July, 1983-88, to obtain indices of vole abundance. The traps were baited with rolled oats and peanut butter and set 5 m apart along single transects (n = 80-120 traps each) through idle mesic sites (Hamerstrom 1979). Traps were set in evening just before sunset and picked up between 0800-0900 hours the following morning. A minimum of 600 trap-nights conducted on calm nights without rain were collected annually. Indices of annual deer mouse abundance were obtained by drift fence sampling (Gibbons and Semlitsch 1981, Vogt and Hines 1982). One drift fence night was defined as a 15-m section of fence open 24 hr; I collected 1000 drift fence nights annually during mid-May through early July, 1984-87.

Statistical Analyses

Null hypotheses regarding raptors and their habitat and general raptor-prey relationships were tested by correlation, regression, ANOVA procedures, and contingency tables (Sokal and Rohlf 1981, Dixon 1983, SAS Institute 1989, Daniel 1990). Non-parametric procedures such as Mann-Whitney tests and Spearman rank correlations were used wherever assumptions for parametric tests were not satisfied. Data sets were tested for homogeneity of variances using F-test (Sokal and Rohlf

1981:402) procedures in BMDP and SAS. I conveyed exact probability levels for test results where $\underline{P} \geq 0.001$ and considered $\underline{P} < 0.1$ to be grounds for rejecting null hypotheses.

Occupancy of a raptor nesting area in successive years may involve the same raptor or raptor pair (Newton 1979, Janes 1984a). However, because birds were not individually marked in this study I was unable to assess site fidelity. In statistical analyses of raptor nesting habitat, I assumed that reoccupancy of nesting areas by the same individuals negligibly influenced assumptions of independence among observations.

RESULTS

Composition of the Breeding Raptor Community

Five species of hawks and 3 species of owls nested on LNWR during 1981-90 (Table II-1 and Table II-2). Only 3 of these species were common: red-tailed hawk, great horned owl, and northern harrier. Short-eared owls were common in 1981-82 but did not occur as nesting raptors in other study years. Based on mean annual nesting densities and estimated densities (Table II-1 and Table II-2), an average of about 89 pairs of raptors occurred on LNWR each year (0.82 raptor pairs/km^2) and the approximate average yearly makeup of the nesting raptor community was 28% red-tailed hawk, 4% Swainson's hawk, <1% ferruginous hawk, 3% Cooper's hawk, 41% northern harrier, 16% great horned owl, 1% long-eared owl, and 7% short-eared owl.

Species Nesting Biology and Nesting Habitat

Red-tailed hawk

Density, Distribution, and Nesting Habitat. Annual nesting density of red-tailed hawks averaged 0.23 occupied nests/km^2 during 1983-90 and was stable among years (Table II-1).

Table II-1. Density (number of occupied nests/km^2) of nesting raptors on LNWR[a] by species, 1983-90.

Year	Red-tailed hawk	Swainson's hawk	Ferruginous hawk	Cooper's hawk	Great horned owl	Long-eared owl[b]
1983	0.213	0.046	0	0.009	0.1[c]	0
1984	0.213	0.065	0	0.009	0.1[c]	0.028
1985	0.240	0.037	0	0.009	0.129	0
1986	0.268	0.046	0	0.018	0.120	0.028
1987	0.213	0.018	0	0.028	0.157	0.018
1988	0.222	0.018	0	0.028	0.120	0
1989	0.222	0.009	0	0.046	0.129	0
1990	0.231	0.009	0.009	0.046	0.129	0
Mean	0.228	0.031	0.001	0.024	0.131[d]	0.009
SD	0.018	0.019	0.003	0.015	0.012	0.012

[a] Excludes northern harriers and short-eared owls.
[b] (Asio otus).
[c] Great horned owls were incompletely censused in 1983 and 1984 and data presented for these years are minimum densities.
[d] Mean annual great horned owl density based on 1985-90 data.

All nests of red-tailed hawks were in trees. Quaking aspen was the most available tree on LNWR and most frequently supported occupied nests of red-tailed hawks (93.7% of tree clumps available compared with 97.5% of nest occupancies [n = 197]; X^2 = 4.12, 1 df, P = 0.043). The other nests were in American elm (Ulmus americana). There was a strong, direct correlation between density of aspen tree clumps and cumulative nest occupancy (r_s = 0.712, P < 0.001) in each 2.59-km^2 section. But, correlation between cumulative nest occupancy and wetland abundance was poor (r_s = 0.165, P = 0.262) even though abundance of wetlands and of aspen tree clumps/section were weakly correlated (r_s = 0.250, P = 0.086).

Table II-2. Estimated density (number of active nests/km^2) of northern harriers and short-eared owls on LNWR, 1981-89, determined from annual surveys of native prairie plots.

	Sample plots searched		Estimated density			
			Northern harrier		Short-eared owl	
Year	n	km^2 total	Mean	90% CI[a]	Mean	90% CI[a]
1981	14	5.8	1.57	1.16-1.99	0.60	0.26-0.95
1982	12	4.2	1.87	1.14-2.61	1.28	0.32-2.25
1983	13	4.7	0.29	0.01-0.59[b]	0	
1984	13	4.7	0.70	0.21-1.18	0	
1985	12	4.2	0.41	0.11-0.70	0	
1986	13	7.0	0.32	0.03-0.60	0	
1987	13	6.7	0.68	0.33-1.04	0	
1988	13	5.7	0.28	0.05-0.50	0	
1989	13	5.7	0.20	0.01-0.42	0	
Mean		5.4		0.34[c]		0.06[c]
SD		1.0		0.47		0.13

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[a] Ninety percent confidence interval on estimated mean.

[b] Minimum number of active northern harrier nests in 1983 was based on counts of nests recorded on native prairie on LNWR because lower interval bound on estimate of mean was 0.

[c] Mean annual density conservatively based on average of lower bounds of interval estimates.

Red-tailed hawk nests were in larger than average aspen tree clumps (Table II-3). Nests were constructed at similar heights and in trees of similar diameter (dbh) as used by the congeneric Swainson's hawk, but red-tailed hawks selected taller aspen (Table II-4).

Table II-3. Size of aspen tree clumps and distribution of size categories of clumps that accommodated occupied nests of red-tailed, Swainson's, Cooper's hawks, and great horned owls on LNWR during 1983-90, and comparison to aspen available on the area.

	Aspen clumps used			% of aspen clump use by size category[a]					
		Size (ha)							
Species	*n*	*x*	SD	I	II	III	IV	X^2 [b]	*P*
Red-tailed hawk	69	0.67	0.41	10.1	31.9	23.2	34.8	69.3	< 0.001
Swainson's hawk	16	0.41	0.22	31.3	37.5	18.8	12.5	3.6	0.311
Cooper's hawk	9	0.87	0.44	0	11.1	33.3	55.6	25.2	< 0.001
Great horned owl	40	0.76	0.44	10.0	22.5	22.5	45.0	59.6	< 0.001
Aspen tree clump availability, LNWR:									
	518	0.36	0.37	53.7	23.9	11.2	11.2		

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[a] Areas (ha) for categories of aspen clumps were: category I, 0.05-0.25; category II, 0.26-0.50; category III, 0.51-0.75; category IV, >0.75.

[b] Chi-square analysis of use compared to availability.

Table II-4. Sites selected in aspen clumps by red-tailed, Swainson's, and Cooper's hawks for construction of nests.[a]

	Tree dbh (cm)	Tree ht. (m)	Nest ht. (m)	% nest ht.: tree ht.	Edge distance (m)	*n* nest sites
Red-tailed hawk						
mean	23.54[e]	12.05[d,e]	9.16[e]	76.0[e]	7.51[e]	50
SD	4.89	2.50	2.25	8.4	7.49	
Swainson's hawk						
mean	21.41	10.09[c]	8.25[e]	81.5[e]	8.31[e]	15[b]
SD	3.83	1.55	1.69	7.7	7.20	
Cooper's hawk						
mean	20.01[c]	9.47[c]	6.21[c,d]	65.4[c,d]	15.08[c,d]	13
SD	6.02	2.04	1.51	4.1	8.58	

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[a] Includes only nests of known origin.

[b] Excludes a shrub nest site in 1987.

[c] Significantly different from red-tailed hawk ($P < 0.1$) based on Kruskal-Wallis multiple comparison using Dunn's test (Daniel 1990:241).

[d] Significantly different from Swainson's hawk ($P < 0.1$).

[e] Significantly different from Cooper's hawk ($P < 0.1$).

Nest Success and Productivity. Mean annual nest success and productivity of red-tailed hawks were 56% and 0.86 young/occupied nest (Table II-5). Less than two-thirds of nests were successful in 5 of 7 years studied, and annual productivity never exceeded 1.3 young/occupied nest. I was unable to collect success and productivity data from red-tailed hawks in 1987 and suspect productivity was higher that year than other years. During other work on LNWR in July 1987, I observed adult red-tailed hawk pairs still staunchly defended their nests, implying they had young. Nest defense by pairs that failed in reproduction subsided much earlier in other years.

Table II-5. Annual reproductive parameters of red-tailed hawks on LNWR.[a]

Year	No. occupied nests	No. nests successful	Nest success (%)	No. young produced	No. young/ occupied nest
1983	23	14	60.9	23	1.00
1984	23	8	34.8	15	0.65
1985	26	22	84.6	31	1.19
1986	29	23	79.3	36	1.24
1988	24	11	45.8	19	0.79
1989	24	11	45.8	15	0.63
1990	25	10	40.0	13	0.52
mean	24.9	14.1	55.9	21.7	0.86
SD	2.0	5.5	18.1	8.2	0.26

[a] Nest success and productivity were not determined in 1987.

Lowest mean annual nest success and productivity (Table II-5) occurred in a year with a severe spring blizzard (1984) and during 3 years of extreme drought (1988-90). On 27-29 April 1984, temperatures ranged -10 to 4°C, accompanied by 30-60 kph winds and a 40-cm snowfall that remained on the ground for 3-4 days. This occurred when red-tailed hawks were beginning incubation. On 12-14 May 1983, a less severe blizzard occurred (15 cm of snow, 20-40 kph winds, -3 to 3°C) when the hawks were in mid-incubation. In these 2 years, hatching of successful red-tailed hawk nests occurred later than in other years (1983-84 mean was 26 May compared to 21 May in other years; $\underline{t} = 4.16$, $\underline{P} < 0.001$). Severe drought in 1988-90 that coincided with low red-tailed hawk nest success and productivity was characterized by lack of water in >95% of seasonal and semi-permanent wetlands by mid-May, above average spring and summer temperatures (monthly averages 3-5°C above normal [FWS, unpubl. refuge files]), more frequent than normal windspeeds of 25-40 kph, and low average relative humidity (<20%). Annual precipitation was low in 1988 (33.5 cm compared to 42.2 cm average for 1936-80) but average in 1989-90 (FWS, unpubl. refuge files).

Although 56% of nest occupancies by red-tailed hawks during 7 years produced young, brood sizes were small. Of 98 broods of large young observed, 48%, 51%, and 1% were of 1, 2, and 3 young (compared to equal proportions, $\underline{X}^2 = 45.4$, df = 2, $\underline{P} < 0.001$).

Great Horned Owl

Density, Distribution, and Nesting Habitat. Annual nesting density of great horned owls on LNWR averaged 0.13 occupied nests/km^2 during 1983-90 and was stable among years (Table II-1).

Great horned owls tended to occupy nests situated among areas of greatest aspen tree clump density ($\underline{r}_s = 0.324$, $\underline{P} = 0.016$) and wetland abundance ($\underline{r}_s = 0.278$, $\underline{P} = 0.056$), 2 habitat variables that had weak autocorrelation (see red-tailed hawk). Selection of nesting areas by great horned owls may have been partly influenced by availability of large stick nests.

All nests occupied by great horned owls were stick nests in trees. Nearly all were in aspen (98.2% of 55 nest occupancies for which a nest site could clearly be ascribed), in part a function of nest site selection by species on which great horned owls depended for stick nests. Original builders of 27 nests of known origin that were used by great horned owls included Swainson's hawks (14.3% of nests used), Cooper's hawks (3.7%), and black-billed magpies (Pica pica)(11.1%), but most (70.3%) were constructed by red-tailed hawks and nearly all these were used by the owls >1 nesting season. Great horned owls typically exchanged use of such nests with red-tailed hawks in successive years, with long-term presence of stick nests apparently contingent on maintenance provided by the hawk's intermittent tenure.

I could not precisely assess availability of stick nests constructed by various species mainly because nests noted at the beginning of the study were of uncertain origin. Great horned owls seemed to use nests built by red-tailed hawks and Swainson's hawks in proportion to their availability and those of Cooper's hawks less than expected based on availability. The few black-billed magpie nests used by great horned owls were occupied 2-4 years after being built, by which time canopies of the nests had collapsed. Magpie nests in shrub were unused by great horned owls even though they comprised >75% of magpie nest sites. Stick nests built by American crows (Corvus brachyrhynchos) were not used by great horned owls (except possibly 1) even though many (1-2/km^2) were available on LNWR through the mid-1980s. Crow nests were smaller than stick nests used by great horned owls (Table II-6).

Nest sites used by great horned owls closely resembled those of red-tailed hawks on which the owl mostly depended for nest structures. Nest trees averaged 11.6 m high and 23.1 cm dbh (SD = 2.3, 4.0), with nests situated 9.1 m high (SD = 2.3)(n = 38 sites), similar to respective statistics for red-tailed hawks (Table II-4). Aspen tree clumps in which great horned owls nested were larger than expected based on availability on LNWR (Table II-3) but did not differ in size from those used by red-tailed hawks (Mann-Whitney test, P = 0.225). Nests used by the owl averaged 10.8 m from edges of tree clumps (SD = 8.4).

Table II-6. Dimensions of stick nests built by American crows compared to nests used by great horned owls on LNWR.

	Width (cm)		Depth (cm)		
Species	mean	SD	mean	SD	*n*
American crow	33.0	2.2	22.9	5.3	14
Great horned owl	49.0	7.7	32.2	10.5	37
Difference, *P*[a]	< 0.001		0.002		

[a] Result of Mann-Whitney test.

Nest Success and Productivity. Mean annual nest success and productivity of great horned owls were 41% and 0.72 young/occupied nest (Table II-7). Annual nest success and productivity varied markedly and exceeded 67% and 1.3 young/occupied nest, respectively, in only 2 of 8 years.

High productivity of great horned owls in 1987 corresponded to a moderate peak in abundance of meadow voles (Fig. II-2). Correlation between annual productivity and summer vole abundance was poor (r_s = 0.154, P = 0.805), however, only because highest great horned owl productivity in 1985 coincided with a moderate peak in vole abundance that began in summer 1984 and ended before I trapped voles the following summer (Fig. II-2). In early spring 1985 I commonly observed voles and vole sign (runways and grassy nests, widespread girdling of brush stems) and voles comprised 87% of the number of prey items represented in 52 pellets collected from great horned owl nests in April (R. Murphy, unpubl. data). The vole population had declined sharply, however, by midsummer 1985 when I surveyed vole relative abundance (Fig. II-2). I propose that both years of high nest success and productivity of great horned owls coincided with moderate abundance of meadow voles in winter and early spring.

Table II-7. Annual reproductive parameters of great horned owls on LNWR.

Year	No. occupied nests	No. nests successful	Nest success (%)	No. young produced	No. young/ occupied nest
1983	≥10	0	0	0	0
1984	≥10	3	30.0[a]	3	0.30[a]
1985	15	14	93.3	29	1.93
1986	13	4	30.8	6	0.46
1987	17	13	76.5	25	1.47
1988	13	4	30.8	8	0.62
1989	14	4	28.6	8	0.57
1990	14	5	35.7	6	0.43
mean	14.3[b]	5.9	40.7[a]	10.6	0.72[a]
SD	1.4	4.6	27.8	9.8	0.60

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[a] Nest success and productivity (mean number of young per occupied nest) were maximum numbers because ≥10 occupied nests occurred in 1983 and in 1984.

[b] Average based on 1985-90 data because total numbers of occupied nests were undetermined in 1983-84.

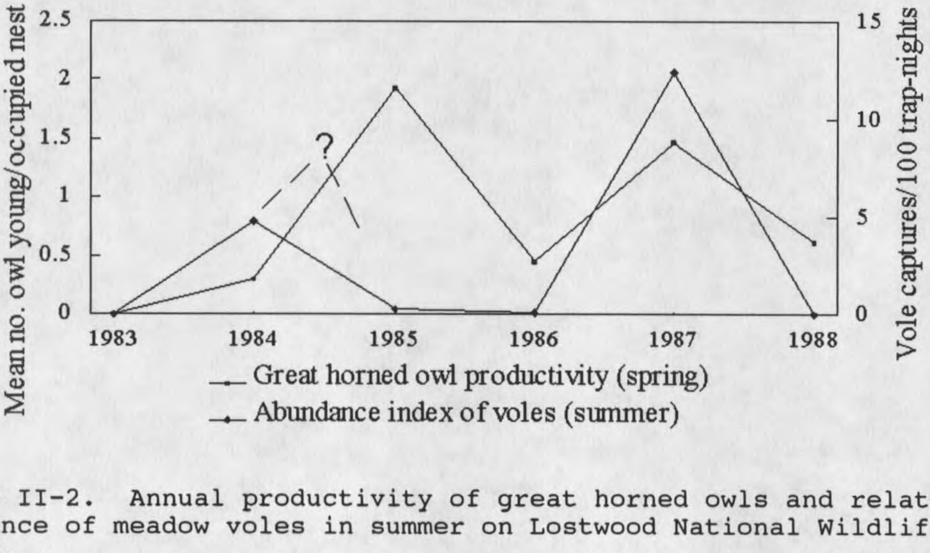

Figure II-2. Annual productivity of great horned owls and relative abundance of meadow voles in summer on Lostwood National Wildlife Refuge.

Sharp-tailed grouse and deer mice were the only other vertebrate species common on LNWR during winter through early spring that were abundant enough to be potentially important great horned owl prey. Annual productivity of great horned owls was not correlated with April censuses of male grouse (r_s = -0.018, P = 0.969) and appeared to be negatively correlated with numbers of deer mice captured in drift fences during late spring-early summer (r_s = -1.00, P = 0.1, n = 4 years).

Spring blizzards that reduced productivity of red-tailed hawks had no noticeable impact on great horned owls which were brooding large, downy young by late April-early May. Low nest success and productivity experienced by great horned owls during 1988-90 (Table II-7), however, paralleled inimical effects of severe drought on nesting red-tailed hawks.

Swainson's Hawk

Density, Distribution, and Nesting Habitat. Annual nesting density of Swainson's hawks on LNWR averaged 0.03 occupied nests/km^2 and declined during this study (Table II-1).

Swainson's hawk occupied nests were on the periphery (<1 km from the boundary) of LNWR, except for a nesting area that was disturbed annually through the 1980s by prescribed fire, hay harvest, and tillage associated with native grass seedings. Nesting by Swainson's hawks (cumulative nest occupancies) was unrelated to aspen clump density (r_s = 0.172, P = 0.243) and wetland abundance (r_s = -0.037, P = 0.805).

Nearly all nests of Swainson's hawks were in quaking aspen (96.3% of n = 27 nests, compared to 93.7% of tree clumps available (X^2 = 0.0, P = 1.0). Aspen tree clumps used by Swainson's hawks were smaller in area (ha) than those used for nesting by other hawks (P < 0.1; Kruskal-Wallis multiple comparison using Dunn's test [Daniel 1990:241]) and did not differ from sizes of clumps that were available (Table II-3). Otherwise, nest sites selected by Swainson's hawks were similar to those of red-tailed hawks except Swainson's hawks built nests in shorter trees

(Table II-4). One Swainson's hawk nest was a in shrub (roundleaf hawthorn [Crateagus chrysocarpa]).

Nest Success and Productivity. Seventeen of 28 (60.7%) total nest occupancies were successful. Productivity averaged 1.14 young/occupied nest but was highly variable (SD = 1.11), including 4 broods (24% of broods observed) of 3 young. In 1983 only 1 juvenile Swainson's hawk was produced from 5 occupied nesting areas, possibly due to the aforementioned May blizzard that occurred about a week before egg-laying (mean laying date = 22 May).

Cooper's Hawk

Density, Distribution, and Nesting Habitat. Annual nesting density of Cooper's hawks on LNWR averaged 0.02 occupied nests/km^2 and was increasing during this study (Table II-1).

Although Cooper's hawks nested in largest aspen tree clumps available (Table II-3), they did not necessarily nest in areas with highest densities of aspen clumps. Nesting areas (n = 6) varied from 2.3-15.4 tree clumps/km^2 (mean = 8.5, compared to 4.8 on LNWR). But, 2 nesting areas with near or below average density of aspen had extensive tall shrub or nearby farmsteads with shelterbelts where Cooper's may have foraged (Peterson and Murphy 1992).

Cooper's hawks nested exclusively in quaking aspen. The hawk nested in tree clumps that were larger in area than those used by Swainson's hawks but not red-tailed hawks ($P < 0.1$, Kruskal-Wallis multiple comparison using Dunn's test)(Table II-3). Compared to other hawks, Cooper's hawks placed nests lower relative to tree height and much farther from aspen clump edges (Table II-4). Also, a higher proportion of nest sites selected by this hawk were within closed canopies (>60% overhead cover) compared to sites selected by red-tailed hawks though not by Swainson's hawks (Table II-8).

Table II-8. Canopy closure above nests[a] constructed in trees by red-tailed, Swainson's, and Cooper's hawks.

	Canopy closure classes[b], % of nest sites selected				
Species[c]	None	Low	Moderate	High	n
Red-tailed	2.1	18.8	66.7	12.5	48
Swainson's	7.1	28.6	28.6	35.7	14
Cooper's	0	15.4	30.8	53.8	13

[a] Canopy closure estimated for area above nest within a cylinder of 1-m radius centered on nest (see Methods).

[b] Classes of percentage canopy closure were none (0-10%), low (11-30%), moderate (31-60%), and high (>60%).

[c] H_o of similar distributions among species: X^2 = 14.15, 2 df, P = 0.007. H_o, pairwise comparisons: Cooper's versus red-tailed, X^2 = 10.59, 2 df, P = 0.005; Cooper's versus Swainson's, X^2 = 1.58, 2 df, P = 0.451.

Nesting Success and Productivity. Fourteen of 21 (66.7%) nest occupancies by Cooper's hawks were successful. Mean productivity was 2.38 young/occupied nest (SD = 1.9). No Cooper's hawk young were reared in the most severe drought year of 1988, but productivity in 1989 and 1990 drought years averaged 2.4 for 10 nest occupancies. I believe most unsuccessful Cooper's hawk nests failed during or before incubation, based on lack of sign of young. One nest with 3-week old young was depredated by great horned owls.

Northern Harrier and Short-eared Owl

Estimated Density and Nesting Habitat. Estimates of annual nesting densities of northern harriers on LNWR averaged 0.34 active nests/km^2 based on lower bounds of 90% confidence intervals (Table II-2). As indices of annual abundance, point estimates of density (means in Table II-2) suggested marked annual variation in nesting density of northern harriers on LNWR. This annual index correlated strongly with change in relative abundance of voles in summer during 1983-88 (r_s = 0.928, P = 0.008). A vole abundance index was not obtained in 1981-82, but peak abundance of nesting northern harriers those years coincided with what clearly were peak years of vole abundance based on tremendous numbers of voles observed daily through summer (K. Smith and A. Kruse, pers. comm.).

During 1981-89, short-eared owls only nested in 1981 and 1982, and respective estimates of minimum annual densities were 0.26 and 0.32 active nests/km^2 (lower confidence interval bounds, Table II-2). The only other year that short-eared owls were observed through mid-breeding season (June) was 1987; only 2 unpaired birds were observed past April and both were weakly territorial. Although no survey for northern harriers and short-eared owls was conducted in 1990, I did not see short-eared owls during other work on LNWR in spring-summer that year. Occurrence of nesting short-eared owls in 1981-82 coincided with peaks in estimated nesting densities of northern harriers and vole abundance.

All nests of northern harriers and short-eared owls found on survey plots were on the ground in uplands or dry parts of wetland basins. Northern harrier nests (*n* = 55) nearly all were in dense ground cover in native uplands, usually (52% of nests) centered in 0.05-0.5 ha patches of western snowberry sometimes mixed with silverberry (*Eleagnus commutata*) or Wood's rose (*Rosa woodsii*), or in snowberry and other brush mixed with 5-50% herbaceous cover (40% of nests). A few nests were in grass-dominated sites (4%) or in dry parts of wetland basins (4%). Mean vegetation height-density (Robel visual obstruction index) at 52 northern harrier nests in late spring was 3.5 dm (SD = 1.7), compared with averages of about 1.0-2.0 dm for native cover available. Vegetation height-density at 14 short-eared owl nest sites averaged 1.2 dm (SD = 1.1) and was lower than that at northern harrier nests (Mann-Whitney test, $P < 0.001$). Although most short-eared owl nests were in brush-dominated sites, only 21% were in sites surrounded solely by brush (>95% canopy cover) and 71% were in sites where brush was mixed with herbaceous plants. One short-eared owl nest was in a dry part of a wetland basin.

Nest Success and Productivity. I monitored 33 northern harrier nests on survey plots long enough to obtain success and productivity data. Mayfield nest success was 65.2% for active nests. Most (8 of 9) nest failures occurred during incubation and mainly were due to predation by undetermined species of mammals. Mayfield productivity based on 33 nests averaged 2.54 young/active nest (SD = 2.5). For 13 short-eared owl nests, Mayfield nest success was 40.8% for active nests. Productivity of short-eared owls could not be accurately estimated because the owlets moved from their nests at an early age (Clark 1975) and brood members were hard to account for. A minimum mean of 1.00 young/active nest (SD = 1.30; without Mayfield correction) was observed.

Other Nesting Raptors

Ferruginous Hawk. The single nest occupancy by ferruginous hawks occurred on top of a nest (7.3 m high in aspen) constructed 2 years previously by Swainson's hawks. The nest was in an area prescribe-burned a year before the ferruginous hawk nesting and there was cropland and heavily grazed mixed grass prairie on adjacent private land. A single young ferruginous hawk was produced.

Long-eared Owl. Nesting long-eared owls occurred in only 3 of 8 years studied and mean annual nesting density averaged 0.01 occupied nests/km^2 (Table II-1). Long-eared owls occupied stick nests that had been built in previous years by American crows and black-billed magpies. Five nests used by the owls averaged 4.4 m above ground, and all were in quaking aspen averaging 7.9 m high and 15.0 cm dbh (SD = 1.2, 2.2, and 3.7). Mean distance to tree clump edge and mean clump size were 12.0 m and 0.8 ha (5.7 and 0.4). Three to 5 young were reared in each of 4 long-eared owl nests that were successful out of 7 occupied nests for which nest success was documented.

Non-nesting Raptors

Presence of Floaters and Unpaired Territorial Raptors

Floaters (non-territorial individuals of same species that nested on LNWR) occurred annually but were rare (10-20 total observations/year) and ephemeral which made them difficult to study as Newton (1979:148) pointed out. Hawks that were floaters typically were unpaired and in immature plumage. I did not observe clear evidence of any unpaired hawks that were territorial (defended a nesting area) for >2-3 weeks. It was more difficult to ascertain status of some apparently errant great horned owls and long-eared owls.

Other Raptors

Unpaired American kestrels (*Falco sparverius*) and merlins (*F. columbarius richarsonii*) occasionally were observed into mid-breeding season (June), but did not occupy nests on LNWR even though they occasionally nest in northwestern North Dakota (Stewart 1975). Burrowing owls (*Athene cunicularia*) were not observed even though a pair annually occupied a nest 6 km northeast, on the edge of the Drift Plain (pers. obs.). Thirteen other species of raptors were observed in spring or in late summer (Murphy and Green 1992; Appendix Table 1).

DISCUSSION

Breeding Biology and Habitat of Nesting Raptors

LNWR has high abundance of nesting raptors. Based on lower confidence interval bounds of survey estimates for northern harriers and short-eared owls and yearly censuses of other raptors, total annual nesting density for 8 species of raptors averaged about 0.8 occupied nests/km^2 and ranged from about 0.5 in drought years to 2.0 in years of high vole abundance. Collective abundance of nesting raptors on other areas in midwest and western states include 1.1 occupied nests/km^2 on cliff-lined river surrounded by shrubsteppe in Idaho (U.S. Bureau of Land Management 1979), about 0.7 occupied nests/km^2 on mixed farmland

and woodlot in Michigan (Craighead and Craighead 1956:214), and about 0.4-0.7 occupied nests/km^2 in mixed hardwood draw, riparian, and prairie habitat in southwestern North Dakota (1978 estimate based on a stratified, random sample [Postovit 1979]). I attribute the high nesting density of raptors on LNWR to contiguous grassland, wetland, and woodland habitats that were highly dispersed, a relatively diverse prey base in spring and summer, and scarcity of humans on the area.

Red-tailed Hawk and Great Horned Owl

Nesting densities of red-tailed hawks and great horned owls on LNWR were comparable to those in favorable habitats such as aspen parkland in Canada and mixed woodlots and farmland in the eastern deciduous forest biome, but higher than previously reported in North Dakota (Table II-9). Except, nesting great horned owls were nearly as abundant on a township composed mainly of cropland and pasture next to LNWR (Part III).

Distribution and abundance of breeding raptors ultimately can be explained in terms of 2 resources: prey and nest sites (Newton 1979). Nesting red-tailed hawks and great horned owls were abundant on LNWR due to dispersion of aspen tree clumps that provided hunting perches and nest sites, a premise supported for both species by strong correlation between cumulative nest occupancies and aspen tree clump density. Both species depend on tall perches to forage for prey (Dunstan 1970, Orde and Harrell 1977, Rudolph 1978, Ballam 1984, Janes 1984b) Peterson 1979). Red-tailed hawks typically use large trees in which to build their bulky nests (McGovern and McNurney 1986, Santana C. et al. 1986, Bechard et al. 1990) and great horned owls often rely on red-tailed hawk nests for breeding as observed in this study and in many other areas (Dunstan and Harrell 1973, Springer and Kirkley 1978, Toland 1990). Red-tailed hawk abundance on LNWR may also benefit from scarcity

Table II-9. Nesting densities (occupied nests or pairs/km^2) of red-tailed hawks and great horned owls in various studies.

Source	Location	Density	Habitat[a]	n years, nests[b]
Red-tailed hawk				
Petersen 1979	se Wisconsin	0.243	DF	4,71
Bohm 1977	c Minnesota	0.215[c]	DF	3,72
Kirkley and Springer 1980	c Ohio	0.161	DF	1,59
Toland 1990	c Missouri	0.135	DF	7,140[d]
McInvaille and Keith 1974	c Alberta	0.133	AF	6,131
Sargeant et al. 1992	s Alberta and s Saskatchewan	0.158[e]	AF	3,49
Gilmer et al. 1983	sc North Dakota	0.009	PF	3,21
Sargeant et al. 1992	e North Dakota	0.008[f]	PF	2,2
Part III	nw North Dakota	0.156	AF	2,25
this study	nw North Dakota	0.228	IA	8,197
Great horned owl				
Orians and Kuhlman 1956	se Wisconsin	0.085	DF	3,48
Petersen 1979	se Wisconsin	0.133	DF	4,45
Belyea 1976	s Michigan	0.047	DF	5,22
Kirkley and Springer 1980	c Ohio	0.122	DF	1,59
Rusch et al. 1972	c Alberta	0.044	AF	4,28
Gilmer et al. 1983	sc North Dakota	0.017	PF	3,43
Gaines and Kohn 1982	c North Dakota	0.016	PF	1,14
Sargeant et al. 1992	e North Dakota	0.047[f]	PF	2,11
Part III	nw North Dakota	0.112	AF	2,18
this study (1985-90)	nw North Dakota	0.131	IA	6,86

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[a] Habitat and land use generalized as: eastern deciduous and other woodland and farmland (DF), aspen parkland and farmland (AF), prairie and farmland (PF), idle prairie changing to aspen parkland (IA).

[b] Total number of years and occupied nests.

[c] Density recalculated after correcting for apparent error.

[d] Total number of active nests reported.

Table II-9. Continued

[e] Mean calculated from 12 complete count data presented in Appendix Table 15 in Sargeant et al. (1992), from 8 26-km^2 aspen parkland study areas in Alberta and Saskatchewan.
[f] Mean calculated from 10 data presented in Appendix Table 15 in Sargeant et al. (1992) from 6 21- to 23-km^2 study areas in eastern North Dakota.

of potentially competing congeners, Swainson's and ferruginous hawks, although these Buteo spp. can live sympatrically and successfully partition most resources (Schmutz et al. 1980, Bechard et al. 1990, Restani 1991).

Abundance of seasonal and semi-permanent wetland basins correlated with cumulative nest occupancies of great horned owls but not red-tailed hawks. Wetlands are sources of great horned owl prey on LNWR and nearby mixed land use in northwestern North Dakota (Part IV and Part VI). Affiliation with wetlands has been suggested for great horned owls in the Aspen Parkland and Great Lakes regions (McInvaille and Keith 1974, Petersen 1979). Lack of correlation between wetlands and red-tailed hawks on LNWR was surprising because increased red-tailed hawk nesting coincided with increased aspen tree clump density, and there was a direct correlation between aspen and wetland abundance. Thus, the hawk selected areas having wetland abundance lower than expected based on aspen clump density. I propose this occurred due to frequent selection by great horned owls of stick nests built by the hawk. Because red-tailed hawks arrived 2-3 weeks after great horned owls began incubation, the hawk may have been forced to build new nests in nearby habitats less optimally associated with wetlands. Canada geese (Branta canadensis maxima) similarly initiated nesting in old red-tailed hawk nests near wetlands just before red-tailed hawks returned (n = 5 instances, 1984-87) as observed at Buteo spp. stick nests in Alberta (Schmutz et al. 1988).

Red-tailed hawk nests were in aspen tree clumps that were larger in area than average. The hawk used large aspen trees (>25 cm dbh) where available but many red-tailed hawk nesting areas lacked large aspen, or great horned owls occupied nests in clumps with large trees when the hawk arrived in spring. Twice red-tailed hawks built atop remnants of old crow nests in small aspen (15 and 18 cm dbh)(pers. obs.). Both occurrences were in the most productive great horned owl nesting season and clumps of large trees used previously for nesting by the hawks were occupied by owls. Because red-tailed hawks at LNWR used a variety of nest tree sizes, I suggest their annual nest distribution was limited more by not having tree clumps effectively dispersed as hunting perches.

Nesting densities of red-tailed hawks and great horned owls were stable among years despite significant annual changes in wetlands that supported many potential prey on LNWR. For example, abundance of waterfowl declined during 1988-90 as nearly all wetland basins dried up (90% confidence interval mean of estimated total ducks in late May 1988-90: 5189, 2911, and 1189; FWS, unpubl. refuge files). Also, decreased primary production that accompanied severe drought years presumably diminished upland prey populations (e.g., meadow voles). Red-tailed hawks and great horned owls are versatile predators (Bent 1938, Errington 1938, 1967, Palmer 1988) and probably maintain stable nesting densities because of their dietary flexibility. Long-term numerical stability is characteristic of nesting densities of red-tailed hawks but not of great horned owls that nest in aspen parkland (Houston 1987) or parkland-boreal forest ecotone (McInvaille and Keith 1974, Adamcik et al. 1979).

In contrast to stable numbers of nesting pairs, nest success and productivity of great horned owls and red-tailed hawks on LNWR varied dramatically among years and generally were low. This variable and low reproductive success was due to decreases in abundance or vulnerability of prey. Great horned owl reproductive success related to annual vole abundance, and low productivity of both great horned owls and red-tailed hawks coincided with severe drought that reduced wetland prey. But, low nest success and productivity of red-tailed hawks also related to reduced prey vulnerability or foraging effort during spring storms that occurred at critical times in the hawk's reproductive cycle. These storms affected reproduction of raptors elsewhere in North Dakota (Allen et al. 1986). Although not a factor during this study, vulnerability of voles to great horned owls in late winter could be reduced by deep snows (Errington et al. 1940, McInvaille and Keith 1974, Baker and Brooks 1981).

Annual productivity of great horned owls on LNWR was more erratic than that of red-tailed hawks and contrasted sharply with great horned owls 350 km north that demonstrated regularly cyclic productivity linked with fluctuating abundance of snowshoe hares (Houston 1987). Great horned owls at LNWR were too far south to profit from a snowshoe hare prey base yet too far north to benefit from cottontail rabbits typically important as winter prey in other northcentral and western states (Errington et al. 1940, Petersen 1979, Phillips et al. 1990), and white-tailed jackrabbits have been scarce locally since the 1940s (FWS, unpubl. refuge files). Winter food availability directly affects reproductive physiology of the great horned owl in northern parts of its range (McInvaille and Keith 1974, Adamcik et al. 1979). I propose that availability of vole prey on LNWR in winter and early spring is the most significant determinant of great horned owl nest success and productivity. These reproductive parameters exceeded 50% and 1 young/occupied nest only in 2 years, both of which coincided with good winter and spring vole availability. Other prey either were scarce in winter or had abundance levels unrelated to yearly great horned owl reproductive success. Abundance of voles in winter strongly influences great horned owl clutch size in aspen parkland-boreal forest ecotone of central Alberta (Adamcik et al. 1979).

Mean annual productivity of 0.86 and 0.72 young/occupied nest for red-tailed hawks and great horned owls observed in this study were among the poorest recorded in the northern Great Plains and adjacent regions (Table II-10), and were far below respective minimum levels of 1.31-1.36 and 1.47 young/occupied nest needed to sustain populations (Henny 1972, Henny and Wight 1972). Red-tailed hawks on LNWR never acheived the minimum level in any year and great horned owls reached or exceeded it in only 2 of 8 years. My data indicate overall productivity is so low for nesting red-tailed hawks and great horned owls on LNWR that these raptors must depend on recruitment from other areas to maintain high breeding densities.

Nest success of LNWR red-tailed hawks was closer to those in other studies (Table II-10) but was low (<65%) most years. Thus, productivity was low because sizes of broods were small; half had only 1 young. Broods of 1 are less common in redtail populations elsewhere (Orians and Kuhlman 1956, Bohm 1977, Peterson 1979, Cress and Langley 1988).

Interspecific interaction between breeding red-tailed hawks and great horned owls is common, usually with the hawk being negatively affected through nest abandonment or depredations (Springer and Kirkley 1978, Hagar 1957, Luttich et al. 1971, Houston 1975, Bosakowski et al. 1988). I noted lack of success at only 1 red-tailed hawk nest that could be attributed to great horned owls (remains of a large nestling hawk along with owl contour feathers in the red-tailed hawk nest). Conversely, in 1985 both species nested successfully 120 m apart in the same aspen clump. Toland (1990) noted mutual tolerance between sympatric red-tailed hawks and great horned owls nesting in Missouri, presumably due to adequate prey and temporal partitioning of activities.

Table II-10. Comparison of nest success and productivity of red-tailed hawks and great horned owls on LNWR with other populations.

Source	Location	% nest success[a]	Young/ nest[b]	n years, nests[c]
Red-tailed hawk				
Orians and Kuhlman 1956	se Wisconsin	62	1.2	2,66
Petersen 1979	se Wisconsin	72	1.3	4,81
Bohm 1977	c Minnesota	61	1.1	2,72
Johnson 1975	sc Montana	53	1.4	2,137
Seidensticker and Reynolds 1971	sc Montana	50	0.9	2,54
Gilmer et al. 1983	sc North Dakota	72	1.5	3,54
Part III	nw North Dakota	84	1.4	2,25
this study	nw North Dakota	56	0.9	7,174
Great horned owl				
Kirkley and Springer 1980	c Ohio	75[d]	1.3	1,56
Orians and Kuhlman 1956	se Wisconsin	43	1.2	3,51
Petersen 1979	se Wisconsin	66	1.1	4,45
Rusch et al. 1972	c Alberta	64	1.4	4,28
Seidensticker and Reynolds 1971	sc Montana	64	1.2	2,11
Gilmer et al. 1983	sc North Dakota	84	1.6	3,75
Part III	nw North Dakota	56	1.1	2,18
this study	nw North Dakota	41	0.7	8,115

[a] Based on average annual success = 100 * (number of occupied nests with ≥1 large or fledging age young/total number of occupied nests).

[b] Average annual mean number of large or fledging-age young per occupied nest.

[c] Total numbers of years and occupied nests.

[d] Success for Kirkley and Springer (1980) derived from "failure rate" of 25% which apparently excluded several "non-nesting" pairs.

Cooper's Hawk

Nesting Cooper's hawks increased from 1 nest occupied in 1983-85 to 5 in 1989-90. Although the hawk pioneered on LNWR in the early 1980s (Part I), its nesting density at the close of my study approached those reported from more heavily wooded habitats (Table II-11).

Table II-11. Nesting densities (occupied nests or pairs/km^2) of Cooper's hawks reported from various studies.

Source	Location	Density	Habitat[a]	*n* years, nests[b]
Rosenfield and Anderson 1983	c Wisconsin	0.058[c]	DF	3,7
Rosenfield et al. 1991	se Wisconsin	0.302	DP	1,9
Craighead and Craighead 1956	se Michigan	0.079	DF	3,22
Reynolds and Wight 1978	w Oregon	0.048[d]	MW	2,9
Postovit 1979	sw North Dakota	0.052[e]	PW	1,4
this study	nw North Dakota	0.046[f]	IA	2,10

[a] Habitat and land use generalized as: eastern deciduous and other woodland and farmland (DF), eastern deciduous woodland and pine plantation (DP), montane coniferous woodland (MW), prairie and riparian woodland (PW), idle prairie changing to aspen parkland (IA).

[b] Total number of years and occupied nests.

[c] Data from Blaine study area.

[d] Data from Corvallis study area.

[e] Postovit's density figure was an estimate of the population mean, based on a stratified random sample, 1978 data.

[f] Data from 1989-90.

Reproductive data for Cooper's hawks in northern Great Plains are scant (e.g., Stewart 1975:90). Mean nest success and productivity for 21 nest occupancies on LNWR compared closely with reports from the Great Lakes region and far western states (Table II-12) and suggested Cooper's hawks on LNWR were reproductively healthy. Cooper's hawks were more successful and productive per nest occupancy and acheived normal reproductive performance compared to red-tailed hawks and great horned owls on LNWR. Although drought in 1988-90 affected other raptors and no Cooper's hawk young were reared in the most severe drought year of 1988, new Cooper's hawk nesting areas were established and average productivity occurred in 1989 and 1990. Decreased productivity of Cooper's hawks occurred in California in years of drought (Asay 1987).

Table II-12. Comparison of nest success and productivity of Cooper's hawks on LNWR with other populations.

Source	Location	% nest success[a]	Young/ nest[b]	n years, nests[c]
Craighead and Craighead 1956	se Michigan	--	2.2	3,22
Rosenfield and Anderson 1983	Wisconsin	69[d]	2.4[d]	3,83
Hennessey 1978	n Utah	54	1.6	2,43
Reynolds and Wight 1978	Oregon	69[d]	2.1[d]	6,24
Asay 1987	s California	--	2.3[d]	4,55
this study	nw North Dakota	67	2.4	8,21[e]

[a] Based on average annual success = 100 * (number of occupied nests with ≥ 1 large young/total number of occupied nests).
[b] Average annual mean number of large young per occupied nest.
[c] Sample size: total number of years and occupied nests.
[d] Averages based on active nests; average based on occupied nests presumably would have been lower than this figure.
[e] Derived from pooling of all nest occupancies from 1983-90.

Cooper's hawks placed nests much lower relative to nest tree height and far from tree clump edges compared to other hawks and used nest sites that were well-sheltered above by tree canopy. These attributes indicate selection of closed tree canopy for nest sites on LNWR, which seems universal in the Cooper's hawk (Palmer 1988).

Swainson's Hawk and Ferruginous Hawk

Nesting Swainson's hawks decreased from 4-7 occupied nests in 1983-85 to 1-2 in 1987-90 and average annual nesting density was 0.03 occupied nests/km^2. Higher densities of the hawk occur elsewhere in the northern Great Plains (Table II-13) although populations may fluctuate among years (Gilmer and Stewart 1984, Schmutz and Hungle 1989). Nesting Swainson's hawks on an adjacent township were more than twice as common as on LNWR (Part III).

Table II-13. Nesting densities (occupied nests or pairs/km^2) of Swainson's hawks reported from various studies.

Source	Location	Density	Habitat[a]	n years, nests[b]
Schmutz et al. 1980	se Alberta	0.158[c]	PR	2,152
Olendorff 1975	ne Colorado	0.033	PR	1,68
Dunkle 1977	se Wyoming	0.149	PF	1,55
Sargeant et al. 1992	e North Dakota	0.105[d]	PF	2,24
Gilmer and Stewart 1984	sc North Dakota	0.051	PF	3,193
Part III	nw North Dakota	0.075	AF	2,16
this study	nw North Dakota	0.031	IA	8,27

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[a] Habitat and land use generalized as: prairie rangeland, prairie and farmland (PF), aspen parkland and farmland (AF), idle prairie changing to aspen parkland (IA).

[b] Total number of years and occupied nests.

[c] Calculated from reported 76 Swainson's hawk nests on 480 km^2 each of 2 years.

[d] Mean calculated from 10 data presented in Appendix Table 15 in Sargeant et al. (1992) from 6 21- to 23-km^2 study areas in eastern North Dakota.

Abundance of nesting raptors is limited ultimately by prey or nest sites (Newton 1979). Availability of nest sites was adequate but foraging habitat inadequate for Swainson's hawks on LNWR. Some Swainson's hawk nest site characteristics overlapped with those of red-tailed hawks which suggested potential for competitive exclusion, but Swainson's hawks showed no preference for size (area) of aspen tree clumps for nest sites or for aspen tree clump density, and also nested in shrub. On LNWR, trees or tall shrubs that could have supported stick nests of Swainson's hawks occurred on each 2.59-km^2 section. Except for a nesting area that frequently was cultivated and prescribe-burned, Swainson's hawks occupied nests exclusively along the boundary of LNWR and hunted adjacent private lands (pers. obs.). This nest distribution and foraging pattern combined with lack of nest site limitation on LNWR and greater abundance of nesting Swainson's hawks on an adjacent area of different land use (Part III) implied foraging habitat was deficient.

I propose Swainson's hawk foraging habitat was inadequate on LNWR because prey could not be accessed or detected by the hawk. In the northern Great Plains, nesting Swainson's hawks use a variety of vertebrate prey species (Schmutz et al. 1980, Gilmer and Stewart 1984, Part V) many of which commonly occur on LNWR (e.g., mice or voles, Passeriforms and other birds, amphibians). But regardless of prey abundance, Swainson's hawks cannot successfully forage in tall, dense vegetation (Bechard 1982, Janes 1985) such as idle prairie on LNWR. Swainson's hawk prey were accessible on adjoining lands where most prairie was grazed heavily and croplands and haylands were disturbed frequently by tillage or harvest. Mean Robel height-density of idle prairie vegetation on LNWR during spring and summer in the 1980s were about 0.5-1.5 and 1-2 dm (FWS, unpubl. refuge files) but height-density indices on adjacent grazed prairie were about half as great.

Productivity of Swainson's hawks on LNWR was slightly lower than reported elsewhere in the northern Great Plains and in northwestern states although nest success was comparable (Table II-14). In 1983 only 1 juvenile Swainson's hawk was produced from 5 nesting pairs, possibly due to the May blizzard that occurred about a week before egg-laying.

Only 1 ferruginous hawk occupied nest occurred during this study although 2 were observed on LNWR in 1982 (Piehl 1983; FWS, unpubl. refuge files). Where native prairie predominates in other areas of the northern Great Plains, ferruginous hawk nesting densities are about 0.01-0.10 occupied nests/km^2 (Lokemoen and Duebbert 1976, Gilmer and Stewart 1983, Schmutz et al. 1980, Schmutz 1984), much greater than the 8-year average of 0.001 observed in this study. Ferruginous hawks probably were rare on LNWR for some of the same reasons that Swainson's hawks were uncommon. Potential nest sites were available but foraging habitat was inadequate because ferruginous hawks also cannot forage in tall, dense vegetation (Wakeley 1978, Jasikoff 1982, Schmutz 1987).

Table II-14. Comparison of productivity and success of Swainson's hawks on LNWR with other populations.

Source	Location	% nest success[a]	Young/nest[b]	_n_ years, nests[c]
Henny et al. 1984	Oregon	68	1.2	3,25
Cottrell 1981	se Oregon	56	1.3	2,16[e]
Bechard 1983	se Washington	--	1.1[d]	4,87
Olendorff 1975	ne Colorado	55	1.2[d]	3,119
Dunkle 1977	se Wyoming	60	1.2	1,55
Gilmer and Stewart 1984	sc North Dakota	64	1.6	3,270
this study (LNWR)	nw North Dakota	61	1.1	8,28[e]

[a] Based on average annual success = 100 * (number of occupied nests with ≥1 large young/total number of occupied nests).
[b] Average annual mean number of large young per occupied nest.
[c] Sample size: total number of years and occupied nests.
[d] Reported mean number of young per active nest; productivity per occupied nest presumably was lower than this figure.
[e] Derived from pooling of all nest occupancies from 1983-90.

Also, nesting ferruginous hawks in the northern Great Plains rely heavily on Richardson's ground squirrels (S. richardsonii) as prey (Schmutz et al. 1980, Gilmer and Stewart 1983, Schmutz and Hungle 1989) but the ground squirrel occurs in short vegetative cover such as heavily grazed areas (Jones et al. 1983) and thus is scarce on LNWR. Last, ferruginous hawks avoid heavily treed areas regardless of availability of prey (Schmutz et al. 1980, Schmutz 1984).

Northern Harrier and Short-eared Owl

Estimated northern harrier nesting density on LNWR was high. The annual mean of 0.34 active nests/km^2 was conservatively estimated and densities could be several times greater especially in years of high vole abundance. In North Dakota, a statewide mean density of 0.19 northern harrier pairs/km^2 was estimated by Stewart and Kantrud (1972) and the harrier was considered a major bird species. Annual counts of it on FWS Breeding Bird Surveys in North Dakota are among the highest for any state or province (U.S. Fish and Wildlife Service 1987). Other densities reported for North Dakota and mid-continent North America range considerably from 0.05 to >1.0 nests or pairs/km^2 (reviewed in Palmer 1988). Sutherland's (1987) high report of 1.35 nests/km^2 was from a 11-km^2 island on a central North Dakota reservoir.

Northern harriers on LNWR exhibit a close but not obligatory relationship with voles that is well-known (Hamerstrom 1979, Simmons et al. 1986, Grant et al. 1991). Conversely, short-eared owls normally only breed in areas of high microtine abundance (Clark 1975). Indeed, nesting by short-eared owls in only the first 2 of 9 years studied coincided with an obvious peak in vole abundance on LNWR, and observation of few, single owls in 1 other breeding season coincided with moderate vole abundance.

Nearly all northern harrier nests were in uplands in brush-dominated sites but some also were in grassy sites and in wetlands, suggesting nest sites were selected based on plant physiognomy rather than species composition. Dense, tall nest cover provided by a variety of woody and herbaceous plants was used in Alberta and Saskatchewan (Sealy 1967) and central Wisconsin (Hamerstrom and Kopeny 1981). Short-eared owls used sparser, more herbaceous nest cover on LNWR, a general difference Palmer (1988) recognized.

Nest success and productivity of northern harriers on LNWR was average or slightly higher than reported for other harrier populations in and near the northern Great Plains (Table II-15). Few reproductive data from North America exist for short-eared owls. My estimate of 41% Mayfield nest success was similar to Kantrud and Higgins (1992) report of 38% for 59 nests of the owl in North Dakota, South Dakota, eastern Montana, and Manitoba during 1963-91 (based on Mayfield correction; included the 13 data from LNWR presented herein).

Table II-15. Comparison of nest success and productivity of northern harriers on LNWR with other populations.

Source	Location	% nest success[a]	Young/ nest[b]	*n* years, nests[c]
Craighead and Craighead 1956	se Michigan	--	1.3	3,19
Toland 1986	sw Missouri	66	2.2	2,15
Hamerstrom et al. 1985	c Wisconsin	73	2.2	25,330[d]
Hammond and Henry 1949	nc North Dakota	72	2.2	3,60
Sutherland 1987	c North Dakota	59	2.2	2,29[d]
this study	nw North Dakota	65[e]	2.5[e]	8,33[d]

[a] Based on average annual success = 100 * (number of occupied nests with ≥1 large young/total number of occupied nests).
[b] Average annual mean number of large young per occupied nest.
[c] Sample size: total number of years and occupied nests.
[d] Data from all study years pooled.
[e] Estimate based on active nests and corrected for unsuccessful nests not detected by periodic nest searches (Mayfield 1961, 1975).

Long-eared Owl

Along with the Cooper's hawk, long-eared owls are known to nest in North Dakota but have questionable population status due to lack of information (Anonymous 1986). Previous nest records of long-eared owls for northwestern North Dakota are few, all from the Des Lacs River valley 30 km northeast (Stewart 1975:159). Although long-eared owls either were absent or uncommon on LNWR during years of this study, 7 nests were occupied on 22 km^2 in 1982 (FWS, unpubl. refuge files) which coincided with peak northern harrier abundance and occurrence of nesting short-eared owls. This indirectly suggested a link with vole abundance as noted for long-eared owls in Europe (Village 1981). Average annual nesting density of 0.01 occupied nests/km^2 for long-eared owls on LNWR was lower than an estimated 0.05/km^2 for an area of woody draws and riparian and prairie habitat in southwestern North Dakota (1978 stratified sample [Postovit 1979]). Long-eared owls on LNWR relied on Corvids to provide nest sites, a relationship observed elsewhere (Bent 1938, Mikkola 1983, Marks 1986).

Almost no nest success and productivity data exist for long-eared owls in North Dakota (Stewart 1975:159). My observation of 3-5 young reared in each of 4 successful out of 7 occupied nests was within ranges of about 35-60% nest success and 2-4 young/occupied nest reported by others in North America (Craig and Trost 1979, Thurow and White 1984, Marks 1986).

SUMMARY, CONCLUSIONS, AND IMPLICATIONS

Overall abundance of breeding raptors during 1981-90 on LNWR was high. Excluding unpaired and non-territorial birds, conservative estimates of total density for 8 species of nesting raptors ranged from about 0.5 occupied nests/km^2 in years of severe drought to about 2.0 occupied nests/km^2 when voles were abundant. The raptor community was characterized by high, stable densities of red-tailed hawks and great horned owls that exhibited erratic but generally low productivity, and high but fluctuating densities of northern harriers with normal productivity. Nesting by short-eared owls occurred infrequently but at high densities as could be expected for a nomadic, monophagic raptor. The community included few nesting Swainson's hawks, almost no ferruginous hawks, and no burrowing owls, species endemic or nearly so in the plains of western North America. The Cooper's hawk, a woodland raptor, increased through the study and long-eared owls nested occasionally.

Numbers of red-tailed hawk and great horned owl pairs did not respond to changes in habitat conditions and prey populations presumably due to dietary flexibility in these raptors (Luttich et al. 1970), McInvaille and Keith 1974, Adamcik et al. 1978, 1979). However, reproductive output of red-tailed hawks deviated from normal levels for the species in response to declines in prey abundance attributed to severe drought, and to short-term unavailability of prey from spring storms which breeding strategies can hardly anticipate (Adamcik et al. 1979). Breeding strategies of great horned owls on LNWR are distinctive for a northern population of the species because Leporid prey that significantly influence great horned owl demographics elsewhere are scarce on LNWR. Significant numerical change among years in the owl's nesting population should have occurred based on fluctuating populations of other northern great horned owls (Adamcik et al. 1978, Houston 1987, Phillips et al. 1990), but was not observed. The owls remained on territories through winter but had to rely on scarce prey from few taxa compared with owl populations elsewhere. I proposed that overwinter availability of voles determined whether great horned owls on LNWR become physiologically and behaviorally prepared for breeding. Great horned owls responded to 2 moderate peaks in vole abundance by increased nesting effort and success and by acheiving normal productivity for the species.

Patterns of reproductive output or nesting density of several species suggested the nesting raptor community generally exhibits "boom and bust" phenomena from year to year, not unlike other vertebrate fauna that breed in dynamic environments (e.g., northern prairie waterfowl). An important implication of this is that studies of only 2-3 years length easily could convey a biased view of demographic patterns of northern prairie raptors. For example, a ferruginous hawk population in Utah appeared to increase in initial years of a study but then declined precipitously over following years and the hawk eventually was extirpated (Woffinden and Murphy 1989).

Red-tailed hawks and great horned owls on LNWR clearly were favored by presence of large (>0.5 ha) aspen tree clumps for nest sites, surrounded by more aspen tree clumps for hunting perches. Occurrence of occupied nests of either species was greatest where aspen tree clumps were most prevalent (6-17/km^2). Nesting by the owl also correlated with wetland presence, which may have related to forage preferences. Great horned owls relied mainly on red-tailed hawks to provide nest sites.

Swainson's hawks used aspen tree clumps on LNWR that were significantly smaller in area than those used by other hawks and occasionally nested in shrub sites. There was no strong relationship between density of aspen tree clumps and occurrence of occupied Swainson's hawk nests. At least half of LNWR had too many tree clumps to be suitable habitat for nesting ferruginous hawks, as per Schmutz (1984) and Schmutz et al. (1980). My observations suggested that food supply restricted these 2 hawks on LNWR mainly by widespread, dense vegetative cover that precluded foraging and caused related lack of Richardson's ground squirrel prey.

Cooper's hawks used large (>0.75 ha) aspen tree clumps for nesting compared to what was available on LNWR and placed nests in sites protected by closed canopies. Nesting by the hawk was not restricted to areas with high densities of aspen clumps, suggesting the hawk was flexible about its foraging habitat needs relative to nest site selection.

Northern harriers nested in dense, tall upland cover, usually western snowberry and other brush but also in grassy or wetland sites, suggesting nest sites were selected based on plant physiognomy rather than species composition. Short-eared owls nested in shorter and more herbaceous upland cover. Nest sites for both were widely available and no restriction in nesting distribution was apparent for either.

Habitat management based on rest or periodic but light impact (e.g., low-intensity grazing) favors the raptor assemblage present on LNWR in the 1980s, one capable of existing in predominantly brush- and tree-invaded prairie habitats. My data indicate that average reproduction in 2 of 3 dominant raptor species (red-tailed hawks and great horned owls but not northern harriers) is below that needed to sustain the respective populations; presumably recruitment from other areas maintains observed breeding densities. Furthermore, habitat clearly is marginal or inadequate for several other species of nesting raptors that are uncommon or rare on LNWR but more abundant elsewhere in the northern Great Plains (e.g., Swainson's hawk, ferruginous hawk).

Habitat management practices that decrease density and size of aspen tree clumps, decrease brush (i.e., snowberry), and increase vertical structural diversity of grass-forb communities would favor increased foraging opportunities for Swainson's and ferruginous hawks on LNWR but probably disfavor red-tailed hawks and great horned owls. Cooper's hawks might be reduced under such management. Abundances of nesting northern harriers and short-eared owls probably would change little because resultant habitat mosaics still would amply provide for nest sites and increase availability of vole prey. Habitat treatments in small (1-2 km^2) blocks would be most appropriate for northern harriers and other ground-nesting birds that are similarly philopatric, because treatment in large blocks could conceivably displace nesting birds. These habitat management practices would compliment management for many other prairie-dependent wildlife species (Ryan 1986, 1990).

LITERATURE CITED

ADAMCIK, R. S., A. W. TODD, and L. B. KEITH. 1978. Demographic and dietary responses of great horned owls during a snowshoe hare fluctuation. Can. Field-Nat. 92:156-166.

---, ---, and ---. 1979. Demographic and dietary responses of red-tailed hawks during a snowshoe hare fluctuation. Can. Field-Nat. 93:16-27.

ALLEN, G. T., R. K. MURPHY, K. STEENHOF, and S. W. PLATT. 1986. Late fledging dates, renesting, and large clutches of prairie falcons. Wilson Bull. 98:463-465.

ANONYMOUS. 1986. List of North Dakota's threatened and endangered biota. North Dakota Outdoors 49:28-32.

ARMBRUSTER, J. S. 1983. Impacts of coal surface mining on 25 migratory bird species of high federal interest. U.S. Fish Wildl. Serv. FWS/OBS 83/35. 348pp.

ASAY, C. E. 1987. Habitat and productivity of Cooper's hawks nesting in California. Calif. Fish Game 73:80-87.

BAKER, J. A., and R. J. BROOKS. 1981. Raptor and vole populations at an airport. J. Wildl. Manage. 45:390-396.

BALLAM, J. M. 1984. The use of soaring by the red-tailed hawk (Buteo jamaicensis). Auk 101:519-524.

BECHARD, M. J. 1982. Effect of vegetative cover on foraging site selection by Swainson's hawk. Condor 84:153-159.

---. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. Wilson Bull. 95:233-242.

---, B. W. ZOELLICK, and M. NICKERSON. 1985. Accuracy in determining the age of nestling red-tailed hawks. J. Wildl. Manage. 49:226-228.

---, R. L. KNIGHT, D. G. SMITH, and R. E. FITZNER. 1990. Nest sites and habitats of sympatric hawks (Buteo spp.) in Washington. J. Field Ornithol. 61:159-170.

BELYEA, G. Y. 1976. A nesting study of the red-tailed hawk in southern Michigan. Ph. D. Thesis, Mich. State Univ. 73pp.

BENT, A. C. 1938. Life histories of North American birds of prey, part 2. Smithsonian Inst., U.S. Natl. Mus. Bull. 170, Washington, D.C. 465pp.

BOHM, R. T. 1977. A study of nesting red-tailed hawks in central Minnesota. Loon 50:129-137.

BOSAKOWSKI, T., R. SPEISER, and D. G. SMITH. 1988. Nesting ecology of forest-dwelling great horned owls, Bubo virginianus, in the eastern deciduous forest biome. Can. Field-Nat. 103:65-69.

BROWN, L. 1974. Data required for effective study of raptor populations. Raptor Res. Rep. 2:9-20.

---, and D. AMADON. 1989. Eagles, hawks and falcons of the world, 2nd ed., Vol. 1 and 2. Wellfleet Press, Secaucus, New Jersey. 945pp.

CLARK, R. J. 1975. A field study of the short-eared owl, Asio flammeus (Pontoppidan), in North America. Wildl. Monogr. 47:1-67.

COTTRELL, M. J. 1981. Resource partitioning and reproductive success of three species of hawks (Buteo spp.) in an Oregon prairie. M.S. Thesis, Oregon State Univ., Corvallis. 72pp.

CRAIG, T. H., and C. H. TROST. 1979. The biology and nesting density of breeding American kestrels and long-eared owls on the Big Lost River, southeastern Idaho. Wilson Bull. 91:50-61.

CRAIGHEAD, F. C., Jr., and D. P. MINDELL. 1981. Nesting raptors in western Wyoming, 1947 and 1975. J. Wildl. Manage. 45:865-872.

CRAIGHEAD, J. J., and F. C. CRAIGHEAD. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania. 443pp.

CRESS, G. A., and W. M. LANGLEY. 1988. Effect of annual and habitat variations in prey on the growth and productivity of red-tailed hawks (Buteo jamaicensis). Trans. Kans. Acad. Sci. 91:96-102.

DIXON, W. J., ed. 1983. BMDP statistical software. Univ. California Press, Berkeley. 733pp.

DANIEL, W. W. 1990. Applied non-parametric statistics. PWS-KENT Publishing Co., Boston, Mass. 635pp.

DUEBBERT, H. F., and A. M. FRANK. 1984. Value of prairie wetlands to duck broods. Wildl. Soc. Bull. 12:27-34.

DUNKLE, S. W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. Auk 94:65-71.

DUNSTAN, T. C. 1970. Post-fledging activites of juvenile great horned owls as determined by radio-telemetry. Ph.D. Thesis, Univ. South Dakota, Vermillion. 110pp.

---, and B. E. HARRELL. 1973. Spatiotemporal relationships between breeding red-tailed hawks and great horned owls in South Dakota. Raptor Res. 7:49-54.

ERRINGTON, P. L. 1938. The great horned owl as an indicator of vulnerability in prey populations. J. Wildl. Manage. 2:190-205.

---. 1967. Of predation and life, 1st ed. University of Iowa Press, Ames, Iowa. 277pp.

---, F. HAMERSTROM, and F. N. HAMERSTROM Jr. 1940. The great horned owl and its prey in north-central United States. Iowa Agric. Exp. Stn. Res. Bull. 227:758-850.

EVANS, D. L. 1982. Status reports on twelve raptors. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Wildl. 238. 68pp.

FOX, G. A. 1971. Recent changes in the repoductive success of the pigeon hawk. J. Wildl. Manage. 35:122-128.

FYFE, R. W., and R. R. OLENDORFF. 1976. Minimizing the dangers of nesting studies to raptors and other sensitive species. Can. Wildl. Serv. Occas. Pap. 23. 16pp.

GABRIELSON, I. N. 1943. Wildlife refuges. MacMillan, New York. 257pp.

GAINES, R. C., and S. C. KOHN. 1982. Raptor use of hardwood draws in central North Dakota. Prairie Nat. 14:55-58.

GIBBONS, J. W., and R. D. SEMLITSCH. 1981. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimlayana 7:1-16.

GILMER, D. S., and R. E. STEWART. 1983. Ferruginous hawk populations and habitat use in North Dakota. J. Wildl. Manage. 47:146-157.

---. 1984. Swainson's hawk nesting ecology in North Dakota. Condor 86:12-18.

---, P. M. KONRAD, and R. E. STEWART. 1983. Nesting ecology of red-tailed hawks and great horned owls in central North Dakota and their interactions with other large raptors. Prairie Nat. 15:133-143.

GRANT, C. V., B. B. STEELE, and R. L. BAYN. 1991. Raptor population dynamics in Utah's Uinta Basin: the importance of food resource. Southwest. Nat. 36:265-280.

GRIER, J. W., and R. W. FYFE. 1987. Preventing research and management disturbance. Natl. Wildl. Fed. Sci. Tech. Ser. 10:173-182.

HAGAR, D. C., Jr. 1957. Nesting populations of red-tailed hawks and horned owls in central New York state. Wilson Bull. 69:263-272.

HAMERSTROM, F. 1969. A harrier population study. Pages 367-383 in J. J. Hickey, ed. Peregrine falcon populations: their biology and decline. Univ. Wisc. Press, Madison, Wisconsin.

---. 1979. Effect of prey on predator: voles and harriers. Auk 96:370-374.

---, and M. KOPENY. 1981. Harrier nest-site vegetation. Raptor Res. 15:86-88.

HAMMOND, M. C. 1969. Notes on conducting waterfowl breeding population surveys in the north central states. Can. Wildl. Serv. Rep. Ser. 6:238-254.

---, and C. J. HENRY. 1949. Success of marsh hawk nests in North Dakota. Auk 66:271-274.

HENNESSEY, S. P. 1978. Ecological relationships of Accipiter in northern Utah with special emphasis on the effects of human disturbance. M.S. Thesis, Utah State Univ., Logan. 66pp.

HENNY, C. J. 1972. An analysis of the population dynamics of selected avian species with special reference to changes during the modern pesticide era. U.S. Bur. Sport Fish Wildl. Wildl. Res. Rep. 1. 99pp.

---, and H. M. WIGHT. 1972. Population ecology and environmental pollution: red-tailed and Cooper's hawks. U.S. Bur. Sport Fish Wildl. Wildl. Res. Rep. 2:229-250.

---, L. J. BLUS, and T. E. KAISER. 1984. Heptachlor seed treatment contaminates hawks, owls and eagles of Columbia Basin, Oregon. Raptor Res. 18:41-48.

HICKEY, J. J., ed. 1969. Peregrine falcon populations. Univ. Wisconsin Press, Madison. 596pp.

HIGGINS, K. F., L. M. KIRSCH, H. F. DUEBBERT, A. T. KLETT, J. T. LOKEMOEN, H. W. MILLER, and A. D. KRUSE. 1977. Construction and operation of a cable-chain for nest searches. U.S. Fish Wildl. Serv., Wildl. Leafl. 512. 14pp.

---, L. M. KIRSCH, A. T. KLETT, and H. W. MILLER. 1992. Waterfowl production on the Woodworth Station in south-central North Dakota, 1965-81. U.S. Fish Wildl. Serv. Resour. Publ. 180. 79pp.

HOUSTON, C. S. 1975. Close proximity of red-tailed hawk and great horned owl nests. Auk 92:612-614.

---. 1987. Nearly synchronous cycles of the great horned owl and snowshoe hare in Saskatchewan. U.S. For. Serv. Gen. Tech. Rep. RM-142:56-58.

JANES, S. W. 1984a. Fidelity to breeding territory in a population of red-tailed hawks. Condor 86:200-203.

---. 1984b. Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. Ecology 65:862-870.

---. 1985. Habitat selection in raptorial birds. Pages 159-188 in M. L. Cody, ed. Habitat selection in birds. Academic Press, Orlando, Fla.

JASIKOFF, T. M. 1982. Habitat suitability index models: ferruginous hawk. U.S. Fish Wildl. Serv. Biol. Rep. FWS/OBS-82/10.10. 18pp.

JENSEN, R. E. 1972. Climate of North Dakota. Natl. Weather Serv., North Dakota State Univ., Fargo. 48pp.

JOHNSGARD, P. A. 1988. North American owls: biology and natural history. Smithsonian Inst. Press, Washington,D.C. 295pp.

JOHNSON, J. L., J. F. FRANKLIN, and R. G. KREBILL. 1984. Research natural areas: baseline monitoring and management. U.S. For. Serv. Gen. Tech. Rep. INT-173. 84pp.

JOHNSON, S. J. 1975. Productivity of the red-tailed hawk in southwestern Montana. Auk 92:732-736.

JONES, J. K., Jr., D. M. ARMSTRONG, R. S. HOFFMAN, and C. JONES. 1983. Mammals of the Northern Great Plains. Univ. Nebraska Press, Lincoln, Nebraska. 379pp.

KANTRUD, H. A., and K. F. HIGGINS. 1992. Nest and nest site characteristics of some ground-nesting, non-passerine birds of northern grasslands. Prairie Nat. 24:67-84.

---., G. L. KRAPU, and G. A. SWANSON. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85:111pp.

KENNEDY, P. L. 1980. Raptor baseline studies in energy development. Wildl. Soc. Bull. 8:129-135.

KIRKLEY, J. S., and M. A. SPRINGER. 1980. Nesting populations of red-tailed hawks and great horned owls in central Ohio. Raptor Res. 14:22-28.

KIRSCH, L. M., H. F. DUEBBERT, and A. D. KRUSE. 1978. Grazing and haying effects on habitats of upland nesting birds. Trans. North Am. Wildl. Conf. 43:486-497.

KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, and K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the Prairie Pothole Region. U.S. Fish Wildl. Serv. Resour. Publ. 158. 24pp.

KOCHERT, M. N. 1986. Raptors. Pages 323-349 in A. Y. Cooperrider, R. J. Boyd and H. R. Stuart, eds. Inventory and monitoring of wildlife habitat. U.S. Bur. Land Manage., Denver, Colo.

KRAENZEL, C. F. 1966. The Great Plains in transition. Univ. Oklahoma Press, Norman. 428pp.

KRUSE, A. D., and J. L. PIEHL. 1986. The impact of prescribed burning on ground-nesting birds. Proc. N. Am. Prairie Conf. 9:153-156.

LOKEMOEN, J. T., and H. F. DUEBBERT. 1976. Ferruginous hawk nesting ecology and raptor populations in northern South Dakota. Condor 78:464-470.

LUTTICH, S., D. H. RUSCH, E. C. MESLOW, and L. B. KEITH. 1970. Ecology of red-tailed hawk predation in Alberta. Ecology 51:190-203.

---, L. B. KEITH, and J. D. STEPHENSON. 1971. Population dynamics of the red-tailed hawk (Buteo jamaicensis) at Rochester, Alberta. Auk 88:75-87.

MARKS, J. S. 1986. Nest-site characteristics and reproductive success of long-eared owls in southwestern Idaho. Wilson Bull. 98:547-560.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255-261.

---. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456-466.

MCGOVERN, M., and J. M. MCNURNEY. 1986. Densities of red-tailed hawk nests in aspen stands in the Piceance Basin, Colorado. Raptor Res. 20:43-45.

MCINVAILLE, W. B., Jr., and L. B. KEITH. 1974. Predator-prey relations and breeding biology of the great horned owl and red-tailed hawk in central Alberta. Can. Field-Nat. 88:1-20.

MIKKOLA, H. 1983. Owls of Europe. Buteo Books, Vermillion, S. Dakota. 397pp.

MORITSCH, M. Q. 1983. Photographic guide for aging nestling red-tailed hawks. U.S. Bur. Land Manage., Snake River Birds Prey Proj., Boise, Idaho. 21pp.

MURPHY, R. K. 1990. Vertebrate fauna of Lostwood National Wildlife Refuge: an annotated checklist. U.S. Fish Wildl. Serv., refuge leaflet publ.

---, and M. T. GREEN. 1992. Migrant peregrine falcons in northwestern North Dakota in spring. J. Raptor Res. 26:101-102.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota. 399pp.

ODUM, E. P. 1971. Fundamentals of ecology. W.B. Saunders Co., Philadelphia, Pa. 574pp.

OLENDORFF, R. R. 1975. Population status of large raptors in northeastern Colorado - 1970-1972. Raptor Res. Rep. 3:185-205.

ORDE, C. J., and B. E. HARRELL. 1977. Hunting techniques and predatory efficiency of nesting red-tailed hawks. Raptor Res. 11:82-85.

ORIANS, G., and F. KUHLMAN. 1956. Red-tailed hawk and horned owl populations in Wisconsin. Condor 58:371-385.

PALMER, R. S., ed. 1988. Handbook of North American birds, Vol. 4 and 5. Yale Univ. Press, New Haven, Conn. 433 and 465pp.

PETERSEN, L. 1979. Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. 111. 63pp.

PETERSEN, L. R., and D. R. THOMPSON. 1977. Aging nestling raptors by 4th primary measurement. J. Wildl. Manage. 41:587-590.

PETERSON, D. J., and R. K. MURPHY. 1992. Prey delivered to two

Cooper's hawk, Accipiter cooperii, nests in northern mixed grass prairie. Can. Field-Nat. 106:In Press.

PHILLIPS, R. L., and A. E. BESKE. 1990. Distribution and abundance of golden eagles and other raptors in Campbell and Converse counties, Wyoming. U.S. Fish Wildl. Serv. Fish Wildl. Tech. Rep. 27. 31pp.

---, A. H. WHEELER, J. M. LOCKHART, T. P. MCENEANEY, and N. C. FORRESTER. 1990. Nesting ecology of golden eagles and other raptors in southeastern Montana and northern Wyoming. Fish Wildl. Tech. Rep. 26. 13pp.

PIEHL, J. L. 1983. The cottonwood goose. North Dakota Outdoors 45(11):1.

POSTOVIT, H. R. 1979. Population estimates of breeding raptors in the North Dakota badlands. M.S. Thesis, North Dakota State Univ., Fargo. 50pp.

---, and B. C. POSTOVIT. 1989. Mining and energy development. Natl. Wildl. Fed. Sci. Tech. Ser. 12:167-172.

POSTUPALSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Raptor Res. Rep. 2:21-31.

RESTANI, M. 1991. Resource partitioning among three Buteo species in the Centennial Valley, Montana. Condor 93:1007-1010.

REYNOLDS, R. T., and H. M. WIGHT. 1978. Distribution, density, and productivity of accipiter hawks breeding in Oregon. Wilson Bull. 90:182-196.

ROBEL, R. J., J. N. BRIGGS, A. D. DAYTON, and L. C. HULBERT. 1970. Relationship between visual obstruction measurements and weight of grassland vegetation. J. Range Manage. 23:295-297.

ROSENFIELD, R. N., and R. K. ANDERSON. 1983. Status of the Cooper's hawk. Wis. Dep. Nat. Resour., Endangered and Threatened Species Invest. Study No. 208. 20pp.

---, J. BIELEFELDT, R. K. ANDERSON, and J. M. PAPP. 1991. Accipiters. Natl. Wildl. Fed. Sci. Tech. Ser. 15:42-49.

RUDOLPH, S. G. 1978. Predation ecology of coexisting great horned and barn owls. Wilson Bull. 90:134-137.

RUSCH, D. H. 1983. Great horned owl. Pages 87-88 in Davis, ed. CRC handbook of census methods for terrestrial vertebrates. CRC Press, Boca Raton, Fla.

---, E. C. MESLOW, P. D. DOERR, and L. B. KEITH. 1972. Response of great horned owl populations to changing prey densities. J. Wildl. Manage. 36:282-296.

RYAN, M. R. 1986. Nongame management in grassland and agricultural ecosystems. Pages 117-139 in J. B. Hale, L. B. Best and R. L. Clawson, eds. Non-game management in the Midwest: a developing art. Northcent. Sec., The Wildl. Soc., Grand Rapids, Mich.

---. 1990. A dynamic approach to the consevation of the prairie ecosystem in the Midwest. Pages 91-106 in J. M. Sweeney, ed. Management of dynamic ecosystems. North Cent. Sect., The Wildl.

Soc., West Lafayette, Ind.

SANTANA C., E., E. N. LABOY, J. A. MOSHER, and S. A. TEMPLE. 1986. Red-tailed hawk nest sites in Puerto Rico. Wilson Bull. 98:561-570.

SARGEANT, A. B., R. J. GREENWOOD, M. A. SOVADA, and T. L. SHAFFER. 1993. Distribution and abundance of predators that affect duck production - Prairie Pothole Region. U.S. Fish Wildl. Serv. Resour. Publ. 194. In Press.

SAS INSTITUTE, I. 1989. SAS/STAT user's guide, version 6, 4th ed., Vol. 2. SAS Institute, Inc., Cary, NC. 846pp.

SCHEAFFER, R. L., W. MENDENHALL, and L. OTT. 1990. Elementary survey sampling. PWS-KENT, Boston, Mass. 390pp.

SCHMUTZ, J. K. 1977. Relationship between three species of the genus Buteo (Aves) coexisting in the prairie-parkland ecotone of southeastern Alberta. M.S. Thesis, Univ. Alberta, Edmonton. 126pp.

---. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. J. Wildl. Manage. 48:1180-1187.

---. 1987. The effect of agriculture on ferruginous and Swainson's hawks. J. Range Manage. 40:438-440.

---. 1989. Hawk occupancy of disturbed grasslands in relation to models of habitat selection. Condor 91:362-371.

---, and D. J. HUNGLE. 1989. Populations of ferruginous and Swainson's hawks increase in synchrony with ground squirrels. Can. J. Zool. 67:2596-2601.

---, S. M. SCHMUTZ, and D. A. BOAG. 1980. Coexistence of three species of hawks (Buteo spp.) in the prairie-parkland ecotone. Can. J. Zool. 58:1075-1079.

---, W. D. WISHART, J. ALLEN, R. BJORGE, and D. A. MOORE. 1988. Dual use of nest platforms by hawks and Canada geese. Wildl. Soc. Bull. 16:141-145.

SEALY, S. G. 1967. Notes on the breeding biology of the marsh hawk in Alberta and Saskatchewan. Blue Jay 25:63-69.

SEIDENSTICKER, J. C., IV, and H. V. REYNOLDS III. 1971. The nesting, reproductive performance, and chlorinated hydrocarbon residues in the red-tailed hawk and great horned owl in south-central Montana. Wilson Bull. 83:408-418.

SIMMONS, R., P. BARNARD, B. MACWHIRTER, and G. L. HANSEN. 1986. The influence of microtines on polygyny, productivity, age, and provisioning of breeding northern harriers: a 5-year study. Can. J. Zool. 64:2447-2456.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. W.H. Freeman Co., New York, NY. 859pp.

SPRINGER, M. A., and J. S. KIRKLEY. 1978. Inter and intraspecific interactions between red-tailed hawks and great horned owls in central Ohio. Ohio J. Sci. 78:323-328.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Natl. Wildl. Fed. Sci. Tech. Ser. 10:157-170.

STEWART, R. E. 1975. Breeding birds of North Dakota. Tri-college Center for Environmental Studies, Fargo, North Dakota. 295pp.

---, and H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Dep. Inter. Bur. Sport Fish. Wildl. Res. Publ. 92. 57pp.

---, and ---. 1972. Population estimates of breeding birds in North Dakota. Auk 89:766-788.

SUTHERLAND, J. E. 1987. The predation ecology of the northern harrier (_Circus_ _cyaneus_ _hudsonius_) on Mallard Island, North Dakota. M.S. Thesis, Univ. North Dakota, Grand Forks. 164pp.

THUROW, T. L., and C. M. WHITE. 1984. Nesting success and prey selection of long-eared owls along a juniper/sagebrush ecotone in southcentral Idaho. Murrelet 65:10-14.

TOLAND, B. R. 1986. Nesting ecology of northern harriers in southwest Missouri. Trans. Mo. Acad. Sci. 20:49-57.

---. 1990. Nesting ecology of red-tailed hawks in central missouri. Trans. Mo. Acad. Sci. 24:1-16.

U.S. BUREAU OF LAND MANAGEMENT. 1979. Snake River Birds of Prey Special Research Report. U.S. Bureau of Land Management, Boise, Idaho. 142pp.

U.S. FISH AND WILDLIFE SERVICE. 1987. Migratory nongame birds of management concern in the United States: the 1987 list. U.S. Fish Wildl. Serv. Off. Migr. Bird Manage., Washington, D.C. 27pp.

---. 1990. Conservation of avian diversity in North America. U.S. Fish Wildl. Serv. Off. Migr. Bird Manage. 22pp.

---. 1991. Endangered and threatened wildlife and plants. Code Fed. Reg. Title 50, part 17.11.

VILLAGE, A. 1981. The diet and breeding of long-eared owls in relation to vole numbers. Bird Study 28:215-224.

VOGT, R. C., and R. L. HINES. 1982. Evaluation of techniques for assessment of amphibian and reptile populations in Wisconsin. Pages 201-217 _in_ N. J. Scott, ed. Herpetological communities: a symposium of the society for the study of amphibians and reptiles and Herpetologist's League. U.S. Fish Wildl. Serv. Res. Rep. 13.

WAKELEY, J. S. 1978. Factors affecting the use of hunting sites by ferruginous hawks. Condor 80:316-326.

WIENS, J. A. 1984. The place of long-term studies in ornithology. Auk 101:202-203.

WOFFINDEN, N. D., and J. R. MURPHY. 1989. Decline of a ferruginous hawk population: a 20-year summary. J. Wildl. Manage. 53:1127-1132.

PART III

NESTING BIOLOGY OF RAPTORS ON MIXED LAND USE IN NORTHWESTERN NORTH DAKOTA

INTRODUCTION

Although North Dakota has a relatively diverse avifauna (Stewart 1975), study of breeding birds has been unevenly distributed over the state and mostly devoted to waterfowl (Anseriformes). Other than records in Stewart and Kantrud (1972) and Stewart (1975), almost no data on nongame bird distribution and demography are available for northwestern North Dakota to help protect nongame birds from negative land use impacts such as fossil fuel extraction and coal-fired power generation. A recent study reports such data for raptors (Falconiformes and Strigiformes) on Lostwood National Wildlife Refuge (LNWR) in northwestern North Dakota (Part II) but relevancy of findings to areas of more typical land use is only speculative. Raptor abundance and distribution data also are useful to wildlife managers because some raptors potentially influence local production of other migratory birds (Sargeant et al. 1992). Objectives of this study were to determine nesting density and reproductive success of raptors on a township area with an array of habitat and land use attributes characteristic of the Missouri Coteau landform in Burke County, northwestern North Dakota.

STUDY AREA

I studied breeding raptors except northern harriers (Circus cyaneus) on Lucy Township (93 km^2) in Burke County (48°40′N;102°35′W) during 1986-87. Land use was a mix of dryland grain farming and cattle ranching. Habitat composition was 41% native (Stipa-Agropyron) prairie (about half grazed heavily by domestic livestock and half grazed lightly or idle) with scattered tall shrubs such as hawthorn (Crateagus chrysocarpa) and chokecherry (Prunus virginiana); 31% cropland, a third of which annually was fallow; 19% seasonal, semipermanent, and permanent wetlands (classification according to Stewart and Kantrud [1971]); 5%

tame hay; 2% small (<1 ha), scattered clumps of quaking aspen (Populus tremuloides) trees (mean = 4.7 clumps/km^2, SD = 3.4); and 2% roads, farmsteads, and shelterbelts. The area was sparsely inhabited by humans (1 farmstead/8 km^2). Lucy Township lies within the Missouri Coteau glacial moraine which is characterized by rolling to hilly, knob-and-kettle topography (Bluemle 1977). Climate is semi-arid with cold winters and warm summers. Annual precipitation was 46 cm in 1986 and 31 cm in 1987 compared to 42 cm average.

Vertebrate wildlife that were common and potentially important to nesting raptors as prey included grebes (Podicipediformes), ducks (Anserinae), sharp-tailed grouse (Tympanuchus phasianellus), gray partridge (Perdix perdix), rails and coot (Rallidae), Passeriforms especially sparrows (Emberizinae) and blackbirds (Icterinae), meadow vole (Microtus pennsylvanicus), deer mouse (Peromyscus maniculatus), ground squirrels (Spermophilus spp.), tiger salamander (Ambystoma tigrinum) and leopard frog (Rana pipiens). White-tailed jackrabbits (Lepus townsendii) were widespread but scarce.

Raptors that nested were migratory except great horned owls (Bubo virginianus) occurred year-round and likely were sedentary as elsewhere in North America (Johnsgard 1988).

METHODS

I systematically censused hooting great horned owls in March (Rusch 1983) and then searched all potential raptor nesting habitat on foot on 80.3 km^2 (access was denied on the remainder of the township) in early April and again in late May-early June. Nest locations were plotted on USGS topographic maps (1:24,000). I am confident all raptor nests were found. I took precautions to minimize disturbance to nesting raptors during searches (Fyfe and Olendorff 1976) and observed nests from >300-400 m away during potentially sensitive courtship and incubation stages of nesting. After I presumed eggs had hatched, I visited nests to assess their fate and count young.

Standardized raptor breeding terminology (Postupalsky 1974) was used. An occupied nest was a nest at which any of the following were observed: (1) an adult in an incubating position, (2) eggs, (3) young, (4) occurrence of a raptor pair at least through the time when incubation normally occurred, or (5) occurrence of a newly constructed or refurbished stick nest within 0.2 km of where territorial behavior by a raptor pair had been observed in spring. A meaningful indicator of raptor productivity is the average number of large young produced per occupied nest (Postupalsky 1974). I considered an occupied nest successful if it produced at least 1 large (>3 weeks old) nestling and unsuccessful or failed if it did not. Nest success was the proportion of occupied nests that was successful. The term reproductive success encompassed nest success and productivity. Nesting density was based on occupied nests found on 80.3 km^2 searched; I ignored raptor nests on remaining parts of the study area where access was denied. Although I did not attempt to determine clutch size or whether eggs were laid, any raptor pair that occupied a nest was referred to as nesting.

RESULTS AND DISCUSSION

Red-tailed hawks (Buteo jamaicensis), great horned owls, and Swainson's hawks (B. swainsoni) were most common nesting raptors on Lucy Township in 1986-87 (Table III-1). Uncommon nesting raptors were Cooper's hawks (Accipiter cooperii), American kestrels (Falco sparverius), and long-eared owls (Asio otus), species having almost no previous nest records in northwestern North Dakota north and west of the Missouri and Des Lacs Rivers (Stewart 1975). Northern harriers appeared more abundant than any other species of raptor but were not censused. No ferruginous hawks (B. regalis) nested on Lucy Township although there was an occupied nest 0.5 km south of the township both years. All raptor nests were in quaking aspen, except American kestrels used a nest cavity in a large eastern cottonwood (P. deltoides).

Table III-1. Composition and density (occupied nests/km^2) of nesting raptors[a] on Lucy Township, 1986-87.

Species	1986	1987	Mean, 1986-87
Red-tailed hawk	0.149	0.162	0.156
Swainsons' hawk	0.075	0.075	0.075
Coopers' hawk	0.012	0.012	0.012
American kestrel	0	0.012	0.006
Great horned owl	0.112	0.112	0.112
Long-eared owl	0.012	0	0.006
Total	0.360	0.373	0.367

[a] Excludes northern harrier.

Nesting Density and Distribution

Red-tailed hawk and great horned owl nesting density averaged 0.16 and 0.11 occupied nests/km^2 (Table III-1), higher than 0.01-0.05 previously reported for these species elsewhere in North Dakota (Postovit 1979, Gaines and Kohn 1982, Gilmer et al. 1983, Sargeant et al. 1992) except nesting red-tailed hawks were half again as common on nearby LNWR (Part II). Nesting densities of red-tailed hawks and great horned owls were relatively high on Lucy Township mainly because of well-dispersed aspen tree clumps that provided elevated hunting perches and nest site substrates on which these raptors depend (Petersen 1979, Janes 1984, 1985). Averages of 3-5 aspen tree clumps/km^2 characterize the Missouri Coteau of Burke County as aspen parkland; aforementioned areas of North Dakota reporting densities of red-tailed hawks and great horned owls had fewer trees.

Average Swainson's hawk nesting density of 0.08 occupied nests/km^2 (Table III-1) was higher than 0.05 reported for the Missouri Coteau in southcentral North Dakota (Gilmer and Stewart 1984) but lower than an average of about 0.11 from 6 21- to 23-km^2 study areas in eastern North Dakota (from Appendix 15 in Sargeant et al. 1992). Most heavily treed parts of Lucy Township that had up to 1 red-tailed hawk nest/km^2 were void of Swainson's hawks, as Schmutz (1980) noted in southeastern Alberta; interspecific competition may have partly influenced this distribution pattern (Janes 1985). Conversely, Swainson's hawks were absent from an intensively cultivated, 10-km^2 area of the township where no other raptors nested except a pair of American kestrels.

Reproductive Success

Red-tailed hawks exhibited high average annual nest success and productivity (Table III-2). Mean productivity of 1.4 young/occupied nest compared favorably with estimated minimums of 1.3-1.4 required for population stability (Henny and Wight 1972) and was close to 1.5 reported by Gilmer et al. (1983) for 3 years in southcentral North Dakota. Average red-tailed hawk productivity during 1986-87 on Lucy Township may have exceeded long-term trends, however; productivity of the hawk on nearby LNWR was similar (1.2) to Lucy Township in 1986 and was not monitored but suspected to be high in 1987, but averaged 0.9 young/occupied nest for 7 years studied (Part II).

Nest success and productivity of Lucy Township great horned owls were 56% and 1.1 young/occupied nest during 1986-87 (Table III-2), lower than averages of 84% and 1.6 reported for the owl during 3 years in southcentral North Dakota (Gilmer et al. 1983) though similar to data from nearby states (Seidensticker and Reynolds 1971, Petersen 1979). Great horned owl productivity on Lucy Township was <1.5 estimated by Henny (1972) to be required for population stability. Great horned owl nest success and productivity were low in 1986 and high in 1987, a contrast closely paralleled by great horned owls on LNWR in 1986-87 (31% and 0.5 young/occupied nest in 1986, 77% and 1.5 in 1987 [Part II]).

Table III-2. Nest success[a] and productivity (average number of large young per occupied nest) of common nesting raptors on Lucy Township, 1986-87.

	1986			1987			Mean, 1986-87[c]	
Species	*n*[b]	% nest success[a]	Young/ nest	*n*	% nest success	Young/ nest	% nest success	Young/ nest
Red-tailed hawk	12	75.0	1.17[d]	12	92.3	1.69	83.7	1.43
Swainson's hawk	6	(1)	0.33	6	(4)	0.67	41.7	0.50
Great horned owl	9	(3)	0.56	9	(7)	1.67	55.5	1.11

[a] Percentage nest success reported only where *n* occupied nests >9, otherwise number of successful nests presented parenthetically.

[b] Number of occupied nests.

[c] Means for Swainson's hawk and great horned owl based on pooled count totals from 1986-87 because <10 occupied nests were observed annually.

[d] Includes counts of minimum number of young at 3 successful nests.

Similarity of red-tailed hawk and great horned owl reproductive success between Lucy Township and LNWR in 1986-87 suggests that factors influencing annual reproductive success of these raptors are uniform locally regardless of land use. Weather extremes affected 1 or both raptors and overwinter abundance of meadow voles (*Microtus pennsylvanicus*) was believed to most significantly affect great horned owl reproductive success on LNWR (Part II).

Swainson's hawk nest success and productivity were 42% and 0.5 (Table III-2) which were very low compared to 60-68% and 1.1-1.6 reported for nearby LNWR (Part II), southcentral North Dakota (Gilmer and Stewart 1984), and other northern Great Plains states (Olendorff 1975, Dunkle 1977). Swainson's hawk reproductive success on Lucy Township in 1986-87 probably underrepresented the long-term average. In both years decreases in brood sizes coincided with unusually cool, wet weather (daily minimum temperatures of 6-15°C; daily rains of up to 1-3 cm) during early to mid-July when Swainson's hawk young were 1-3 weeks old. Brood reduction during similar weather occurred in Swainson's hawks in Washington (Bechard 1983).

The single American kestrel nest fledged 4 young and the long-eared owl nest was unsuccessful. Success of single nests occupied by Cooper's hawks in 1986 and 1987 was undetermined in 1986 and 3 large young were produced in 1987.

CONCLUSIONS

This study indicated nesting red-tailed hawks and great horned owls are more common on the Missouri Coteau of northwestern North Dakota than implied by Stewart (1975) and in comparison to other rural parts of the state. This mainly was because aspen tree clumps were dispersed on my study area as well as on much of the northwestern Coteau, and trees were less prevalent in areas surveyed by other authors. Nesting Swainson's hawks were about equally abundant on Lucy Township as in other studies even though they avoided heavily treed areas with high local densities of red-tailed hawks and great horned owls and an intensively cultivated area. Reproductive success of major raptors likely reflected conditions encountered during 2 years of the study rather than long-term trends, which emphasizes need for longer periods of study.

LITERATURE CITED

BECHARD, M. J. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. Wilson Bull. 95:233-242.

BLUEMLE, J. P. 1977. The face of North Dakota: the geologic story. North Dakota Geol. Surv. Educ. Ser. 11. 73pp.

DUNKLE, S. W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. Auk 94:65-71.

FYFE, R. W., and R. R. OLENDORFF. 1976. Minimizing the dangers of nesting studies to raptors and other sensitive species. Can. Wildl. Serv. Occas. Pap. 23. 16pp.

GAINES, R. C., and S. C. KOHN. 1982. Raptor use of hardwood draws in central North Dakota. Prairie Nat. 14:55-58.

GILMER, D. S., and R. E. STEWART. 1984. Swainson's hawk nesting ecology in North Dakota. Condor 86:12-18.

---, P. M. KONRAD, and R. E. STEWART. 1983. Nesting ecology of red-tailed hawks and great horned owls in central North Dakota and interactions with other large raptors. Prairie Nat. 15:133-143.

HENNY, C. J. 1972. An analysis of the population dynamics of selected avian species with special reference to changes during the modern pesticide era. U.S. Bur. Sport Fish Wildl. Wildl. Res. Rep. 1. 99pp.

---, and H. M. WIGHT. 1972. Population ecology and environmental pollution: red-tailed and Cooper's hawks. U.S. Bur. Sport Fish Wildl. Wildl. Res. Rep. 2:229-250.

JANES, S. W. 1984. Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. Ecology 65:862-870.

---. 1985. Habitat selection in raptorial birds. Pages 159-188 _in_ M. L. Cody, ed. Habitat selection in birds. Academic Press, Orlando, Fla.

JOHNSGARD, P. A. 1988. North American owls: biology and natural history. Smithsonian Inst. Press, Washington, D.C. 295pp.

OLENDORFF, R. R. 1975. Population status of large raptors in northeastern Colorado - 1970-1972. Raptor Res. Rep. 3:185-205.

PETERSEN, L. 1979. Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. 111. 63pp.

POSTOVIT, H. R. 1979. Population estimates of breeding raptors in the North Dakota badlands. M.S. Thesis, North Dakota State Univ., Fargo. 50pp.

POSTUPALSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Raptor Res. Rep. 2:21-31.

RUSCH, D. H. 1983. Great horned owl. Pages 87-88 _in_ D. E. Davis, ed. CRC handbook of census methods for terrestrial vertebrates. CRC Press, Boca Raton, Fla.

SARGEANT, A. B., R. J. GREENWOOD, M. A. SOVADA, and T. L. SHAFFER. 1993. Distribution and abundance of predators that affect duck production - Prairie Pothole Region. U.S. Fish Wildl. Serv. Resour. Publ. 194. In Press.

SCHMUTZ, J. K., S. M. SCHMUTZ, and D. A. BOAG. 1980. Coexistence of three species of hawks (_Buteo_ spp.) in the prairie-parkland ecotone. Can. J. Zool. 58:1075-1079.

SEIDENSTICKER, J. C., IV, and H. V. REYNOLDS III. 1971. The nesting, reproductive performance, and chlorinated hydrocarbon residues in the red-tailed hawk and great horned owl in south-central Montana. Wilson Bull. 83:408-418.

STEWART, R. E. 1975. Breeding birds of North Dakota. Tri-college Center for Environmental Studies, Fargo, North Dakota. 295pp.

---, and H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Dep. Inter. Bur. Sport Fish. Wildl. Res. Publ. 92. 57pp.

---. 1972. Population estimates of breeding birds in North Dakota. Auk 89:766-788.

PART IV

PREY OF NESTING RED-TAILED HAWKS AND GREAT HORNED OWLS ON LOSTWOOD NATIONAL WILDLIFE REFUGE, NORTH DAKOTA

INTRODUCTION

Red-tailed hawks (*Buteo jamaicensis*) recently invaded and great horned owls (*Bubo virginianus*) have increased on Lostwood National Wildlife Refuge (LNWR) in northwestern North Dakota due to succession from mixed grass prairie to aspen parkland (Part I). Information on diets of these raptors is needed by resource managers to assess the species' needs and relations with other fauna; such data are available from few areas in the northern Great Plains (e.g., Gilmer et al. 1983). This paper summarizes composition of prey of red-tailed hawks and great horned owls observed at nests on LNWR during a long-term study of raptor nesting ecology (Part II).

STUDY AREA AND METHODS

LNWR encompasses 108 km^2 in Burke and Mountrail counties, North Dakota (48°37'N;102°27'W). It is rolling to hilly (elev. 685-747 m), semi-arid grassland interspersed with numerous (*n* = 4,200) temporary to permanent wetland basins and clumps of quaking aspen (*Populus tremuloides*) trees (*n* = 518; size range 0.05-3 ha, mean 0.3 ha). Physiography, geology, soils, habitat composition, climate, and history of LNWR are detailed in Part I.

Vertebrate wildlife that were common potential prey included grebes (Podicipediformes), ducks (Anserinae), sharp-tailed grouse (*Tympanuchus phasianellus*), American coot (*Fulica americana*) and other rails (Rallidae), Passeriforms especially sparrows (Emberizinae) and blackbirds (Icterinae), meadow vole (*Microtus pennsylvanicus*), deer mouse (*Peromyscus maniculatus*), jumping mouse (*Zapus* spp.), ground squirrels (*Spermophilus* spp.), and tiger salamander (*Ambystoma tigrinum*) (Murphy 1990). White-tailed jackrabbits (*Lepus townsendii*) were widespread and scarce and other Leporids (snowshoe hare [*L. americanus*] and eastern cottontail [Sylvilagus floridanus]) were rare and narrowly distributed.

I observed fresh prey items (i.e., prey still edible by nesting raptors) during climbs (1-2/nest/nesting season) to assess productivity at great horned owl nests during late April-early May and at red-tailed hawk nests during late June-early July (Part II), similar to Gilmer et al. (1983). Prey were identified and left in nests. Data were pooled from all years for both raptor species and were summarized by relative (percentage) frequency by dividing the number of individuals in each prey category by the total number of prey items observed.

RESULTS AND DISCUSSION

Forty-nine fresh prey were observed during about 200 climbs to red-tailed hawk nests and 53 fresh prey were observed during 78 climbs to great horned owl nests during 1983-90. I acknowledge that small prey were more likely to be overlooked than large prey by my methods but assume effect of the bias was low. Birds were important prey of red-tailed hawks and especially of great horned owls on LNWR (Table IV-1). Mammals generally comprise most red-tailed hawk prey during summer in other parts of the northern Great Plains (Schmutz et al. 1980, Gilmer et al. 1983) and elsewhere (reviewed in Palmer 1988). Nesting great horned owls also generally rely on mammals (Snyder and Wiley 1976). In southcentral North Dakota, however, birds were dominant prey of great horned owls (Gilmer et al. 1983), and both great horned owls and red-tailed hawks used northern pocket gophers (Thomomys talpoides) and cottontails, species absent and scarce (respectively) on LNWR. Rodents and Leporids generally make up most prey of great horned owls in other northcentral states and in adjacent provinces (Errington et al. 1940, Petersen 1979, Houston 1987).

Table IV-1. Prey of red-tailed hawks during summer and of great horned owls during spring on Lostwood National Wildlife Refuge, based on observation of fresh prey at nests during 1983-90.

	Red-tailed hawk		Great horned owl	
Prey[a]	n	% frequency	n	% frequency
Mammals				
Richardson's and thirteen-lined ground squirrels (S. richardsonii, S. tridecemlineatus)	10	20.4	0	--
Meadow vole and jumping mouse	4	8.2	6	11.3
White-tailed jackrabbit (juvenile)	1	2.0	5	9.4
Least weasel (Mustela nivalis)	1	2.0	0	--
Total mammals	16	32.7	11	20.8
Birds				
Horned or Eared grebe (Podiceps auritus, P. nigricollis)	0	--	3	5.7
American coot	2[b]	4.1	12	22.6
Sora and Virginia rail (Porzana carolina, Rallus limicola)	0	--	2	3.8
Duck[c]	18[d]	36.7	14	26.4
Sharp-tailed grouse	5[e]	10.2	5	9.4
Blackbird[f]	1	2.0	6	11.3
Unknown small Passeriforms (juveniles)	5	10.2	0	--
Total birds	31	63.3	42	79.2
Other prey				
Smooth green snake (Opheodrys vernalis)	1	2.0	0	--
Band-winged grasshopper (Oedipodinae)	1	2.0	0	--
Total	49	100.0	53	100.0

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[a] Prey were adult size unless otherwise indicated.

[b] Both coot prey were juveniles.

[c] Adult duck prey included mallard (Anas platyrhynchos), northern pintail (A. acuta), blue-winged teal (A. discors), northern shoveler (A. clypeata), gadwall (A. strepera), American wigeon (A. americana), and lesser scaup (Aythya affinis).

[d] Duck prey of red-tailed hawk included 9 juveniles.

[e] Grouse prey of red-tailed hawk included 3 juveniles.

Table IV-1. Continued.

[f] Blackbird prey of red-tailed hawk was red-winged blackbird (Agelaius phoeniceus). Blackbird prey of great horned owl included yellow-headed blackbird (Xanthocephalus xanthocephalus), common grackle (Quiscalus quiscula), and brown-headed cowbird (Molothrus aeneus).

About 43% of red-tailed hawk prey and 64% of great horned owl prey were species directly associated with wetlands (e.g., American coot, ducks, red-winged blackbird, and yellow-headed blackbird) even though this habitat comprised 20% of LNWR. Use of wetland prey by both raptors was greater than expected from wetland availability (chi-square goodness-of-fit test; $X^2 = 14.6$ [hawk] and 61.8 [owl], df = 1, both $P < 0.001$). Thus, prey groups most important were birds from wetlands (Table IV-1) especially Rallids for great horned owls and ducks for both raptors. Half of duck prey of red-tailed hawks were ducklings (all Anas spp.), all but 1 of these <1 week old. Female ducks made up 79% of 14 adult duck prey of great horned owls. I did not estimate prey biomass composition but believe wetland birds contributed most prey biomass used by nesting great horned owls based on frequency of grebes, American coot, and ducks observed. Wetland birds dominated biomass of the owl's diet on nearby private lands of northwestern North Dakota (Part VI).

Another important prey group of red-tailed hawks was ground squirrels (Table IV-1). Most (80%) were Richardson's ground squirrels that may have been captured on grazed prairie adjacent to LNWR. Franklin's ground squirrels (S. franklinii) occurred on LNWR but were not observed as prey of either red-tailed hawks or great horned owls.

Although dietary overlap between sympatric red-tailed hawks and great horned owls has been studied based on prey remains or pellets at nests (e.g., Gilmer et al. 1983), a 6-week disparity in nesting chronology between the species on LNWR rendered such comparisons weak. In summer, nearly half of mammal and bird prey of red-tailed hawks were juveniles whereas small (<300 g) jackrabbits were nearly the only juvenile vertebrate prey available in spring when great horned owl diets were recorded; the owls used this prey (Table IV-1). Great horned owls would have preyed on different age classes and perhaps species of prey in summer compared to spring as observed on nearby areas of different land use (Part VI).

This cursory survey suggests birds especially those from wetlands are most important prey of nesting red-tailed hawks and great horned owls on LNWR during each raptor's respective nestling period. Great horned owls seemed particularly tied to wetland prey which supports observations of strong affinity for wetland habitats by the owls on LNWR (Part II). Relative composition of red-tailed hawk and great horned owl diets on LNWR were similar to those of conspecifics nesting in southcentral North Dakota (Gilmer et al. 1983) except that red-tailed hawks on LNWR relied more on bird prey, and ducks were more important to both the hawk and owl on LNWR.

LITERATURE CITED

ERRINGTON, P. L., F. HAMERSTROM, and F. N. HAMERSTROM Jr. 1940. The great horned owl and its prey in north-central United States. Iowa Agric. Exp. Stn. Res. Bull. 227:758-850.

GILMER, D. S., P. M. KONRAD, and R. E. STEWART. 1983. Nesting ecology of red-tailed hawks and great horned owls in central North Dakota and their interactions with other large raptors. Prairie Nat. 15:133-143.

HOUSTON, C. S. 1987. Nearly synchronous cycles of the great horned owl and snowshoe hare in Saskatchewan. U.S. For. Serv. Gen. Tech. Rep. RM-142:56-58.

MURPHY, R. K. 1990. Vertebrate fauna of Lostwood National Wildlife Refuge: an annotated checklist. U.S. Fish Wildl. Serv., refuge leaflet publ.

PALMER, R. S., ed. 1988. Handbook of North American birds, Vol. 4 and 5. Yale Univ. Press, New Haven, Conn. 433 and 465pp.

PETERSEN, L. 1979. Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. 111. 63pp.

SCHMUTZ, J. K., S. M. SCHMUTZ, and D. A. BOAG. 1980. Coexistence of three species of hawks (Buteo spp.) in the prairie-parkland ecotone. Can. J. Zool. 58:1075-1079.

SNYDER, N. F. R., and J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20. 96pp.

PART V

SWAINSON’S HAWK SUMMER DIET AND PREDATION ECOLOGY IN RELATION TO HABITAT IN NORTHWESTERN NORTH DAKOTA

INTRODUCTION

Swainson's hawks (Buteo swainsoni) nest mainly throughout the midcontinent prairies and western intermountain grasslands of North America (Palmer 1988). Local abundance of breeding pairs relates to land use especially extent of annually tilled cropland (Gilmer and Stewart 1984, Schmutz 1984, 1987, 1989). Aside from obvious impacts on nest site availability, mechanisms by which land use influences Swainson's hawk abundance remain somewhat speculative. In southeastern Alberta nesting Swainson's hawks were most abundant where 11-30% of land was annually tilled and cropped; reproductive success appeared higher at nests more closely associated with such croplands (Schmutz 1984, 1987). Schmutz (1987) hypothesized that Swainson's hawks shifted from their main prey, Richardson's ground squirrels (Spermophilus richardsonii), to mice and voles (species unspecified) as the landscape changed from grassland to cropland. But, published reports of prey use by Swainson's hawks insufficiently explain variation in diet among nesting pairs. An understanding of such variation could elucidate the hawk's relationship with its habitat and enhance Swainson's hawk conservation.

My initial null hypotheses were that different prey groups (e.g., small mammals, Passeriforms, amphibians) were used by nesting Swainson's hawks in equal proportions, that these proportions did not vary among nesting pairs, and that land use or habitat did not influence hawk diets. Thus, objectives of this study were to quantify composition of prey used by Swainson's hawks nesting on an area of varied land use and habitat in midcontinent North America, assess variation in prey use among pairs, and examine relationships between use of prey and habitat surrounding nest sites.

STUDY AREA

Diets of nesting Swainson's hawks were studied during July to mid-August, 1986 and 1987 on Lucy Township and adjacent lands of similar habitat and land use in Burke County, northwestern North Dakota (93 km^2; 48°40'N;102°35'W). Land use was a mix of dryland grain farming and cattle ranching. Habitat composition on Lucy Township was 41% native (Stipa-Agropyron) prairie (about half grazed heavily by domestic livestock and half grazed lightly or idle) with scattered tall shrubs such as hawthorn (Crataegus spp.) and chokecherry (Prunus virginiana); 31% cropland, a third of which annually was fallow; 19% seasonal, semi-permanent, and permanent wetlands (classification according to Stewart and Kantrud [1971]); 5% tame hay; 2% small (<1 ha), scattered clumps of quaking aspen (Populus tremuloides) trees (mean = 4.7 clumps/km^2, SD = 3.4); and 2% roads, farmsteads, and shelterbelts. The area was sparsely inhabited by humans (1 farmstead/8 km^2).

Lucy Township lies within the Missouri Coteau glacial moraine which is characterized by rolling to hilly topography (Bluemle 1977). Climate is semi-arid with cold winters and warm summers. Annual precipitation was 46 cm in 1986 and 31 cm in 1987 compared to a 42-cm average (precipitation data from adjacent Lostwood National Wildlife Refuge [LNWR], unpubl. refuge files).

Nesting biology of raptors on Lucy Township during 1986-87 was described in Part III. Commonly nesting species of raptors were red-tailed hawk (B. jamaicensis)(0.16 occupied nests/km^2), Swainson's hawk (0.08/km^2), northern harrier (Circus cyaneus)(probably >0.2/km^2), and great horned owl (Bubo virginianus)(0.11/km^2).

METHODS

Each spring I systematically searched 80 km^2 of Lucy Township (access was denied on 13 km^2) for occupied nests of raptors (Part III) and subsequently monitored prey use by all Swainson's hawk pairs that produced large (>3 week old) nestlings. I augmented the sample of hawk diets with like data from all Swainson's hawk nests found on similar land use and habitat within the Missouri Coteau up to 10 km north, south, and east of Lucy Township.

Data Collection and Interpretation

I checked Swainson's hawks nests to count and estimate the age of young after I presumed eggs had hatched. When nestling hawks were about 4 weeks old, I tethered them on platforms that were about 2 m above ground in sheltered sites <9 m from nests (Petersen and Keir 1976). Tether platforms subsequently were visited daily between 1000-2000 hours for about 2-3 weeks after which the fledging-age young were released. At daily visits I identified each fresh (edible) prey item, marked it by cutting off a foot and left it on the platform, and then identified and removed all discarded (inedible) remains. During a visit I avoided duplicating my count of any prey item by conservatively choosing the lowest number of items represented by discarded remains and fresh items, including fresh items noted at the previous visit (Craighead and Craighead 1956, Collopy 1983).

I assessed efficacy of using discarded remains and fresh items to reveal prey delivered by adult Swainson's hawks at 25% of tether platforms. The sample was stratified according to brood size but was not entirely random because I tried to use sites where observation blinds (1 x 2 x 1.5 m) could be partly hidden by shrub. A blind was placed about 20 m from each platform in the sample and then gradually was moved to within ≤4-8 m during several days. At midday about every other day, an observer accompanied me on my routine visit to 1 of these platforms, entered the blind, and remained there until 15 min after sunset. The observer reentered the blind 1 hr before sunrise the following morning and remained there until I revisited the platform at midday. The 2 consecutive, half-days of platform observation composed an observation unit of about 15 hr length for comparing numbers of prey delivered by adult hawks to those revealed by fresh items and discarded remains. I used these observations to correct for biases in determining dietary composition by multiplying numbers of prey based on fresh items and discarded remains by correction factors.

I report overall dietary makeup in terms of relative (percentage) frequency and biomass. Percentage frequency was calculated by dividing the number of individuals in each prey species category by the total number of prey items observed, and percentage biomass was estimated by multiplying the number of individuals of each prey category by their respective mean weight, then dividing the subtotal of each prey category by the grand total prey weight (Marti 1987).

For each prey category that comprised >1% frequency of prey pooled from all hawk tether platforms, I estimated the average biomass (in g) or number of prey killed daily by each Swainson's hawk pair. I referred to these estimated averages as daily kill rates in terms of biomass (DKR-biomass) or numbers (DKR-numbers). DKR-biomass (g/day) was estimated for a given tether platform by multiplying the corrected percentage biomass of each prey category times daily food needs of adults and young combined (Craighead and Craighead 1956:312). I assumed that: (1) composition of prey consumed by adults was the same as that delivered to their tethered young and (2) each adult and young Swainson's hawk required an average of 150 g of prey daily (Craighead and Craighead 1956, Olendorff 1974, Kirkley and Gessaman 1990). The assumption of similar diets was supported by observations from blinds of partially consumed prey delivered by adults. DKR-numbers were estimated by dividing daily biomass intake of each prey category by respective mean prey weights. I assumed that biomass of prey captured by adult Swainson's hawks equalled that consumed by adults and young.

Pellets (castings) regurgitated by tethered young also were collected at each visit to tether platforms. I assessed whether numbers of prey represented by remains in pellets augmented numbers of prey identified from fresh items and discarded remains by analyzing contents of pellets collected from 2-3 consecutive observation units at tether platforms observed from blinds. Based on knowledge of raptor pellet formation (Duke et al. 1975, Yalden and Yalden 1985), I assumed prey consumed during a given set of consecutive units were represented by remains in pellets gathered at the end of each unit and on the following visit. I acknowledge that these collections of pellets possibly included prey consumed before observation began but contend this only made my assessment conservative. Pellets were air-dried and individually dissected. Bones, teeth, and feathers were compared with reference specimens. Hair was identified with keys (Adorjan and Kolenosky 1969, Moore et al. 1974). For small (<50 g) mammals, only 1 prey item of a given species was credited to a pellet unless numbers of bones or teeth indicated otherwise (Fitch et al. 1946).

Prey Weights

Weights assigned the prey were obtained mainly from specimens I collected on the study area (Appendix Table 2), and from literature (Dane 1965, Oring 1968, Greenwood 1975, Jones et al. 1983, Dunning 1984; U.S. Fish Wildl. Serv. [FWS], Northern Prairie Wildl. Res. Center, unpubl. mss). Age of fresh items and discarded remains on platforms were classified where possible; weights of juvenile prey relative to those of adults of the same species were: (1) large juvenile (adult weight x 0.75), (2) 2/3 grown (adult weight x 0.66), and (3) 1/2 grown (0.5 x adult weight). For prey of undetermined age, I used conspecific prey from tether platforms as a reference and assigned the average weight. For undetermined species of juvenile duck prey, lengths of tarsi (tarsometatarsi) were compared to a composite curve of tarsus length versus weight for mallard (*Anas platyrhynchos*), gadwall (*A. strepera*), and blue-winged teal (*A. discors*)(Appendix Fig. 1) which represented large, medium, and small breeding ducks. Ages of duckling prey were classified according to Gollop and Marshall (1954). I assigned each invertebrate prey (Orthoptera) a weight of 1 g.

Habitat Measurements

I defined nesting area as the area within 1 km of a tether platform. This was about the maximum distance from nests I observed adult Swainson's hawks in mid-summer (several adults were individually marked by distinct plumage), and a 2-km diameter area was about the size of the hawk's home range reported by Craighead and Craighead (1956:263). All habitat units within each Swainson's hawk nesting area were classified into 1 of the following: aspen tree clump, seasonal wetland, semi-permanent wetland, cropland, hayland (tame hay), pasture (moderately to heavily grazed native prairie), idle prairie (rested ≥ 2 years), and miscellaneous (farmstead, road right-of-way). Area (ha) of each habitat was measured on aerial photographs (1:15,840). Within each nesting area I also measured area of each habitat unit within 100 m of a perch >6 m high because Swainson's hawks sometimes hunt from elevated perches (Janes 1984). I also measured distance (m) from tether platform to nearest seasonal wetland, semi-permanent wetland, cropland, hayland, pasture, idle prairie, and to next nearest aspen tree clump; hereafter I refer to these variables simply as distance to (e.g.) cropland. Distance from each tether platform to LNWR was measured to account for possible effects of different land use, habitat, and prey populations on the wildlife refuge on diets of Swainson's hawks that nested near the refuge boundary.

Statistical Treatment of Data

Null hypotheses regarding Swainson's hawk diets and relationships between diet and habitat were tested by correlation, ANOVA procedures, and contingency tests (Sokal and Rohlf 1981, Dixon 1983, Daniel 1990). Non-parametric procedures were used wherever assumptions for parametric tests were not satisfied. Data sets were tested for homogeneity of variances using F-test procedures in BMDP (Sokal and Rohlf 1981:402). I conveyed exact probability levels for test results where $P \geq 0.001$ and considered $\underline{P} < 0.1$ to be grounds for rejecting null hypotheses.

I used Spearman rank correlation (coefficient $\underline{r}_s$) to measure association between daily occurrence of amphibian prey at tether platforms and total amount of rainfall (recorded on nearby LNWR [FWS, unpubl. refuge files]) during the previous 72 hr. Occurrence of amphibian prey was expressed as mean numbers/day/tether platform within years; pairs of daily means and associated rainfall from both years were pooled for a single analysis after checking between-year difference.

A hypothesis of no overall between-year difference in DKR-numbers of important prey categories used by Swainson's hawk families was tested by using mulivariate ANOVA (under PROCGLM in SAS [SAS Institute 1989]). Univariate analyses of variance were used if overall year effect was significant in the mulivariate test.

Multivariate, linear regression models (Neter et al. 1985) were used to untangle variation in DKR-biomass of important prey categories among Swainson's hawk families. Because of assumed lack of independence, the database excluded 1 season's data (randomly omitted) for individual nesting areas monitored both in 1986 and 1987. In this database, I also assumed independence between adult hawks tending nesting areas 1 year and those tending mutually exclusive nesting areas in the alternate year but could not verify this because birds were not individually marked in this study (other than several hawks with distinctive plumages). Where appropriate, prey abundance indices were entered as independent variables to account for year effects. I used the stepwise regression procedure in BMDP (Dixon 1983) with DKR-biomass of prey as dependent variables to select 5-8 best, potential independent (habitat or year effect) variables. Then I explored all possible 2- and 3-variable models to find any that explained (respectively) >40% and >50% of variation in dependent variables. Independent variables not normally distributed were log transformed. Correlation was used to check for multicollinearity among independent variables and residual plots were examined for the assumption of constant variance. I reported standardized regression coefficients and associated _P_-values (probability of _t_ in reduced model test for coefficient) to convey relative importance and validity of independent variables in each model.

RESULTS

Efficacy of Tether Platforms and Correction for Biases

I obtained 15 approximately 15-hr observation units from 4 tether platforms which included 141 prey deliveries (mean = 0.66 items/hr, SD = 0.33) observed from blinds. One platform had 1 young hawk, 2 had 2, and 1 had 3. Adult Swainson's hawks at another site (with 1 young) appeared disturbed by the blind; observations were terminated and the data were excluded from analysis. About 10% of prey observed delivered had anterior portions partly consumed (excludes 5 small prey items consumed by adults after being proffered but ignored by apparently sated young).

Notable differences in handling by tethered young of 2 prey types led to contrasts in detectability between the types. I found an average of 43% of small (<50 g) prey items, excluding birds, for 4 platform sites (Table V-1). Young Swainson's hawks either (1) swallowed such prey whole or otherwise ate them entirely, leaving no discarded remains, or (2) left only gastrointestinal tracts or 1-3 small hair clumps or pieces of skin. This low detectability (LD) group included meadow voles (_Microtus pennsylvanicus_), deer mice (_Peromyscus maniculatus_), tiger salamanders (_Ambystoma tigrinum_), and northern leopard frogs (_Rana pipiens_) and made up 90% of delivered prey. In contrast, I detected 79% of birds and large (≥50 g) mammals (Table V-1). Juvenile Passeriforms, ducklings, Richardson's ground squirrels, and thirteen-lined ground squirrels (_S. tridecemlineatus_) comprised this high detectability (HD) group. Tethered young plucked and scattered feathers or large pieces of hide from HD items, ensuring their detection. Skeletal remains and gastrointestinal tracts also were unconsumed parts of HD prey. Based on mean detectability of LD prey and 11 of 14 HD prey detected (Table V-1), correction factors in this study were 1/0.434 = 2.3 for LD and 1/0.786 = 1.3 for HD prey. Variation in detectability of LD prey among tether platform sites was low (SD = 8%; Table V-1) and I assumed similar low variance in detectability of HD prey.

Table V-1. Numbers of low detectability (LD) and high detectability (HD) prey items observed during daily visits to 4 Swainson's hawk tether platforms, compared with total numbers of prey observed delivered by adult hawks.

			LD items		HD items
Site	_n_ young	_n_ observation units (hr)	_n_ detected/ _n_ delivered	%	_n_ detected/ _n_ delivered
A	2	3 (41.5)	24/45	53.3	0/0
B	3	5 (73.5)	19/43	44.2	5/5
C	1	3 (40.3)	6/18	33.3	0/1
D	2	4 (59.0)	9/21	42.9	6/8
Mean (SD) % detected				43.4 (8.2)	[a]
Total		15 (214.3)	58/127		11/14

[a] Number of HD items from individual sites insufficient to warrant percentage breakdown and variance estimate.

Examination of pellets added few data. An average sample of 2.25 consecutive observation units was obtained via blinds at each of 4 platform sites; these included 72 LD and 9 HD prey delivered by adult hawks. Pellet analysis increased the average number of LD prey detected daily from 4.2 to 4.5 (SD = 0.3), a non-significant difference (Wilcoxon signed rank test, _P_ = 0.180). I did not detect remains of frogs or salamanders in pellets (_n_ = 8 consumed by tethered young during consecutive observation units) and only 1 of 3 HD items not detected by examining fresh items and discarded remains was revealed in pellets. Because these data suggested pellet analysis did not rectify biases related to prey size and handling by tethered young and overlooked amphibian prey, I did not make further use of pellets to determine Swainson's hawk diets in this study.

Data Base and Tethering of Young

During mid-July to mid-August, 1986-87, I recorded 1284 prey items (fresh items and discarded remains) at 20 Swainson's hawk tether platforms (10 platform sites each year, mean 21 days/platform). After applying corrections for undetected prey, items detected at daily visits represented about (± 90% confidence intervals) 2473 ± 386 total prey individuals and 172.5 ± 34.2 kg of prey biomass delivered by adult Swainson's hawks to their tethered young (mean prey weight about 70 g). Eighteen different nesting areas were represented in this sample; 2 nesting areas were sampled both years.

Average numbers of young Swainson's hawks tethered/platform were 1.5 in 1986 and 1.4 in 1987 (range both years, 1-3/platform). One of 29 tethered juveniles was killed by a raccoon (Procyon lotor), despite sheet metal guards I erected to deter mammalian predators, and another was killed by a great horned owl. This excludes 4 juveniles that died within 48 hr of tethering in 1986 due to food stress during unusually cool, rainy weather that caused widespread nestling mortality at nests of other Swainson's hawks in northwestern North Dakota (Part III; pers. obs.). All such mortality of tethered young occurred when they were about 25-28 days old and was averted in 1987 by waiting to tether young when they were about 33-35 days old, after weather-induced mortality had again occurred among area nestlings.

Generalized Diets of Swainson's Hawks

Because diets of raptors typically are generalized for a locale or region by pooling data from multiple breeding sites and often years (e.g., Gilmer and Stewart 1984), I use this approach for comparison (Table V-2). Major prey (>10% frequency or biomass) of Swainson's hawks

Table V-2. Composition of prey used by 20 Swainson's hawk families in northwestern North Dakota during summer 1986 and 1987, based on prey items pooled from all hawk families.

Prey category	Frequency		Biomass		% of nesting areas where preyed on[a]
	N	%	kg	%	
Mammals[b]					
White-tailed jackrabbit[c]	12	0.5	7.0	4.1	33.3
Ground squirrel	160	6.5	42.1	24.4	88.9
Vole and mouse	1566	63.3	44.0	25.5	100.0
Miscellaneous	8	0.3	1.5	0.9	--
Birds[d]					
Duck	103	4.2	27.3	15.8	88.9
Galliform	57	2.3	20.5	11.9	38.9
Rail and Charadriiform	30	1.2	7.9	4.6	38.9
Passeriform	122	4.9	5.0	2.9	88.9
Miscellaneous	5	0.2	0.9	0.5	--
Amphibian[e]	378	15.3	15.4	8.9	94.4
Reptile[f]	12	0.5	0.9	0.5	16.6
Insect[g]	20	0.8	<0.1	<0.1	22.2
Total[h]	2473	100.0	172.5	100.0	

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[a] Based on _n_ = 18 mutually exclusive nesting areas.

[b] Mammalian prey not specifically identified in table were (1) ground squirrel: mainly Richardson's and thirteen-lined, also (<5 individual prey) Franklin's (_S. franklinii_); (2) vole and mouse: mainly meadow vole and deer mouse, also southern red-backed vole (_Clethrionomys gapperi_), olive-backed pocket mouse (_Perognathus fasciatus_), jumping mouse (_Zapus_ spp.); (3) miscellaneous: short-tailed shrew (_Blarina brevicauda_), muskrat (_Ondatra zibethicus_), Norway rat (_Rattus norvegicus_), least weasel (_Mustela nivalis_).

[c] _Lepus townsendii_.

[d] Bird species were (1) duck: mallard, northern pintail (_A. acuta_), blue-winged teal, American wigeon (_A. americana_), lesser scaup (_Aythya affinis_); (2) Galliform: sharp-tailed grouse (_Tympanuchus phasianellus_) and gray partridge (_Perdix perdix_); (3) rail and Charadriiform: mainly sora (_Porzana carolina_) and American coot (_Fulica americana_), also killdeer (_Charadrius vociferous_), lesser yellowlegs (_Tringa flavipes_), willet (_Catoptrophorus semipalmatus_), upland sandpiper (_Bartramia longicauda_), marbled godwit (_Limosa fedoa_);

Table V-2. Continued

(4) Passeriform: mainly unknown sparrows and unknown blackbirds (Emberizinae and Icterinae), also western kingbird (*Tyrannus verticalis*), eastern kingbird (*T. tyrannus*), horned lark (*Eremophila alpestris*), tree swallow (*Tachycineta bicolor*), black-billed magpie (*Pica pica*), Sprague's pipit (*Anthus spragueii*), vesper sparrow (*Pooecetes gramineus*), savannah sparrow (*Passerculus sandwichensis*), red-winged blackbird (*Agelaius phoeniceus*), western meadowlark (Sturnella neglecta), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), Brewer's blackbird (*Euphagus cyanocephalus*), common grackle (*Quiscalus quiscula*), brown-headed cowbird (*Molothrus ater*); (5) miscellaneous: mourning dove (*Zenaida macroura*), short-eared owl (*Asio flammeus*), northern flicker (*Colaptes auratus*).

[e] Includes tiger salamander and northern leopard frog.

[f] Includes plains garter snake (*Thamnophis radix*) and smooth green snake (*Opheodrys vernalis*).

[g] Insects all were grasshoppers or crickets (Orthoptera: Oedipodinae).

[h] Total numbers and biomass are point estimates based on corrections for size-related biases.

were meadow voles and deer mice, Richardson's and thirteen-lined ground squirrels, ducklings, juvenile sharp-tailed grouse and gray partridge, and tiger salamanders and northern leopard frogs. Predation was unequally distributed among Classes of prey represented (frequency data; $X^2 = 4184$, df = 4, $P < 0.001$). Mammals and birds dominated dietary biomass of Swainson's hawks (55% and 36%), and mammals clearly were most frequently delivered prey (71%)(from Table V-2).

Wetlands were important sources of food for Swainson's hawks. Overall, 49% of total numbers and 42% of total biomass of prey used were species associated directly with wetlands (juvenile muskrats, sora, juvenile coots, ducklings, wetland-dwelling shorebirds, yellow-headed blackbirds, red-winged blackbirds, and amphibians) although wetlands averaged 18.1% (SD = 5.2) of habitat area within 1 km of all nests (data pooled from all tether platforms and from both years: 48.9% frequency and 42.2% biomass compared to 18.1% wetland composition; chi-square goodness-of-fit, both $P < 0.001$).

Variation in Diet

Year Effect

I tested null hypotheses that DKR-numbers of prey did not differ between years. Although there was no overall year effect on use of different prey categories (F = 1.14, df = 17, P = 0.422)(Table V-3), numbers of meadow voles killed daily by hawk pairs appeared much greater in 1987 which coincided with increased vole abundance between years indicated by a snap-trap index on nearby LNWR (0.1 voles/100 trap-nights in 1986 and 12.4 voles/100 trap-nights in 1987 [Part II]).

Table V-3. Variation in estimated daily kill rates of prey[a] by nesting pairs of Swainson's hawks between 1986 and 1987, and among nesting areas[b] within years as indicated by standard deviations (SD).

	Number of prey items/day		Prey biomass (g)/day	
	1986	1987	1986	1987
Prey category	mean (SD)	mean (SD)	mean (SD)	mean (SD)
Ground squirrels				
Richardson's	0.28 (0.43)	0.21 (0.27)	96.0 (146.5)	69.9 (92.4)
Thirteen-lined	0.29 (0.26)	0.15 (0.19)	45.4 (41.0)	25.0 (29.6)
Voles and mice				
Meadow vole	2.65 (2.17)	4.94 (2.23)	82.5 (67.5)	153.7 (69.3)
Deer mouse	1.28 (1.20)	1.05 (0.90)	24.0 (22.5)	19.7 (16.8)
Ducks	0.37 (0.33)	0.22 (0.26)	98.9 (87.6)	59.9 (68.0)
Galliforms	0.14 (0.16)	0.14 (0.18)	48.8 (55.6)	48.3 (63.2)
Rallids and Scolopacids	0.08 (0.09)	0.09 (0.09)	22.3 (24.5)	23.1 (24.0)
Passeriforms	0.57 (0.38)	0.27 (0.25)	23.3 (15.8)	10.9 (10.4)
Amphibians	1.24 (0.94)	1.58 (1.15)	50.6 (38.2)	64.4 (46.8)

[a] Excludes prey or prey groups that comprised <1% dietary composition by frequency.

[b] N = 9 nesting areas sampled each year; locations of nesting areas sampled 1 year were independent (i.e., mutually exclusive) of nesting areas in alternate year.

Variation among Nesting Areas

Habitat was extremely variable among Swainson's hawk nesting areas (Table V-4). The only difference in occurrence of 7 major habitat types between nesting areas off ($\underline{n}$ = 12) and on ($\underline{n}$ = 6) Lucy Township was that nesting areas off the township had less idle prairie on average (overall multivariate ANOVA, $\underline{F}$ = 2.57, df = 17, $\underline{P}$ = 0.085; univariate ANOVA, $\underline{P}$ = 0.066). This was mostly because 1 nesting area on the township overlapped 1.5 km^2 of idle prairie on privately-owned lands and 0.9 km^2 of idle prairie on nearby LNWR that was prescribe-burned during the respective nesting season.

Table V-4. Composition of 7 major habitat types among 18 Swainson's hawk nesting areas, 1986-87.

	% of area < 1 km from nest		
Habitat type	mean	SD	range
Quaking aspen tree clump	2.5	1.7	0.7-5.6
Seasonal wetland	9.7	4.6	6.0-19.8
Semi-permanent wetland	8.4	5.9	0-21.2
Cropland	35.1	16.9	4.8-67.6
Hayland	5.6	5.5	0-19.2
Pasture	13.3	7.2	0-22.3
Idle prairie	20.2	18.4	1.5-75.6

I observed extreme variability in use of prey among different nesting areas (Table V-3). Each prey species or species group in Table V-3 was not represented at 1-5 nesting areas examined except for voles and mice which comprised >50% of numbers of prey delivered at each of 13 nesting areas. Next I present models for important prey species along with germane details on species and age class composition of prey species groups.

Ground squirrels. Richardson's and thirteen-lined ground squirrels were chief ground squirrel prey (Tables V-2 and V-3); only 2 Franklin's ground squirrel prey were noted. Most (>70%) ground squirrels observed on platforms were adult or subadult size (Richardson's, >250 g; thirteen-lined, >125 g).

Fifty-six percent of variation in DKR-biomass of Richardson's ground squirrels among Swainson's nesting areas was explained by a 3-variable model and 43% by a 2-variable model (Table V-5). Both models implied adult Swainson's hawks captured more Richardson's ground squirrels when nests were close to pasture, although residual plots of the respective independent variable suggested slight violation of an assumption of constant variance. A less important variable was cropland area ≤100 m from hunting perches. Variation in DKR-biomass of thirteen-lined ground squirrels was not clearly tied to habitat features.

Voles and mice. Several competing models explained most (to 58%) variation in meadow vole DKR-biomass (Table V-5). The models suggested that Swainson's hawks captured more vole prey as proportion of surrounding land comprised by semi-permanent wetland or wetland area near perches decreased and hayland increased. Hay was cut in July and Swainson's hawks gleaned voles made vulnerable when rank alfalfa-tame grass cover suddenly was reduced. Observations of Swainson's hawks following hay-harvesting machinery and hunting recently cut hayfields support this notion. Annual vole abundance (an index) was an important variable that explained variation in use of meadow vole prey. Idle prairie near perches also was an important variable.

No multivariate models suitably explained variation in deer mouse DKR-biomass. However, deer mouse DKR-biomass was negatively correlated with semi-permanent wetland (% of area within 1 km; $r = -0.495$, $P = 0.021$).

Table V-5. Multiple regression models that best explain variance in daily kill rates (g biomass/d) of mammalian prey by Swainson's hawks at 18 nesting areas.

Model and independent variables	Coefficient		Fit of model		
	Standardized estimate (b′)	P[a]	R^2	F	P
Richardson's ground squirrel					
Model I			0.556	5.85	0.008
Distance to pasture	- 0.52	0.012			
Distance to hayland	0.37	0.062			
Cropland near perches[b]	0.32	0.100			
Model II			0.425	5.55	0.016
Distance to pasture	- 0.48	0.027			
Cropland near perches[b]	0.37	0.080			
Meadow vole					
Model I			0.584	6.54	0.005
Vole abundance index	0.58	0.005			
Idle prairie near perches[c]	0.49	0.014			
Semi-permanent wetland near perches[b]	- 0.34	0.067			
Model II			0.569	6.17	0.007
% semi-permanent wetland	- 0.55	0.012			
% hayland	0.55	0.011			
Idle prairie near perches[b]	0.39	0.053			
Model III			0.561	5.97	0.008
Vole abundance index	0.51	0.013			
Idle prairie near perches[b]	0.39	0.053			
% semi-permanent wetland	- 0.32	0.103			
Model IV			0.466	6.55	0.009
Vole abundance index	0.54	0.013			
Idle prairie near perches[b]	0.48	0.022			

[a] Probability of t in reduced model test for coefficient.

[b] Area (ha) within 1 km of nest that was ≤100 m from any perch (e.g., utility poles, trees) >6 m tall.

Ducks. There were many 2- and 3-variable models that explained most (to 69%) variation in DKR-biomass of juvenile ducks among Swainson's nesting areas (Table V-6). Models suggested that ducklings were preyed on in proportion to good quality duck nesting habitat and particularly to amount (ha) or proximity of brood-rearing habitat surrounding hawk nests. There also was a suggestion that amount of duck brood wetland near tall perches favored predation on ducklings (Models II and V) and that high vole abundance decreased or buffered predation on ducklings (Models III and V).

Table V-6. Multiple regression models that best explain variance in daily kill rates (g biomass/d) of Anatinae prey[a] by Swainson's hawks at 18 nesting areas.

Model and independent variables	Coefficient		Fit of model		
	Standardized estimate (*b*′)	*P*[b]	R^2	*F*	*P*
Model I			0.686	10.21	0.001
% semi-permanent wetland	0.83	0.001			
% idle prairie (log transformed)	0.38	0.027			
Distance to seasonal wetland	- 0.34	0.045			
Model II			0.651	8.72	0.002
% semi-permanent wetland	0.93	< 0.001			
Seasonal wetland near perches[c]	0.48	0.031			
Vole abundance index	- 0.34	0.058			
Model III			0.577	10.24	0.003
% semi-permanent wetland	0.75	0.001			
% idle prairie (log transformed)	0.35	0.060			
Model IV			0.548	9.10	0.002
% semi-permanent wetland	0.74	0.001			
Distance to seasonal wetland	- 0.30	0.108			
Model V			0.452	6.18	0.011
Semi-permanent wetland near perches[c]	0.63	0.005			
Vole abundance index	- 0.33	0.112			

[a] Nearly all Anatinae (98%) prey were juveniles (ducklings).
[b] Probability of *t* in reduced model test for coefficient.
[c] Area (ha) within 1 km of nest that was ≤100 m from any perch (e.g., utility poles, trees) >6 m tall.

Nearly all (98%) Anatinae prey I noted at tether platforms during 1986-87 were ducklings. Class I ducklings (<2.5 weeks old [Gollop and Marshall 1954]) accounted for 42.9% of duckling prey; nearly all the remainder were class II (2.5-5+ weeks old). Mallard, blue-winged teal, and lesser scaup comprised most (>20% frequency each) of known duckling species, and dabbling ducks (*Anas* spp.) made up 81% of ducklings delivered by Swainson's hawks to tether platforms (Table V-7). Species of ducklings were preyed on about in proportion to their presumed occurrence based on the local, adult breeding population. Blue-winged teal and lesser scaup ducklings may have been preyed on more than expected (Table V-7), but I did not test this because I believe these 2 species were more easily identified than other ducklings at platforms.

Table V-7. Composition of duckling prey observed at Swainson's hawk tether platforms[a], mid-summer 1986 and 1987, and mean annual composition of breeding duck pairs on a 0.4 x 28.8-km transect that traversed the north end of the study area[b].

	% of total			% of total	
Species	Duckling prey	Pairs on transect[c]	Genera	Duckling prey	Pairs on transect[c]
Northern pintail	4.5	6	<u>Anas</u>	80.8	74
Mallard	22.7	28	<u>Aythya</u>	19.2	20
Blue-winged teal	36.4	11			
Northern shoveler[d]	0	8			
Gadwall	0	16			
American wigeon	4.5	4			
Lesser scaup	31.8	15			
<u>N</u> total observed	22	195, 403[e]		52	195, 403[e]

---

[a] Data from 10 tether platforms in 1986 and 10 in 1987, at a total of 18 different nesting areas.

[b] Late May adult duck pairs on segment 11 of transect 2, stratum 45 of the North American Waterfowl Breeding Survey (FWS, unpubl. data), based on visibility correction factors for the stratum.

[c] Mean percentage from 1986 and 1987.

[d] <u>Anas clypeata</u>.

[e] Total numbers of duck pairs observed on transect segment in 1986 and 1987, before applying visibility corrections.

Remains of 2 adult ducks, both female blue-winged teal, were found at Swainson's hawk tether platforms. Female blue-winged teal were smallest breeding ducks common on the area (adult female weight 363 g [Dunning 1984]).

<u>Galliforms.</u> Sharp-tailed grouse comprised 59% biomass and 43%

frequency of Galliform prey found at tether platforms and gray partridge formed the balance. Two of 19 grouse prey but ≥ 10 of 25 partridge prey observed were adults (null hypothesis of similar age class proportions; chi-square test of homogeneity, $\underline{X}^2 = 4.73$, df = 1, $\underline{P} = 0.030$).

Sharp-tailed grouse were abundant during both study years on nearby LNWR (FWS, unpubl. refuge files). Six (33%) Swainson's hawk nesting areas I monitored by tether platforms were <1 km from the wildlife refuge. Distance from LNWR was an unimportant independent variable in regression analyses except in predictive models for galliform prey (Table V-8). These models suggested Swainson's hawks near LNWR preyed more on sharp-tailed grouse and gray partridge than hawks nesting farther away. This may have been due to increased abundance of Galliforms near the refuge, but I have no comparative data to support this. Also implied was that Galliforms were preyed on less frequently where tall perches were widespread (Models I and II) and more frequently where pasture was relatively close but idle prairie far from nests (Models I to III).

Amphibians. Tiger salamanders comprised 77.3% frequency and 85.9% biomass of amphibian prey found at Swainson's hawk tether platforms; northern leopard frogs made up the remainder. No 2- or 3-variable models adequately explained variation in amphibian use among Swainson's hawk nesting areas. But, availability of semi-permanent wetland within 1 km of nests correlated with DKR-biomass of amphibians ($\underline{r} = 0.49$, $\underline{P} = 0.037$). Mean daily occurrence of amphibian prey at tether platforms coincided with amount of prior (72 hr) rainfall ($\underline{r} = 0.35$, $\underline{n} = 64$ days during which 3-10 tether platforms were observed, $\underline{P} = 0.005$).

Table V-8. Multiple regression models that best explain variance in daily kill rates (g biomass/d) of Galliform prey by Swainson's hawks at 18 nesting areas.

	Coefficient		Fit of model		
Model and independent variables	Standardized estimate (b')	P[a]	R^2	F	P
Model I			0.650	8.68	0.002
Total area near perches[b]	- 0.63	0.003			
Distance to LNWR	- 0.61	0.002			
Distance to pasture	- 0.51	0.010			
Model II			0.629	7.92	0.002
Distance to LNWR	- 0.62	0.006			
Distance to idle prairie (log transformed)	0.46	0.016			
Total area near perches[b]	- 0.34	0.006			
Model III			0.526	8.32	0.004
Distance to LNWR	- 0.56	0.007			
Distance to idle prairie (log transformed)	0.53	0.009			
Model IV			0.431	5.68	0.015
Distance to LNWR	- 0.59	0.010			
Total area near perches[b]	- 0.44	0.043			

[a] Probability of t in reduced model test for coefficient.

[b] Area (ha) within 1 km of nest that was ≤100 m from any perch (e.g., utility poles, trees) >6 m tall.

DISCUSSION

Comparison to Swainson's Hawks elsewhere

Diets of Swainson's hawks I studied were more diverse than those reported by Schmutz et al. (1980) and Gilmer and Stewart (1984) for other parts of the northern Great Plains (Table V-9), although methods varied somewhat among studies. I found voles and mice, birds, and amphibians more important and Richardson's ground squirrels far less important prey than did these authors. Other, more general studies of Swainson's hawk diets in the northern Great Plains also report greater use of Richardson's ground squirrel than my study (e.g., Houston 1990). Lack of use of northern pocket gophers (compared to Gilmer and Stewart) was explained by their absence on my study area.

Table V-9. Comparison of Swainson's hawk diet diversity, based on biomass proportions of prey categories, among 3 studies in the northern Great Plains of North America.[a]

	southeastern Alberta[b]	southcentral North Dakota[c]	this study
(Dominant habitats)			
grazed and idle grassland	(mainly)	36%	34%[d]
cropland and hayland	8%	58%	41%
wetland	(some)	<5%	18%
Mammals			
Richardson's ground squirrel	89.0	46.6	17.6
Thirteen-lined ground squirrel	1.0	8.8	6.0
Northern pocket gopher	0	36.3	0
White-tailed jackrabbit	13.5	0	4.1
Voles and mice	1.4	2.6	25.5
Birds	9.4	5.7	35.7
Amphibians	0.1	0	8.9
Diversity index[e]	0.819	0.361	0.237
Total prey items observed	979	179	2473 ± 386[f]

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[a] Excludes prey groups that comprised <1% frequency in all studies.
[b] Approximate biomass proportions calculated from average of 2 years in Table 3 of Schmutz et al. (1980).
[c] Biomass proportions in Gilmer and Stewart (1984), based on data pooled from 3 years.
[d] Average composition within 1 km of nests at 18 nesting areas.
[e] Simpson's index: $\underline{D}$ = sum of $\underline{p}_i^2$, where index values ($\underline{D}$) = 0 (high diversity) to 1 (low diversity), and $\underline{p}_i$ = relative proportions of prey groups (see review in Marti [1987]).
[f] Estimated total prey delivered to tether platforms (± 90% confidence interval) based on data pooled from 2 years, with correction for bias applied to $\underline{n}$ = 1284 items detected (Chapter IV).

The moderate use of amphibian prey I observed contrasted sharply with scarcity of use of this type of prey in other studies (Table V-9). I suspect diet study methods used by other researchers overlooked amphibian prey (e.g., see relevant note in Gilmer and Stewart [1984]). These prey were consumed by tethered young but not detected in pellets I analyzed as noted for other Falconiforms (Craighead and Craighead

1956:6, Snyder and Wiley 1976), and did not occur among 207 fresh prey items observed at Swainson's hawk nests on my study area during 1-2 weeks before I tethered young (Appendix Table 3). Dunkle (1977) noted several salamanders and a frog as prey of Swainson's hawks in Wyoming (his records included direct observations of prey deliveries to nests) and Cameron (1913) mentioned frogs as prey of Swainson's hawks in eastern Montana. My observations challenge Palmer's (1988) inclusion of amphibian prey in a list of unusual dietary items of Swainson's hawks.

Wetlands clearly were important sources of food for Swainson's hawks in this study. In central North Dakota, virtually all prey used were upland consociates (Gilmer and Stewart 1984) though about 10-12% of numbers and biomass of Swainson's hawk prey in Alberta were from wetlands (Table 3 in Schmutz et al. [1980]). Although not wetland-dependent, meadow voles were another important prey in this study that often inhabit dense, herbaceous cover on wetland peripheries and within ephemeral and temporary wetlands (Kantrud et al. 1989).

Effect of Habitat and Land Use on Diet

Variation in avian diets is perhaps of greater ecological interest than what an average bird eats (Wiens 1989). Regression models implied that prey with relatively specialized habitat needs generally were used in proportion to availability of their preferred habitat (e.g., Richardson's ground squirrels compared with pasture, ducklings compared with semi-permanent wetlands and nesting cover). In contrast, use of habitat generalist prey could not be readily predicted in relation to habitat or land use by models (e.g., thirteen-lined ground squirrel, deer mouse).

Predation on Richardson's ground squirrels among Swainson's hawk pairs was explained mostly by proximity to pasture, the preferred habitat of this rodent (Jones et al. 1983). Richardson's ground squirrels also may use annually tilled cropland (Jones et al. 1983) and models suggested the ground squirrel may be vulnerable to Swainson's hawks in growing grain when near high perches. Croplands generally are unused by Swainson's hawks until harvest (Bechard 1982) but rodents there might be exploited earlier if perches are nearby.

Most ground squirrel prey found on platforms were adult or subadult size. In Alberta, predation by Swainson's hawks on adult Richardson's or similarly large prey was considered unusual (Schmutz 1987, Schmutz and Hungle 1989). Few other relatively large prey were observed on Swainson's hawk tether platforms in this study. For example, the paucity of adult duck and class III duckling prey indicated Swainson's hawks ignored prey >350-400 g. Avoidance of larger prey by this hawk, other than perhaps injured individuals, was inferred by Schmutz (1987) and Palmer (1988).

Swainson's hawks exhibited dietary (i.e., functional [Solomon 1949]) response to increased meadow vole abundance between years. A relationship between use of voles and amount of hayfield within nesting areas likely related to altered vulnerability of voles during cutting of hay in midsummer. Swainson's hawks characteristically follow hay-harvesters and other farm machinery to catch flushed prey (Schmutz 1987, Palmer 1988), and such vegetation disturbance may be a key aspect of the hawk's foraging ecology (Bechard 1982, Janes 1985, Part I). It was unsurprising that idle prairie was an important explanatory variable because it is optimal vole habitat in the northern Great Plains (Jones et al. 1983:223), although models implied voles in idle prairie were vulnerable when near tall perches. Swainson's hawk use of voles apparently decreased as availability of wetlands in nesting areas increased, presumably because of high importance of wetland prey to the hawk. A negative correlation between use of deer mice and amount of semi-permanent wetlands also suggested Swainson's hawks preyed less on deer mice wherever wetland prey were abundant.

Use of duckling prey related mostly to extent of semi-permanent wetland within nesting areas. Other habitat variables such as percentage cropland or hayland could have been important because even if relatively few ducklings occurred there, they may have been vulnerable.

This notion was not supported by the models, although ducklings (i.e., brood hens) may have completely avoided these habitats.

Use of Galliform prey among Swainson's hawk nesting areas may have decreased as elevated hunting perches increased because aspen tree clumps comprised most perches on the study area, and plains sharp-tailed grouse (T. p. jamesi) avoid areas when aspen and other woody cover predominate (Caldwell 1976, Moyles 1981). Use of Galliform prey probably was associated with pasture because grouse and partridge broods were attracted to pastures to forage and were vulnerable there.

Univariate models correlated use of amphibian prey with amount of semi-permanent wetland in nesting areas and with rainfall. After rains, frogs and especially salamanders clearly were vulnerable to capture by Swainson's hawks as they dispersed across a variety of upland habitats.

Predation on Ducks

The influence of predation by large raptors on production of prairie ducks has received little attention and causes of duckling mortality in the northern Great Plains are poorly understood (Sargeant and Raveling 1992). Swainson's hawk pairs in this study preyed on an estimated 2.6 and 1.5 ducklings/week/nesting area in mid-summer, 1986 and 1987 (from means in Table V-3). This implied about 0.1-0.2 ducklings/week/km^2 taken by Swainson's hawks because nesting density on my study area was about 0.075 occupied Swainson's hawk nests/km^2 in 1986-87 (Part III). But, mean predation on ducklings among all Swainson's hawk pairs probably was about half this because <50% of nesting Swainson's successfully reared young (Part III). Swainson's hawks not rearing young clearly demand less prey, and probably forage more on invertebrates than do pairs feeding young (Johnson et al. 1987, Palmer 1988).

I did not survey availability of duckling prey in Swainson's hawk nesting areas so could not precisely estimate predation rate (proportion of the prey population removed by the hawk). But, I suspect this rate was very low based on estimated daily kill rates, density and nesting success of area Swainson's hawks (Part III), and common occurrence of ducklings in the area. For example, Swainson's hawks probably removed <1% of ducklings present during a month in mid-summer, 1987; local surveys or counts suggested a conservative range of about 35-150 ducklings/km^2 (FWS, unpubl. data, Appendix Table 4) within which I am confident an average for my hawk nesting areas occurred.

All seasonal wetlands and small (<1 ha) semi-permanent wetlands rapidly became dry during June-July, 1987. About 46 and 76% (respectively) of these wetlands on nearby LNWR held water in late May, but only 1 and 24% did by mid-August (FWS, unpubl. refuge files). This presumably caused extensive overland movement by duck broods, making them highly vulnerable to predation and other mortality. Mean daily kill rates of ducklings by Swainson's hawks in 1987, however, was not greater than in 1986 which may reflect impact voles had in reducing predation on ducklings in 1987.

SUMMARY AND CONCLUSIONS

This study reports several key findings on summer diets and predation ecology of Swainson's hawks in an area of mixed land use in the northern Great Plains: (1) wetlands were important sources of prey; (2) makeup of diets varied among nesting hawk pairs due to land use and local habitat diversity; (3) compared to previous reports, ground squirrels especially Richardson's were used less but avian prey were more important and widespread use of amphibian prey was noteworthy; (4) rates of predation on juvenile ducks in mid-summer were low and multivariate models implied meadow voles were important alternate or buffer prey.

Aside from conservation problems in its austral summer range (Palmer 1988), reasonable numbers of nesting Swainson's hawks likely can be maintained in the northern Great Plains mainly by providing occasional small tree clumps or tall shrubs for nest sites (Schmutz 1987). Based on prey use and high dietary flexibility among pairs of nesting Swainson's hawks observed in my study, where possible nest site provisioning should focus on sites close (<1 km) to a mix of wetland, pasture, and hayland. Multivariate models in this study indirectly suggested nesting Swainson's hawks relied on vegetation of relatively short height and density (e.g., pasture) and disturbance of vegetation substrates (e.g., hayfield) for foraging habitat, and used tall perches to exploit prey in dense vegetative cover (e.g., cropland or idle prairie). Although several models suggested perch sites in idle prairie may allow Swainson's hawks to access voles there, widespread tree perch sites and long-term rest of prairie probably disfavor Swainson's hawks (Janes 1985, 1987, Part I, Part II).

LITERATURE CITED

ADORJAN, A. S., and G. B. KOLENOSKY. 1969. A manual for the identification of hairs of selected Ontario mammals. Ont. Dep. Lands For. Res. Rep. Wildl. 90. 64pp.

BECHARD, M. J. 1982. Effect of vegetative cover on foraging site selection by Swainson's hawk. Condor 84:153-159.

BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole, Harrisburg, Pa. 543pp.

BLUEMLE, J. P. 1977. The face of North Dakota: the geologic story. North Dakota Geol. Surv. Educ. Ser. 11. 73pp.

CALDWELL, P. J. 1976. Energetic and population consideration of sharp-tailed grouse in the aspen parkland of Canada. Ph.D. Dissertation, Kansas State Univ., Manhattan. 113pp.

CAMERON, E. S. 1913. Notes on the Swainson's hawk (Buteo swainsoni) in Montana. Auk 30:381-394.

COLLOPY, M. W. 1983. A comparison of direct observations and collections of prey remains in determining the diet of golden eagles. J. Wildl. Manage. 47:360-368.

CRAIGHEAD, J. J., and F. C. CRAIGHEAD. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania. 443pp.

DANE, C. W. 1965. The influence of age on development and reproductive capability of the blue-winged teal (Anas discors Linnaeus). Ph.D. Thesis, Purdue Univ., West Lafayette, Indiana. 171pp.

DANIEL, W. W. 1990. Applied non-parametric statistics. PWS-KENT Publishing Co., Boston, Mass. 635pp.

DIXON, W. J., ed. 1983. BMDP statistical software. Univ. California Press, Berkeley. 733pp.

DUKE, G., A. JEGERS, G. LOFF, and O. EVANSON. 1975. Gastric digestion in some raptors. Comp. Biochem. Physiol., Part A: Comp. Physiol. 50A:649-656.

DUNKLE, S. W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. Auk 94:65-71.

DUNNING, J. B. 1984. Body weights of 686 species of North American birds. Western Bird Banding Asso. Monogr. 1. 38pp.

FITCH, H. S., F. SWENSON, and D. F. TILLOTSON. 1946. Behavior and food habits of the red-tailed hawk. Condor 48:205-237.

GILMER, D. S., and R. E. STEWART. 1984. Swainson's hawk nesting ecology in North Dakota. Condor 86:12-18.

GOLLOP, J. B., and W. H. MARSHALL. 1954. A guide for aging duck broods in the field. Miss. Flyway Counc. Tech. Sect. unpubl. mimeo. 14pp.

GREENWOOD, R. J. 1975. Reproduction and development of four mallard lines. Prairie Nat. 7:9-16.

HOUSTON, C. S. 1990. Saskatchewan Swainson's hawks. Am. Birds 44:215-220.

JANES, S. W. 1984. Influences of territory composition and interspecific competition on red-tailed hawk reproductive success. Ecology 65:862-870.

---. 1985. Habitat selection in raptorial birds. Pages 159-188 in M. L. Cody, ed. Habitat selection in birds. Academic Press, Orlando, Fla.

---. 1987. Status and decline of Swainson's hawks in Oregon: the role of habitat and interspecific competition. Oregon Birds 13:165-179.

JOHNSON, C. G., L. A. NICKERSON, and M. J. BECHARD. 1987. Grasshopper consumption and summer flocks of nonbreeding Swainson's hawks. Condor 89:676-678.

JONES, J. K., Jr., D. M. ARMSTRONG, R. S. HOFFMAN, and C. JONES. 1983. Mammals of the Northern Great Plains. Univ. Nebraska Press, Lincoln, Nebraska. 379pp.

KANTRUD, H. A., G. L. KRAPU, and G. A. SWANSON. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85. 111pp.

KIRKLEY, J. S., and J. A. GESSAMAN. 1990. Water economy of nestling Swainson's hawks. Condor 92:29-44.

MARTI, C. D.. 1987. Raptor food habits studies. Natl. Wildl. Fed. Sci. Tech. Ser. 10:67-80.

MOORE, T. D., L. E. SPENCE, and C. E. DUGNOLLE. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyo. Game and Fish Dep., Cheyenne, Wyo. 177pp.

MOYLES, D. L. J. 1981. Seasonal and daily use of plant communities by sharp-tailed grouse (<u>Pediocetes phasianellus</u>) in the parklands of Alberta. Can. Field-Nat. 95:287-291.

NETER, J., W. WASSERMAN, and M. H. KUTNER. 1985. Applied linear statistical models. Irwin, Inc., Homewood, Illinois. 1127pp.

OLENDORFF, R. R. 1974. Some quantitative aspects of growth in three species of buteos. Condor 76:466-468.

ORING, L. W. 1968. Growth, molts and plumages of the gadwall. Auk 85:355-380.

PALMER, R. S., ed. 1988. Handbook of North American birds, Vol. 4 and 5. Yale Univ. Press, New Haven, Conn. 433 and 465pp.

PETERSEN, L. R., and J. R. KEIR. 1976. Tether platforms - an improved technique for raptor food habits study. Raptor Res. 10:21-28.

SARGEANT, A. B., and D. G. RAVELING. 1992. Mortality during the breeding season. Pages 396-422 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, eds. Ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

SCHMUTZ, J. K. 1984. Ferruginous and Swainson's hawk abundance and distribution in relation to land use in southeastern Alberta. J. Wildl. Manage. 48:1180-1187.

---. 1987. The effect of agriculture on ferruginous and Swainson's hawks. J. Range Manage. 40:438-440.

---. 1989. Hawk occupancy of disturbed grasslands in relation to models of habitat selection. Condor 91:362-371.

---, and D. J. HUNGLE. 1989. Populations of ferruginous and Swainson's hawks increase in synchrony with ground squirrels. Can. J. Zool. 67:2596-2601.

---, S. M. SCHMUTZ, and D. A. BOAG. 1980. Coexistence of three species of hawks (Buteo spp.) in the prairie-parkland ecotone. Can. J. Zool. 58:1075-1079.

SNYDER, N. F. R., and J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20. 96pp.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. W.H. Freeman Co., New York, NY. 859pp.

SOLOMON, M. E. 1949. The natural control of animal populations. J. Anim. Ecol. 18:1-35.

STEWART, R. E., and H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Dep. Inter. Bur. Sport Fish. Wildl. Res. Publ. 92. 57pp.

WIENS, J. A. 1989. Ecology of bird communities: foundations and patterns, Vol. 1. Cambridge Univ. Press, New York. 539pp.

YALDEN, D. W., and P. E. YALDEN. 1985. An experimental investigation of examining kestrel diet by pellet analysis. Bird Study 32:50-55.

PART VI

IMPORTANCE OF DUCKS AND OTHER WETLAND PREY IN DIETS OF GREAT HORNED OWLS DURING BREEDING SEASON, NORTHWESTERN NORTH DAKOTA

INTRODUCTION

Prey use by great horned owls (Bubo virginianus) has been better documented than that of any other North American Strigiform. This owl preys mostly on small to mid-size mammals especially Leporids and small rodents (Errington et al. 1940, Korschgen and Stuart 1972, McInvaille and Keith 1974, Voous 1988) although its list of prey includes diverse sizes and taxa (e.g., Bent 1938). Despite broad knowledge of the great horned owl's diet, little is known about its use of prey in the Prairie Pothole Region (PPR) of midcontinent North America, where nesting waterfowl are abundant (Bellrose 1976). Numerous studies of great horned owl diets have been conducted in the more wooded Great Lakes states (Errington et al. 1940, Orians and Kuhlman 1956, Petersen 1979) and boreal forest ecotone (Rusch et al. 1972, McInvaille and Keith 1974) but implications for predator-prey relationships in the PPR are only speculative. Abundance and distribution of great horned owls in the PPR have increased, concomitant with plantings of trees and suppression of fire since the region was settled by persons of European descent about a century ago (Sargeant et al. 1992, Part I).

The PPR produces about half of North American ducks annually (Smith et al. 1964). Predators, chiefly mammals, significantly limit production of ducks in this region mostly by destroying duck nests but magnitude of predation on adults and especially ducklings is less well documented (Sargeant and Raveling 1992). Information on raptor predation on nesting ducks and their young is particularly scarce and mostly anecdotal. For example, there are no data on differential vulnerability among species or sex cohorts of prairie ducks to predation by raptors, as is available for some mammalian predators (Eberhardt and Sargeant 1977, Sargeant et al. 1984). Study of prey use by great horned owls in the PPR will contribute to these information gaps.

Objectives of this study were: (1) quantify composition of prey used by great horned owls nesting in an area of the PPR with good waterfowl breeding habitat, assess variation in prey use among owl pairs, and examine relationships between use of important prey types and habitat surrounding nest sites; (2) estimate rate of use and describe predation chronology and cohort vulnerability among duck prey.

STUDY AREA

Diets of nesting great horned owls were examined during May to early July, 1986 and 1987 on Lucy Township (93 km^2) and adjacent lands of similar habitat and land use in Burke County, northwestern North Dakota (48°40′N;102°35′W). The study area was within a rolling to hilly glacial moraine known as the Missouri Coteau (Bluemle 1977). Climate was semi-arid with cold winters and warm summers and annual precipitation was 46 cm in 1986 and 31 cm in 1987 compared to a 42-cm average. Land use was a mix of dryland grain farming and cattle ranching. Habitat composition on Lucy Township was 41% native (Stipa-Agropyron) prairie (about half grazed heavily by domestic livestock and half grazed lightly or idle) with scattered tall shrubs such as hawthorn (Crataegus spp.) or chokecherry (Prunus virginiana); 31% cropland, a third of which annually was fallow; 19% seasonal, semi-permanent, and permanent wetlands (classification according to Stewart and Kantrud [1971]); 5% tame grass-alfalfa hay; 2% small (<1 ha), scattered clumps of quaking aspen (Populus tremuloides) trees (mean = 4.7 clumps/km^2, SD = 3.4); and 2% roads, farmsteads, and shelterbelts. The study area was sparsely inhabited by humans (1 farmstead/8 km^2).

Nesting biology of raptors on Lucy Township during 1986-87 was described in Part III. Commonly nesting species of raptors were red-tailed hawk (Buteo jamaicensis)(0.16 occupied nests/km^2), Swainson's (B. swainsoni) hawk (0.08/km^2), northern harrier (Circus cyaneus)(probably >0.2/km^2), and great horned owl (0.11/km^2). Great horned owls occurred year-round and nesting pairs hatched their eggs in early to mid-April.

Density estimates of breeding ducks on a 0.4 x 28.0-km transect (hereafter referred to as segment 11) along the north end of Lucy Township indicated ducks were abundant in the area. About 54 and 104 ducks/km^2 (SD = 9 and 16) occurred on segment 11 in 1986 and 1987, based on expansion factors for stratum 45 of the North American Waterfowl Breeding Population Survey (U.S. Fish Wildl. Serv. [FWS], unpubl. data for segment 11, transect 2, stratum 45). These estimates were slightly lower than 90% confidence interval ranges of 68-105 and 92-144 breeding ducks/km^2 in 1986 and 1987 on Lostwood National Wildlife Refuge (LNWR) which was adjacent (southeast of) Lucy Township (based on stratified random sample; FWS, unpubl. refuge files). Abundance of ducks on segment 11 was below average in 1986 and about average in 1987 (Fig. VI-1). An index of duckling abundance based on minimum (unexpanded) counts of ducklings observed in mid-July on segment 11 (18 ducklings/km^2 in 1986 and 35/km^2 in 1987) suggested greater duckling abundance occurred in 1987, which paralleled abundance of breeding ducks between years.

Some years certain key prey are abundant and buffer raptor predation on other prey (Errington 1932, Darrow 1945, Dasmann 1964). My study occurred in years when populations of meadow voles (_Microtus pennsylvanicus_) and American coots (_Fulica americana_), important buffer prey used by great horned owls (Errington 1967, McInvaille and Keith 1974, Petersen 1979), were below (1986) and above average (1987). Vole abundance was indicated by relative abundance indices on adjacent LNWR (0.1 and 12.4 vole captures/100 snap-trap nights, June 1986 and 1987 [Part II]), and American coot abundance by an aerial count on segment 11 (2.6 and 7.4 coots/km^2, SD = 0.5 and 1.6 [FWS, unpubl. data]). Relative abundance of the deer mouse (_Peromyscus maniculatus_), another potential buffer prey species, probably changed little between years as indicated

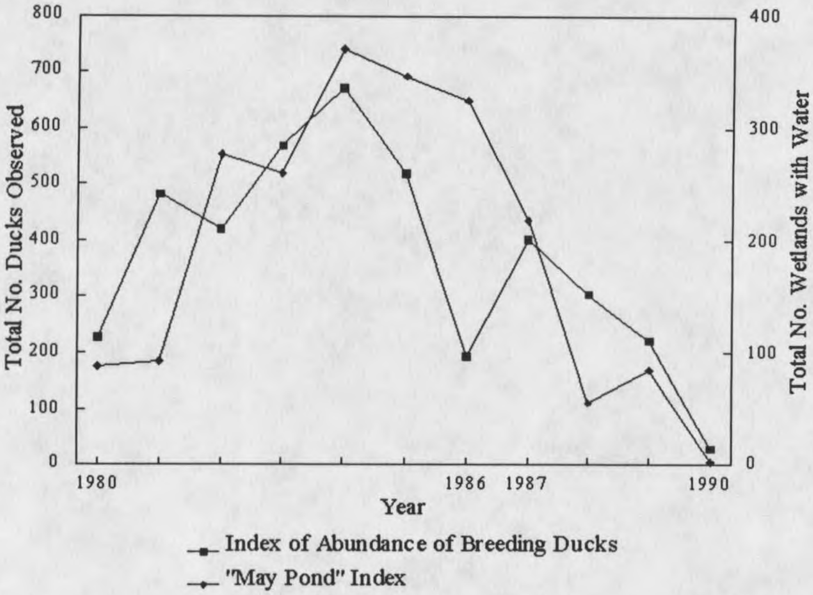

Figure VI-1. Trends in abundance of ducks (uncorrected for visibility biases) and wetlands with water in late May on segment 11, transect 2, stratum 45 of the North American Waterfowl Breeding Population Survey (FWS, unpubl. data).

by relative abundance indices on LNWR (0.17 and 0.12 captures/100 15-m drift-fence nights, mid-May to early July, 1986 and 1987 [FWS, unpubl. data]).

Other vertebrate wildlife that were common and potentially important to nesting great horned owls as prey included grebes (Podicipediformes), sharp-tailed grouse (Tympanuchus phasianellus), gray partridge (Perdix perdix), rails (Rallidae), Passeriforms especially sparrows (Emberizinae) and blackbirds (Icterinae), jumping mouse (Zapus spp.), deer mouse, ground squirrels (Spermophilus spp.), and tiger salamander (Ambystoma tigrinum). White-tailed jackrabbits (Lepus townsendii) were widespread but scarce.

METHODS

Each spring I systematically searched 80 km^2 of Lucy Township (access was denied on 13 km^2) for occupied nests of raptors (Part III) and subsequently monitored prey use by all great horned owl pairs that produced large (>3 week old) nestlings. I augmented this sample of owl diets with like data from all great horned owl nests found on similar land use and habitat within the Missouri Coteau up to 10 km north, south, and east of Lucy Township.

Data Collection

When owlets were 4 weeks old, I tethered them on platforms that were about 2 m above ground in sheltered sites <9 m from nests (Petersen and Keir 1976). I subsequently visited the platforms every 3-4 days between 1000-2000 hours for 6-8 weeks after which young were released. During each visit to tether platforms I weighed owlets and collected all regurgitated pellets and discarded (inedible) prey remains. Fresh (edible) prey were identified, marked by cutting off a foot, and left. I analyzed pellets using standard techniques (Errington 1930, Craighead and Craighead 1956, Marti 1987). I avoided duplicating my count of any prey item by conservatively choosing the lowest number of items represented collectively by pellets, discarded remains, and fresh items, including fresh items noted at the previous visit (Craighead and Craighead 1956, Collopy 1983, Marti 1987). A reference collection of preserved specimens of local fauna was used to help verify identification of prey items.

Data Analyses

I report dietary makeup in terms of relative (percentage) frequency and biomass. Percentage frequency was calculated by dividing the number of individuals in each prey species category by the total number of prey items observed, and percentage biomass was estimated by multiplying the number of individuals of each prey category by their respective mean weight, then dividing the subtotal of each prey category by the grand total prey weight (Marti 1987).

For each prey category that comprised >5% frequency of prey pooled from all owl tether platforms, I estimated the average biomass (in g) or number of prey killed daily by each great horned owl pair. I referred to these estimated averages as daily kill rates in terms of biomass (DKR-biomass) or numbers (DKR-numbers). DKR-biomass (g/day) was estimated for a given tether platform by multiplying the percentage biomass of each prey category times daily food needs of adults and young combined (Craighead and Craighead 1956:312). I assumed that composition of prey consumed by adults was the same as that delivered to owlets, and that each adult and juvenile great horned owl required about 144 g of prey daily (McInvaille and Keith 1974). DKR-numbers were estimated by dividing daily biomass intake (in g) of each prey category by respective mean prey weights.

I compared species composition of adult duck prey observed on great horned owl tether platforms to that of the local breeding population estimated by an annual count of ducks in late May on segment 11 (expanded by correction factors for the stratum [FWS, unpubl. data]). Sex ratios of each species of adult duck prey were compared to an approximate 50:50 sex ratio at hatching and to average spring sex ratios from several locations in North America (Bellrose et al. 1961). Chronology of predation on ducks was summarized by 2-week intervals and by the following age cohorts: adult, Class I duckling, and Class II duckling (age classification according to Gollop and Marshall [1954]). I measured and compared mean DKR-numbers of adult and of juvenile ducks taken by great horned owls during mid-May through June.

Prey Weights

Mean weights of prey were obtained from specimens collected on the study area (nearly all mammals and herptiles, and about half of birds; Appendix Table 5) and from literature (James and Seabloom 1969, Jones et al. 1983, Dunning 1984). For weights of prey represented by remains in owl pellets, I relied mainly on measurement of skeletal elements such as Passeriform synsacra and tarsometatarsi (tarsi) to estimate approximate size and age of prey (Marti 1987). Ossification of major skeletal elements and (for birds) presence of down versus emerging or fully developed contour feathers also were helpful in approximating age and size of prey in pellets. Weights were assigned to juvenile prey relative to those of adults of same species: (1) large juvenile (adult weight x 0.75), (2) 2/3 grown (adult weight x 0.66), and (3) 1/2 grown (0.5 x adult weight). For prey of undetermined age, I used prey observed at tether platforms as a reference and assigned the average weight of conspecific prey for which age could be determined.

Undetermined species of juvenile duck prey could have been any of ≥10 species that varied in size. Therefore, tarsi lengths of unidentified species of ducklings were matched with average weights on an age-growth curve for juvenile mallards (Anas platyrhynchos), gadwalls (A. strepera), and blue-winged teal (A. discors)(Appendix Fig. 1) that represented large, medium, and small breeding ducks. Duckling weight data were from ducklings collected on the study area and from literature (Dane 1965, Oring 1968, Greenwood 1975; FWS, Northern Prairie Wildl. Res. Center, unpubl. mss.).

I assigned each invertebrate prey (Orthoptera) a weight of 1 g.

Habitat Measurements

I defined nesting area as the area within 1 km of a tether platform, roughly the size of a great horned owl home range (Craighead and Craighead 1956:257, Petersen 1979). All habitat units within each owl nesting area were classified into 1 of the following: aspen tree clump, seasonal wetland, semi-permanent wetland, cropland, hayland (tame hay), pasture (moderately to heavily grazed native prairie), idle prairie (rested ≥2 years), and miscellaneous (farmstead, road right-of-way). Area (ha) of each habitat was measured on aerial photographs (1:15,840). Within each nesting area I also measured area of each habitat unit ≤100 m from a perch >6 m high because great horned owls hunt from elevated perches (Marti 1969, Rudolph 1978, Petersen 1979). I also measured distance (m) from tether platform to nearest seasonal wetland, semi-permanent wetland, cropland, hayland, pasture, idle prairie, and to next nearest aspen tree clump (hereafter I refer to these variables simply as e.g., proximity or distance to cropland).

Statistical Treatment of Data

Null hypotheses regarding great horned owl diets and relationships between diet and habitat were tested by correlation, ANOVA procedures, and contingency tests (Sokal and Rohlf 1981, Dixon 1983, Daniel 1990). Non-parametric procedures were used wherever assumptions for parametric tests were not satisfied. Data sets were tested for homogeneity of variances using F-test procedures in BMDP (Sokal and Rohlf 1981:402). I conveyed exact probability levels for test results where $P \geq 0.001$ and considered $P < 0.1$ to be grounds for rejecting null hypotheses.

A hypothesis of no overall between-year difference in frequency proportions of prey used by great horned owls was tested by using the multivariate analysis of covariance procedure in SAS (SAS Institute 1989). Univariate analyses of covariance were used if overall year effect was significant in the multivariate test.

Multivariate, linear regression models (Neter et al. 1985) were used to untangle variation in DKR-biomass or relative biomass of important prey types among great horned owl families. The database excluded 1 season's data (randomly omitted) for individual nesting areas monitored both in 1986 and 1987 because of assumed lack of independence. In this database, I also assumed independence between adult owls tending nesting areas 1 year and those in mutually exclusive nesting areas in the alternate year but could not verify this because birds were not individually marked. Abundance indices of prey used by owls in significantly different frequency proportions between years were entered in regressions to account for year effects. I also included number of tethered young as an independent variable in regressions with DKR-biomass as dependent variables. The stepwise regression procedure in BMDP (Dixon 1983) was used with DKR-biomass or percentage biomass as dependent variables to select 5-8 best, potential independent variables (habitat or year effect variables). Then all possible 2- and 3-variable models were explored to find any that explained (respectively) >40% and >50% of variation in dependent variables. Independent variables not normally distributed were log transformed. I checked for multicollinearity among independent variables by using correlation and examined residual plots for the assumption of constant variance. Standardized regression coefficients and associated P-values (probability of t in reduced model test for coefficient) were reported to convey relative importance and validity of independent variables in each model.

RESULTS

I recorded 1200 prey items at 12 great horned owl tether platforms during 628 platform-days (i.e., a site monitored 1 day) in 1986 and 1700 at 12 tether platforms during 683 platform-days in 1987. Twenty-two different nesting areas were represented in this sample; 2 nesting areas were sampled both years.

One to 3 owlets were tethered on each platform (average 1.8 owlets/platform in 1986 and 2.3/platform in 1987). None of 49 owlets tethered died on platforms; all gained or maintained weight without need for supplemental feeding (Petersen and Keir 1976) and were released while still being fed at a relatively constant rate by tending adults. Evidence of surplus prey on platforms was rare, which supported the assumption that biomass of prey killed equaled that consumed by adults and young.

Generalized Diets of Great Horned Owls

Because diets of raptors typically are generalized by pooling data from multiple breeding sites and often years (e.g., Gilmer et al. 1983), I present data this way for comparison. Avian prey clearly contributed majorities of relative frequency and especially relative biomass of prey delivered (totals from Table VI-1: 64.7% and 83.5%). Mammals comprised

34% frequency and only 17% of biomass delivered, and other Classes of prey contributed insignificant biomass (<2% frequency and 1% biomass in aggregate).

Ducks (10 species; includes juveniles) were the most important prey category; they comprised 35% frequency and 45% biomass of prey found at tether platforms and were used by all owl families both years (Table VI-1). Rails especially American coot (nearly all adults; 70% frequency, 94% biomass of Rallid prey) were the second most important prey and accounted for 11% frequency and 21% biomass. Voles (mainly meadow vole), mice (mainly deer mouse), and Passeriforms (mostly juvenile blackbirds) each contributed >10% frequency of prey and, along with rails, also were used by all owl families. White-tailed jackrabbits (all juveniles) and grebes (nearly all adults) contributed 8% and 6% of overall biomass although jackrabbit prey was not found at 36% of nesting areas. In contrast, Charadriiform prey were widely used but contributed relatively little to overall biomass. Domestic chickens occurred as prey at 1 tether platform (Table VI-1); the owl family fed almost exclusively on chickens and Norway rats (0.7 chickens and 1.2 rats/day found on the tether platform with 3 owlets) from a farmstead 0.5 km away after 250 half-grown cockerels were released into a pen lacking roosting shelter.

Wetlands comprised an average of about 18% of habitat in great horned owl nesting areas, but wetland-dependent prey comprised 57% frequency and 76% biomass of prey in owl diets (pooled data, compared to 18% wetland composition; chi-square goodness-of-fit, both $\underline{P} << 0.001$). These prey mainly were ducks, rails, grebes, and certain Passeriforms (yellow-headed blackbird, red-winged blackbird); other wetland-dependent prey were muskrat, certain shorebirds (e.g., black tern), and tiger salamanders (Table VI-1).

Table VI-1. Composition of prey used by 24 great horned owl families in northwestern North Dakota during May to early July, 1986 and 1987, based on prey items pooled from all owl families.[a]

Prey category	Frequency		Biomass		% of nesting areas where preyed on[b]
	N	%	kg	%	
Mammals[c]					
White-tailed jackrabbit	95	3.3	43.0	7.5	63.6
Ground squirrel	42	1.4	10.1	1.8	81.8
Mouse	385	13.3	6.4	1.1	100.0
Vole	328	11.3	9.7	1.7	100.0
Muskrat	20	0.7	9.5	1.7	36.4
Norway rat	87	3.0	17.7	3.1	45.5
Miscellaneous	14	0.5	1.4	0.2	--
Birds[d]					
Grebe	99	3.4	35.4	6.2	95.5
Duck	1010	34.8	256.5	45.0	100.0
Galliform	34	1.2	17.4	3.1	54.5
Rail	315	10.9	117.1	20.5	100.0
Charadriiform	79	2.7	7.6	1.3	90.9
Passeriform	303	10.4	17.2	3.0	100.0
Domestic chicken	20	0.7	15.5	2.7	4.5
Miscellaneous	18	0.6	3.6	0.6	--
Amphibian[e]	38	1.3	1.9	0.4	50.0
Reptile[f]	1	< 0.1	0.1	< 0.1	4.5
Insect[g]	12	0.4	< 0.1	< 0.1	31.8
Total	2900	100.0	570.1	100.1	

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[a] Total of 12 and 12 nesting areas monitored in 1986 and 1987; 2 nesting areas were monitored both years.

[b] Proportion of 22 nesting areas at which a given species or species group occurred as prey at least once during 1986-87.

Table VI-1. Continued.

[c] Mammalian prey not specifically identified in table were (1) ground squirrel: mainly Richardson's (*S. richardsonii*) and thirteen-lined (*S. tridecemlineatus*), also (<5 individual prey) Franklin's (*S. franklinii*); (2) mice: mainly deer mouse, also western or meadow jumping mouse, olive-backed pocket mouse (*Perognathus fasciatus*), northern grasshopper mouse (*Onychomys leucogaster*), house mouse (*Mus musculus*); (3) voles: mainly meadow vole, also southern red-backed vole (*Clethrionomys gapperi*); (4) miscellaneous: mainly short-tailed shrew (*Blarina brevicauda*) and masked shrew (*Sorex cinereus*), also least weasel (*Mustela nivalis*), striped skunk (*Mephitis mephitis*).

[d] Avian prey not specifically identified in table were (1) grebes: horned or eared grebe (*Podiceps auritus*, *P. nigricollis*), pied-billed grebe (*Podilymbus podiceps*); (2) ducks: green-winged teal (*A. carolinensis*), mallard, northern pintail (*A. acuta*), blue-winged teal, northern shoveler (*A. clypeata*), gadwall, American wigeon (*A. americana*), redhead (*Aythya americana*), lesser scaup (*A. affinis*), ruddy (*Oxyura jamaicensis*); (3) Galliforms: sharp-tailed grouse and gray partridge; (4) rails: mainly American coot and sora (*Porzana carolina*), also (<5 individual prey) Virginia rail (*Rallus limicola*); (5) Charadriiforms: killdeer (*Charadrius vociferus*), American avocet (*Recurvirostera americana*), upland sandpiper (*Bartramia longicauda*), willet (*Catoptrophorus semipalmatus*), common snipe (*Gallinago gallinago*), Wilson's phalarope (*Phalaropus tricolor*), black tern (*Chlidonias niger*); (6) Passeriforms: eastern kingbird (*Tyrannus tyrannus*), horned lark (*Eremophila alpestris*), American crow (*Corvus brachyrhynchos*), house wren (*Troglodytes aedon*), brown thrasher (*Toxostroma rufum*), unknown warblers (Parulinae), unknown sparrows, bobolink (*Dolichonyx oryzivorus*), red-winged blackbird (*Aeglaius phoeniceus*), Western meadowlark (*Sturnella neglecta*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), Brewer's blackbird (*Euphagus cyanocephalus*), common grackle (*Quiscalus quiscula*), brown-headed cowbird (*Molothrus ater*), northern oriole (*Icterus galbula*), unknown blackbirds; (7) miscellaneous (1-3 individuals): American bittern (*Botaurus lentiginosus*), black-crowned night heron (*Nycticorax nycticorax*), Canada goose (*Branta canadensis*)(juvenile), mourning dove (*Zenaida macroura*), northern saw-whet owl (*Aegolius acadicus*), northern harrier, northern flicker (*Colaptes auratus*).

[e] Includes tiger salamander, also (1 individual) northern leopard frog (*Rana pipiens*).

[f] Includes only plains garter snake (*Thamnophis radix*).

[g] Insect prey were grasshopper and cricket (Orthoptera: Oedipodinae) and giant water bug (Hemiptera: Belostomatidae).

Variation in Diet

Year Effect

There was a difference between years in overall use (percentage frequency) of different prey categories by great horned owls (Table VI-2). The relative frequency of voles as prey was greater in 1987 when vole indices were higher than in 1986; this difference was highly significant ($P < 0.01$, Table VI-2). Less significant changes were decreased relative frequency of mouse and passeriform prey from 1986 to

1987. Relative composition of other prey did not differ between years (*P* > 0.1, Table VI-2). Frequency of Rallid prey appeared greater in 1987 when coot abundance indices on segment 11 were higher than in 1986, but the difference was not significant (*P* = 0.142).

Table VI-2. Variation in relative composition of prey[a] of great horned owls between 1986 and 1987, and among nesting areas[b] within years as indicated by standard deviations (SD).

	% frequency[c]				% biomass			
	1986		1987		1986		1987	
Prey category	mean	SD	mean	SD	mean	SD	mean	SD
Mammals								
White-tailed jackrabbit	5.0	3.7	1.9	2.5	10.8	9.5	4.8	6.4
Ground squirrel	2.0	2.5	1.1	0.7	2.1	2.6	1.5	1.6
Mouse[d]	18.1	9.4	11.4	6.7	1.7	1.1	1.0	0.6
Vole[d]	7.0	4.3	14.3	2.8	1.0	0.6	2.2	0.7
Birds								
Grebe	3.2	2.3	2.9	1.7	5.7	4.0	5.5	3.2
Duck	35.5	15.7	32.5	12.1	51.4	18.3	42.3	12.2
Galliform	1.3	3.3	1.2	1.0	2.3	5.9	3.4	2.6
Rallid	7.6	5.3	14.4	7.8	15.9	11.4	25.7	9.2
Charadriiform	3.2	2.4	2.4	3.0	1.6	1.1	1.2	1.3
Passeriform[d]	12.1	5.1	9.0	4.4	3.2	1.8	2.9	2.0
Amphibians	1.9	3.9	0.6	0.7	0.6	1.3	0.2	0.2

[a] Excludes prey or prey groups that comprised <1% dietary composition by frequency.

[b] *N* = 11 nesting areas monitored both in 1986 and 1987; nesting areas sampled 1 year were mutually exclusive (i.e., independent) of nesting areas in alternate year.

[c] Significant difference in overall relative (%) frequency composition between years; multivariate analysis of covariance: Wilks lambda = 0.014, *F* = 18.06, df = 16, *P* = 0.006.

[d] Significant difference in relative (%) frequency between years; univariate analysis of covariance: mouse, *P* = 0.019, vole, *P* = 0.005, Passeriform, *P* = 0.047.

Variation among Nesting Areas

Habitat was variable among great horned owl nesting areas (Table VI-3) and was similar between nesting areas on (n = 8) compared to off (n = 14) Lucy Township except that nesting areas on the township averaged slightly more semi-permanent wetland area (mean ± SD = 33 ± 26 compared with 21 ± 13 ha)(7 major habitat types: overall multivariate ANOVA, F = 3.75, df = 21, P = 0.017; semi-permanent wetland, univariate ANOVA, P = 0.022).

Table VI-3. Composition of 7 major habitat types among 22 great horned owl nesting areas, 1986-87.

	% of area <1 km from nest		
Habitat type	mean	SD	range
Quaking aspen tree clump	3.2	2.4	0.8-8.7
Seasonal wetland	10.1	4.6	2.3-19.8
Semi-permanent wetland	8.1	5.9	0.5-24.0
Cropland	28.4	15.4	3.1-56.7
Hayland	4.6	6.4	0-29.8
Pasture	22.8	14.4	1.9-55.5
Idle prairie	20.1	14.3	0.0-45.1

I observed extreme variability in use of prey among different nesting areas (Table VI-2). For example, percentage biomass comprised by ducks ranged from 28% to 90%. Next I present models for predicting use of prey that comprised >5% overall frequency.

Mice and voles. No multivariate models suitably explained variation in use of mouse prey among great horned owl nesting areas. Mouse DKR-biomass was, however, weakly correlated with percentage cropland in nesting areas (r = 0.377, df = 21, P = 0.084).

Most variation in great horned owl use of vole prey was explained by several competing models (Table VI-4). These implicated extent of hayland in nesting areas or amount (ha) of hayland near elevated perches in nesting areas as important habitat variables. The strong functional (i.e., dietary) response to between-year differences in vole abundance was indicated. Number of tethered young influenced DKR-biomass of vole prey; this independent variable was unimportant in models for other prey I examined.

Table VI-4. Multiple regression models that best explain variance in percentage biomass composition or daily kill rates (g/d) of vole and duck prey used by great horned owls at 22 nesting areas.

Model and independent variables	Coefficient		Fit of model		
	Standardized estimate (*b*′)	*P*[a]	R^2	*F*	*P*
Vole					
Model I (*Y* = % biomass)			0.593	9.47	0.003
Vole abundance index	0.66	0.003			
% hayland (log transformed)	0.31	0.107			
Model II (*Y* = DKR-biomass)			0.513	5.26	0.027
Number of juvenile owls	0.71	0.012			
Hayland near perches[b] (log transformed)	0.43	0.089			
Model III (Y = DKR-biomass)			0.689	8.86	0.002
Vole abundance index	0.51	0.015			
Number of juvenile owls	0.45	0.032			
% hayland (log transformed)	0.36	0.065			
Duck					
Model I (*Y* = DKR-biomass)			0.492	9.19	0.002
% pasture	0.55	0.003			
Distance to nearest road or farmstead	0.39	0.028			
Model II (*Y* = DKR-biomass)			0.414	6.70	0.006
Distance to nearest pasture (log transformed)	- 0.47	0.014			
Distance to nearest road or farmstead	0.45	0.019			

[a] Probability of *t* in reduced model test for coefficient.
[b] Area (ha) within nesting area ≤100 m from perches >6 m tall.

Ducks. No models with relative biomass as the dependent variable adequately explained variation in use of duck prey among owl nesting areas. However, about 41-49% of variation in DKR-biomass of ducks was explained by extent or proximity of pasture and distance to nearest road or farmstead (Table VI-4). I predicted that main components of breeding duck habitat, wetlands and idle prairie (i.e., nesting cover), would explain most variation in use of duck prey among great horned owl nesting areas. These variables were not important, nor were they correlated in univariate models (e.g., DKR-biomass versus percentage semi-permanent wetland in nesting area: $r = 0.063$, df = 21, $P = 0.775$).

Next I examined use of adult and juvenile duck prey separately. Only 1 suitable model resulted for adult ducks; extent (percentage) of pasture and aspen tree clumps explained 37% of variation in DKRs ($R^2 = 0.369$, 21 df, $P = 0.013$; pasture $b' = 0.49$, $P = 0.015$, aspen $b' = 0.32$, $P = 0.099$). Wetlands were unimportant as in previous models for use of duck prey. No multivariate models adequately revealed variation in use of duckling prey although duckling DKR-biomass was correlated with extent of semi-permanent wetland within great horned owl nesting areas ($r = 0.418$, df = 21, $P = 0.053$). From this second analysis, I conclude the positive relationship of pasture to use of duck prey suggested by models in Table VI-4 pertained mostly to adult ducks.

Rallids. No multivariate models adequately explained variation in use of Rallid prey. Both percentage biomass and DKR-biomass among owl nesting areas were correlated with an index of coot abundance from segment 11 ($r = 0.43$ and 0.45, $P = 0.048$ and 0.038), and coot DKR was negatively correlated with the amount of idle prairie within nesting areas that was $\leq$100 m from elevated perches ($r = -0.516$, $P = 0.024$).

Passeriforms. No multi- or univariate models adequately explained variation in use of Passeriform prey.

Profile of Duck Prey

Composition

I counted 102 adult ducks among prey at tether platforms in 1986 and 130 in 1987; all but 4 (all *Anas* spp.) were identified to species level. Blue-winged teal, mallard, gadwall, and ruddy occurred most frequently as prey (Table VI-5). Comparison to composition of adult ducks on segment 11 suggested blue-winged teal were preyed on disproportionately greater than other ducks in both years, and mallards and lesser scaup less than other ducks in 1987 and 1986, respectively.

Table VI-5. Percent species composition of adult duck prey at great horned owl tether platforms and species composition of ducks on a 0.4 x 28.8-km transect that traversed the north end of the study area.[a]

	1986[b]		1987[b]	
Species	% of duck prey	% of population	% of duck prey	% of population
Green-winged teal	0	0	0.8	0.9
Mallard	16.0	20.4	8.6	35.0
Northern pintail	6.0	8.1	5.5	3.4
Blue-winged teal	20.0	12.2	42.2	9.8
Northern shoveler	2.0	8.1	10.2	9.0
Gadwall	23.0	18.7	9.4	12.6
American wigeon	9.0	2.0	2.3	6.2
Redhead	3.0	0	2.3	4.6
Canvasback	0	2.7	0	1.7
Lesser scaup	7.0	19.1	7.8	11.6
Ruddy duck	12.0	8.7	10.9	4.6
N duck prey	100		128	

[a] Late May adult duck pairs on segment 11 of transect 2, stratum 45 of the North American Waterfowl Breeding Survey (FWS, unpubl. data). Data based on visibility corrections for the stratum.

[b] Observed proportions different from those expected based on approximate makeup of the local population: 1986 (excludes green-winged teal and redhead), $\underline{X}^2 = 50.45$, df = 8, $\underline{P} < 0.001$; 1987, $\underline{X}^2 = 181.7$, df = 10, $\underline{P} < 0.001$.

I identified sex of 96.5% of adult duck prey of known species (4 of 8 of unknown sex were ruddy ducks). There were no differences in sex ratios between years for each of 8 species with sample sizes >10 (Fisher exact tests, $P > 0.1$) so respective samples were pooled. Owl predation on male compared to female blue-winged teal did not differ from a 50:50 sex ratio at hatching or an average spring sex ratio for North America, but females of mallard and gadwall were preyed on disproportionately greater than males (Table VI-6). Four undetermined species of dabbling ducks all were females.

Table VI-6. Sex ratios of adult duck prey observed at great horned owl tether platforms during 1986-87 and comparison to 2 hypothetical sex ratios of the duck breeding population.

Species	Adult duck prey		Hypothetical % males in study area population[b]	
	% males	n[a]	Approximate % at hatching	Mean % in spring
Mallard	18.5[c]	27	50	53
Northern pintail	23.1[c]	13	50	59
Blue-winged teal	56.1[d]	73	50	59
Northern shoveler	46.7[d]	15	50	60
Gadwall	22.9[c]	35	50	53
American wigeon	41.7[d]	12	50	55
Redhead	(2 of 5)		--	--
Lesser scaup	38.5[e]	13	50	70
Ruddy duck	73.1[f]	26	50	62

[a] Total number of adults (years combined) for which sex was identified.

[b] Sex ratio data from Bellrose et al. (1961); spring sex ratios were averages from several locations throughout North America.

[c] Sex ratio different from that at hatching and average in spring reported in Bellrose et al. (1961): mallard, $X^2 = 9.48$ and 11.54, $P = 0.002$ and $P < 0.001$; pintail, $X^2 = 2.77$ and 5.53, $P = 0.096$ and 0.019; gadwall, $X^2 = 9.26$ and 11.58, $P = 0.002$ and $P < 0.001$.

[d] Sex ratio not different from that at hatching and average in spring reported in Bellrose et al. (1961): blue-winged teal, $X^2 = 0.88$ and 0.14, $P = 0.349$ and 0.709; shoveler, $X^2 = 0$ and 0.63, $P = 1$ and 0.429; wigeon, $X^2 = 0.31$ and 0.41, $P = 0.579$ and 0.523.

Table VI-6. Continued.

[e] Sex ratio different from average in spring but not from that at hatching; $\underline{X}^2$ = 4.75 and 0.31, $\underline{P}$ = 0.029 and 0.579.

[f] Sex ratio not different from average in spring but different from that at hatching; $\underline{X}^2$ = 0.92 and 4.65, $\underline{P}$ = 0.336 and 0.031.

Only 5 of 778 duckling prey found at tether platforms were identified to species (2 mallard, 1 pintail, 2 blue-winged teal) although 95% of 201 ducklings identified to genera were Anas spp. I did not determine sex of duckling prey. Of 778 duckling prey I found on platforms, 680 (87.4%) were Class I ducklings and the remainder were Class II. It was typical for Class I ducklings to occur in waves (Errington et al. 1940) of similar size individuals in owl pellets collected over 3-4 days.

Chronology

Adult ducks comprised nearly all duck prey in great horned owl diets during May but Class I ducklings made up most of percentage frequency and nearly half of percentage biomass of duck prey by late June (Fig. VI-2). Even though ducklings seldom were preyed on by great horned owls in May, Class I duckling prey were found on tether platforms as early as 11 May, corresponding to hatching of earliest nests of mallard and northern pintail (based on duck nesting data on adjacent LNWR [A. Kruse and B. Bowen, unpubl. data]). In 1986, Class I duckling prey comprised 53% frequency of all great horned owl prey by early July; 8 adult ducks were consumed by 12 owl families during 2 weeks of early July compared to 44 in late May. The transition from adult to juvenile duck prey in late spring contributed to an overall decrease in mean prey weight from about 250 g to about 150 g between late May and late June both years.

There was a 2-week lag in chronology of owl predation on ducks in 1986 compared to 1987 (Fig. VI-2). Adult duck prey occurred twice as frequently as Class I ducklings in early June 1986 but half as frequently in early June 1987, and relative contribution of Class II

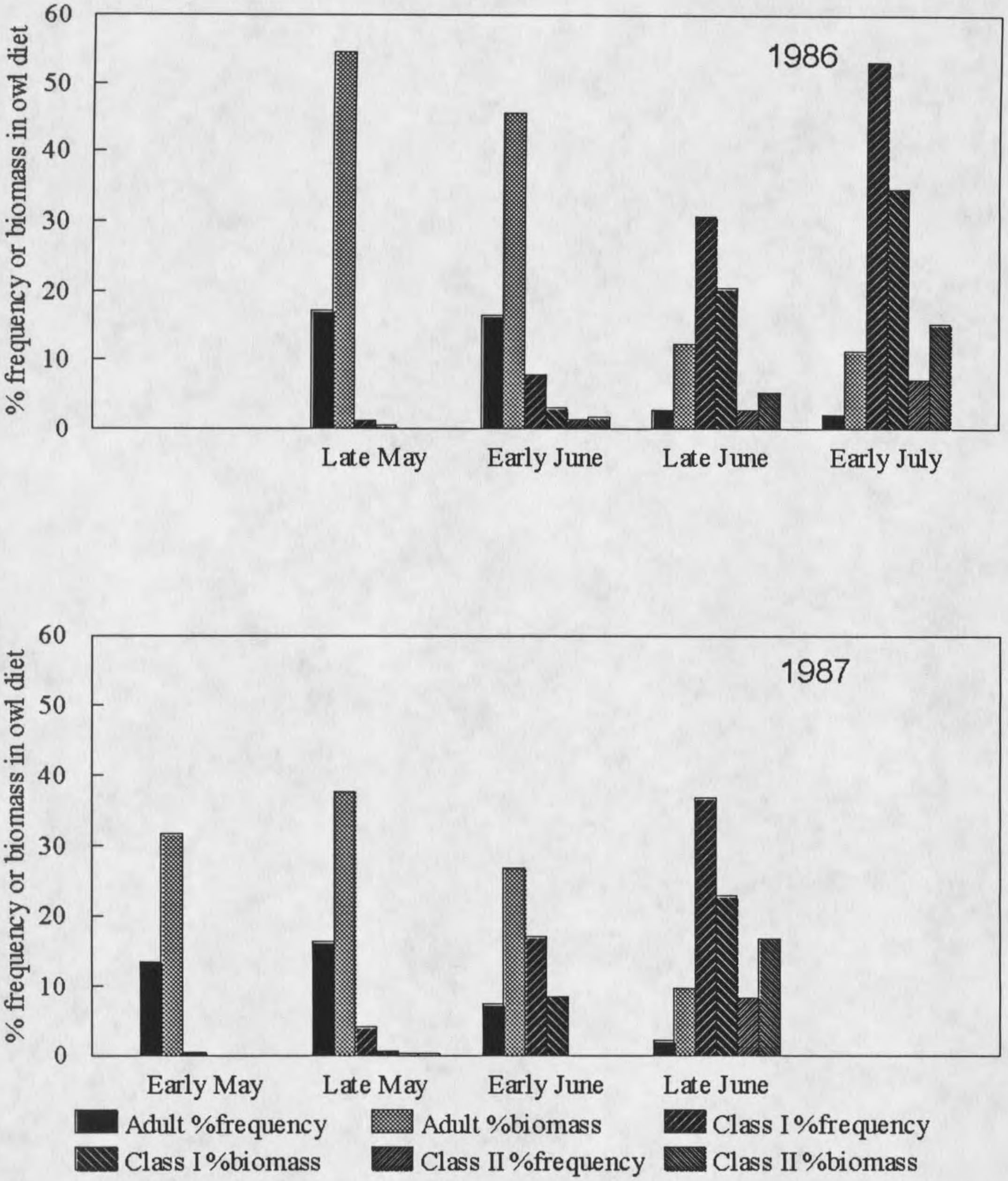

Figure VI-2. Temporal variation in importance of adult duck, Class I duckling, and Class II duckling prey to nesting great horned owls in late spring and early summer, 1986 and 1987 (data incomplete for early May 1986 and early July 1987).

ducklings to great horned owl diets was similar between late June 1987 and early July 1986. The lag coincided with delayed early nesting by ducks in 1986 due to an April snowstorm, followed by May rains that attracted and encouraged nesting by ducks; on LNWR, 39% of duck nests found by searching 500 ha of prairie every 3 weeks in 1986 were initiated by late May, compared with 57% in 1987 (A. Kruse and B. Bowen, unpubl. data).

Rates of Use of Duck Prey

Mean DKR-numbers of adult ducks averaged 0.3/nesting area during about 6 weeks from mid-May through June, 1986 and 1987 (Table VI-7). Highest rates (0.4-0.5 adult ducks/day) as well as the lowest rate (<0.1/day) occurred in nesting areas dominated by pasture, idle prairie, and wetlands. Mean DKR-numbers of juvenile ducks averaged about 0.4 duckling/owl nesting area during mid-May through June 1986 and about 0.9 in 1987; duckling Drs were significantly greater in 1987 (Table VI-7). Dominant habitat varied among nesting areas with highest rates (>1 duckling/day), and the lowest rate (<0.1/day) occurred at a nesting area where owls switched to young domestic chickens released by a farmer in early June. Mean Drs of ducklings exceeded those of adult ducks in 1987.

Table VI-7. Estimated numbers of adult and juvenile ducks killed daily per owl nesting area by great horned owls during mid-May through June, 1986 and 1987.

Year	_n_ owl nesting areas	Adult ducks/day			Ducklings/day		
		Mean	SD	range	Mean	SD	range
1986	11	0.28	0.14	0.04-0.48	0.43[a]	0.47	0.15-1.75
1987	11	0.25[b]	0.10	0.09-0.46	0.87[a,b]	0.50	0.02-1.92

[a] Difference in daily kill rates occurred between years; Mann-Whitney test, _P_ = 0.012.

[b] Difference in daily kill rates between adult and juvenile ducks; Wilcoxon signed ranks test, _P_ = 0.008.

DISCUSSION

Because juvenile great horned owls normally undergo a lengthy period of parental dependency and do little flying for 1-2 months after leaving nests (Petersen 1979, Johnsgard 1988), my tethering of juvenile great horned owls beyond their normal nest departure age of 5-6 weeks (Johnsgard 1988) probably did not significantly decrease their survival. No mortality occurred among tethered owlets, compared with low mortality in other studies (McInvaille and Keith 1974, Petersen and Keir 1976).

Importance of Avian Prey and Wetland Habitats to Owls

Snyder and Wiley (1976) characterized frequency composition of great horned owl diets in North America as 77% mammalian and 6% avian prey. Overwhelming importance of avian, especially duck, prey in my study was unusual though not entirely unique. Cursory surveys of great horned owl diets in northwestern and southcentral North Dakota suggested 79% and 61% frequencies of avian prey, respectively (Part IV, Gilmer et al. 1983). I attribute importance of birds in owl diets to the relatively diverse avifauna associated with the mixed grass prairie and wetlands of the Missouri Coteau (Stewart 1975, Kantrud et al. 1989). At least 50 species of birds were represented in great horned owl diets in this study. Scarcity of other, usually staple prey especially Leporids (Errington et al. 1940) also contributed to high use of avian prey. For example, nesting great horned owls in the nearby Aspen Parkland region of Canada, where wetlands abound, rely heavily on snowshoe hares (Lepus americana) and rodents (Pittman 1925, Bird 1929, Houston 1987).

Prodigious use of wetland prey by nesting great horned owls in late spring and early summer was a major finding of this study. Such prey were far less important to nesting great horned owls in the Great Lakes states (Errington et al. 1940, Petersen 1979) and boreal forest ecotone (Rusch et al. 1972). Use of grebes, sora, yellow-headed and red-winged blackbirds, juvenile muskrat, and especially ducks and coots was so extensive in this study that wetlands had to have been major foraging sites of adult great horned owls. Occurrence of waves of juvenile prey (Errington et al. 1940, Errington 1967) especially Class I ducklings of similar size in owl pellets I collected over 3-4 days suggested adult owls returned repeatedly to forage on the same broods at the same wetland sites, as Olsson (1979) noted for nesting eagle owls (B. bubo) in Sweden. Some adult and juvenile ducks could have been captured by great horned owls in uplands (e.g., hens at nests, broods traveling between wetlands) but others such as coots and grebes occur almost exclusively in wetlands especially semi-permanent types during the breeding season (Kantrud and Stewart 1984, Kantrud 1985).

Only a few valid regression models had worthwhile predictive value for owl use of wetland prey. For example, there was no relationship between use of ducks or coots and proximity and extent of wetlands within owl nesting areas. I believe this implies great horned owls sought wetland prey regardless of distance to or abundance of wetland habitats around tether platforms. Thus, if abundance of wetland-dependent prey related directly to occurrence of wetland habitats, owls did not consistently prey on what was locally most abundant, a relationship McInvaille and Keith (1974) also noted for great horned owls and waterbirds and wetlands in Alberta. Instead, my data align with the assertion of Rusch et al. (1972) that wetlands are an exception to a direct, prey habitat-prey use relationship and that prey are more available and vulnerable to the owl in wetland sites.

Great horned owls may have used wetland-dependent prey extensively because quaking aspen comprised most elevated hunting perches on my study area and occurred mainly on wetland borders. But, owls used prey from wetlands more than prey from uplands even though upland habitats dominated area around aspen tree clumps. I propose that prairie wetlands with adjacent tree clumps are highly profitable patches (Krebs 1973, Pyke et al. 1977) for foraging great horned owls in late spring and summer, probably due to high diversity and density of prey that likely occur in wetlands (Kantrud and Stewart 1984, Kantrud et al. 1989) combined with the nearby, elevated hunting perches.

Dietary Response to Prey Abundance

Great horned owls responded functionally to increased abundances of meadow voles between years. Such responses by the owl to changing prey have been documented elsewhere (e.g., Rusch et al. 1972, Petersen 1979). But, regression models in my study suggested dietary responses toward alternate prey did not significantly influence relative biomass or DKR-numbers ~~Drs~~ of duck prey used by owls. A coincident increase between years in abundance of ducks and voles partly obscured buffering effects but lack of change between years in relative composition of duck prey in owl diets suggested some buffering occurred. Simultaneous, increased abundance of another alternate prey, American coots, probably diminished conspicuousness of buffering by voles. Functional response of great horned owls to a peak in snowshoe hare abundance buffered predation on waterfowl in the boreal forest ecotone of Alberta (Adamcik et al. 1978). In my study, prey-switching by 1 great horned owl family to domestic chickens coincided with lack of subsequent predation on ducks even though I had found adult and juvenile duck prey on the owl tether platform during previous weeks.

Use of other Prey

Relative low importance of Leporid prey in this study was expected because snowshoe hares and cottontails (Sylvilagus spp.) were lacking on the study area and white-tailed jackrabbits were scarce. Extent of predation on juvenile jackrabbits (n = 95 detected on platforms) in light of their apparent scarcity, however, implied selection for Leporid prey by great horned owls as Errington (1967:40) allowed. Leporids are most appropriate prey of great horned owls mainly because of their ideal size (Donazar et al. 1989).

Use of jackrabbit, deer mouse, and ground squirrel prey indicated great horned owls did not hunt wetlands exclusively. Use of ground squirrel prey especially thirteen-lined ground squirrels that are completely diurnal (Jones et al. 1983:144) suggests prairie great horned owls hunt beyond dusk to dawn. Nights are short (about 7 h) in the northern plains in early summer, perhaps too short for adult owls to capture enough prey to feed themselves and several young. Great horned owls could compensate by either extending their crepuscular activity or by selecting largest, most profitable prey available.

Meadow voles were another often-used prey not strictly tied to wetlands although meadow voles inhabit dense, mesic vegetation (Getz 1961, Steele 1977) that typically occurs on wetland peripheries and within ephemeral and temporary wetlands in the PPR (Kantrud et al. 1989). Regression models suggested a link between vole use and hayland, which mainly was upland cover, but owls preyed on voles before hay was harvested beginning in late June and early July. Perhaps owls preyed on voles in hayland even when relatively tall (to 45 cm) vegetation was present, and lack of vegetative litter or mulch in annually cut hayland more critically influenced security of voles than vegetation height. Great horned owls can forage in vegetation up to 45-60 cm tall (Frounfelker 1977) especially when elevated perches are nearby (Petersen 1979); a regression model in this study suggested a direct link between use of vole prey and ha of hayland near hunting perches.

Scarce use of sharp-tailed grouse prey was a startling result because the grouse was very common on my study area. For example, I noted 4 leks on about 25 km^2 of Lucy Township, each with 18-30 displaying male grouse. These leks were within great horned owl nesting areas I monitored beginning in May when grouse were active on leks at dawn and dusk, yet the grouse seemed invulnerable to owl predation. Houston (1960) also found little evidence of predation by great horned owls on sharp-tailed grouse in Saskatchewan and Berger et al. (1963) noted raptors seldom preyed on prairie chickens on leks in Wisconsin.

Ecology of Owl Predation on Ducks

Use of adult duck prey related to proximity and extent of pasture around nests, as per regression models. Also, females of several species of upland-nesting ducks were preyed on disproportionately greater than males. Based on a view of models and sex ratio data in concert, I believe females nesting in pastures were adult ducks most likely to be preyed on by great horned owls in late spring. But, blue-winged teal and ruddy ducks were frequently used adult duck prey for which differential vulnerability disfavoring females was not implied. These exceptions occurred, I believe, because teal and ruddy ducks were small enough (<700 g) that great horned owls could capably manage them over water where male ducks may have been as vulnerable as females; males of other, larger duck species could be managed on land by great horned owls but not as easily over water, away from shore. Because male ducks are not tied to nests, males of the larger species can roost on marshes in relative safety from owl predation. Frequent use of adult coots and grebes, which are moderately large (400-700 g) and almost strictly aquatic birds, support my premise about patterns of owl predation on large birds over water. So, too, did use of blue-winged teal of either sex, both years of the study; it was the duck species most frequently preyed on and was used more than expected based on abundance relative to all duck species.

Excluding teal, female ducks most frequently represented among adult duck prey were mallard and gadwall, which tend to nest in densest upland cover available (Bellrose 1976). Female ducks that nest in May must depend on residual vegetative cover from previous years' growth for concealment because new foliage is just emerging. Because extent and proximity of pasture was an important explanatory variable in regression models for predicting adult duck biomass used by owls, and female mallards and gadwalls contributed much of adult duck biomass to great horned owl diets, I postulate that residual growth in pastures may have inadequately concealed nesting female mallard and gadwall from great horned owls. A regression model also suggested a relationship between owl predation on ducks and extent of aspen clumps. Such elevated hunting perches might allow great horned owls to detect female ducks nesting in all but the densest residual cover in late spring.

Crude estimates of adult duck density from segment 11 in conjunction with observed ~~Drs~~ DKR-numbers and great horned owl nesting density of about 0.11 occupied nests/km^2 (Part III) suggested that in 1986 and 1987 owls depredated 1.4 and 1.3 ducks/km^2 or roughly 3% and 1% of adult ducks present during mid-May through June. These predation rate estimates (proportion of the prey population removed by owls) likely encompass the period (late spring) of peak owl predation on ducks during spring and summer and are not very meaningful outside the context of overall food demands of great horned owls as dictated by owl reproductive success. Not all owl nesting areas successfully produced young and unsuccessful raptor pairs certainly demand less total prey (Craighead and Craighead 1956, Newton 1979). Nesting success of great horned owls on Lucy Township was 33% and 78% in 1986 and 1987 (Part III), so above owl predation rates based on data from successful nests probably overestimated take of ducks/km^2 by all great horned owls, especially in 1986.

Use of duck prey was marked by transition during May to June from mostly adults to juveniles. I believe this change corresponded closely to nesting chronology of area ducks. For example, a 2-week lag in the transition to duckling prey between years probably coincided with delayed early nesting by ducks in 1986 compared with 1987.

The occurrence of multiple numbers of duck broods in wetlands made these most profitable sites for securing duck prey by late June. Nearly all ducklings preyed on in June by great horned owls were Class I, but proportions of duck prey comprised by Class II ducklings had increased by early July when I ended my study. Most available evidence suggests the bulk of duckling mortality occurs in the first 2 weeks (Sargeant and Raveling 1992). My observation that 87% of duckling prey on owl tether platforms were Class I (<2.5 weeks old) supports this pattern for great horned owl predation, although I studied owl diets during the early to mid-nesting season of area ducks, when most juvenile ducks available were Class I ducklings.

I did not survey availability of duckling prey, but an increase in the relative abundance index of ducklings on segment 11 coincided with a significant increase in DKR-numbers of ducklings by great horned owls between years. Moreover, all seasonal wetlands and small (<1 ha), semi-permanent marshes rapidly became dry during June and July in 1987. For example, 73 and 95% (respectively) of these wetland types on adjacent LNWR held water in early May but only 3 and 24% did by mid-July (FWS, unpubl. refuge files). This concentrated duck broods in the few remaining wetlands that held water, which may have made ducklings more vulnerable to great horned owl predation. Thus, greater owl predation on ducklings in 1987 may well have conveyed a heightened state of vulnerability among ducklings (Errington 1938) associated with onset of drought. Based on an owl nesting density of 0.11 occupied nests/km^2 (Part III), mean ~~Drs~~ DKR-numbers of 0.43 and 0.87 ducklings per owl nesting area in 1986 and 1987 equalled about 2 and 4 ducklings/km^2 depredated by great horned owls during mid-May through June.

SUMMARY AND CONCLUSIONS

Great horned owls I studied relied heavily on avian prey associated with prairie wetlands. I believe varied composition of diets among owl pairs was not always clearly related to habitat or land use because wetlands were selected as foraging sites regardless of prevalence or distance from nests, and that availability of adjacent perches was important in determining use of wetlands by owls. Diversity of wetland prey and differences in prey preference among owl pairs also clouded prediction of owl diet based on wetland habitat within nesting areas. Ducks, American coots, deer mice, meadow voles, and Passeriforms especially blackbirds were most important prey overall.

Functional responses to increased annual abundance of voles did not significantly influence use of ducks probably because of a coincident increase in duck abundance and heightened vulnerability of duckling prey caused by impending drought. Predation on adult ducks occurred over a relatively short time period in late spring, before the surge in availability of vulnerable juvenile prey of all kinds by summer; most ducks returned to breed in mid- to late April, just before I had begun to monitor owl diets. Differential vulnerability between sexes of several species potentially was the most important aspect of owl predation on adult ducks. Nesting female ducks are known to be more vulnerable than males to other predators (e.g., red fox [Sargeant et al. 1984]).

This study documented modest removal per unit area of adult ducks and ducklings during late spring by great horned owls nesting in an area of good waterfowl breeding habitat in the PPR. Extent of this predation was partly facilitated by a relatively high nesting density of owls. Here, I also stress importance of considering great horned owl annual reproductive success as an important influence on prey demands during spring and summer; there is some evidence of generally poor annual productivity for great horned owls in northern prairies (Part II), although this needs wider documentation. The impact of great horned owl predation on populations of prairie-nesting ducks must be viewed in the context of whether and how such losses effect overall duck population dynamics (reviewed by Sargeant and Raveling 1992).

LITERATURE CITED

ADAMCIK, R. S., A. W. TODD, and L. B. KEITH. 1978. Demographic and dietary responses of great horned owls during a snowshoe hare fluctuation. Can. Field-Nat. 92:156-166.

BELLROSE, F. C. 1976. Ducks, geese and swans of North America. Stackpole, Harrisburg, Pa. 543pp.

---, T. G. SCOTT, A. S. HAWKINS, and J. B. LOW. 1961. Sex ratios and age ratios in North American ducks. Illinois Nat. Hist. Surv. Bull. 27:391-474.

BENT, A. C. 1938. Life histories of North American birds of prey, part 2. Smithsonian Inst., U.S. Natl. Mus. Bull. 170, Washington, D.C. 465pp.

BERGER, D. D., F. HAMERSTROM, and F. N. HAMERSTROM Jr. 1963. The effect of raptors on prairie chickens on booming grounds. J. Wildl. Manage. 27:778-791.

BIRD, R. D. 1929. The great horned owl in Manitoba. Can. Field-Nat. 43:79-83.

BLUEMLE, J. P. 1977. The face of North Dakota: the geologic story. North Dakota Geol. Surv. Educ. Ser. 11. 73pp.

COLLOPY, M. W. 1983. A comparison of direct observations and collections of prey remains in determining the diet of golden eagles. J. Wildl. Manage. 47:360-368.

CRAIGHEAD, J. J., and F. C. CRAIGHEAD. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania. 443pp.

DANE, C. W. 1965. The influence of age on development and reproductive capability of the blue-winged teal (Anas discors Linnaeus). Ph.D. Thesis, Purdue Univ., West Lafayette, Indiana. 171pp.

DANIEL, W. W. 1990. Applied non-parametric statistics. PWS-KENT Publishing Co., Boston, Mass. 635pp.

DARROW, R. W. 1945. Relation of buffer species abundance to fox predation on grouse nests. Trans. North Am. Wildl. Conf. 5:270-273.

DASMANN, R. F. 1964. Wildlife biology. Wiley and Sons, New York. 231pp.

DIXON, W. J., ed. 1983. BMDP statistical software. Univ. California Press, Berkeley. 733pp.

DONAZAR, J. A., F. HIRALDO, M. DELIBES, and R. R. ESTRELLA. 1989. Comparative food habits of the eagle owl Bubo bubo and the great horned owl Bubo virginianus in six Palearctic and Nearctic biomes. Ornis Scandinavica 20:298-306.

DUNNING, J. B. 1984. Body weights of 686 species of North American birds. Western Bird Banding Asso. Monogr. 1. 38pp.

EBERHARDT, L. E., and A. B. SARGEANT. 1977. Mink predation on prairie marshes during the waterfowl breeding season. Pages 33-43 in R. L. Phillips and C. Jonkel, eds. Predator Symposium. Univ. Montana, Missoula.

ERRINGTON, P. L. 1930. The pellet analysis method of raptor food habits study. Condor 32:292-296.

---. 1932. Studies on the behavior of the great horned owl. Wilson Bull. 44:212-220.

---. 1938. The great horned owl as an indicator of vulnerability in prey populations. J. Wildl. Manage. 2:190-205.

---. 1967. Of predation and life, 1st ed. University of Iowa Press, Ames, Iowa. 277pp.

---, F. HAMERSTROM, and F. N. HAMERSTROM Jr. 1940. The great horned owl and its prey in north-central United States. Iowa Agric. Exp. Stn. Res. Bull. 227:758-850.

FROUNFELKER, C. R. 1977. Prey selection of the great horned owl with reference to habitat and prey availability. M.S. Thesis, Univ. Idaho, Moscow. 62pp.

GETZ, L. L. 1961. Factors influencing the local distribution of Microtus and Synaptomys in southern Michigan. Ecology 42:110-119.

GILMER, D. S., P. M. KONRAD, and R. E. STEWART. 1983. Nesting ecology of red-tailed hawks and great horned owls in central North Dakota and their interactions with other large raptors. Prairie Nat. 15:133-143.

GOLLOP, J. B., and W. H. MARSHALL. 1954. A guide for aging duck broods in the field. Miss. Flyway Counc. Tech. Sect. unpubl. mimeo. 14pp.

GREENWOOD, R. J. 1975. Reproduction and development of four mallard lines. Prairie Nat. 7:9-16.

HOUSTON, C. S. 1960. 1960 - the year of the owls. Blue Jay 18:105-110.

---. 1987. Nearly synchronous cycles of the great horned owl and snowshoe hare in Saskatchewan. U.S. For. Serv. Gen. Tech. Rep. RM-142:56-58.

JAMES, T. R., and R. W. SEABLOOM. 1969. Aspects of growth in the white-tailed jackrabbit. Proc. North Dakota Acad. Sci. 23:7-14.

JOHNSGARD, P. A. 1988. North American owls: biology and natural history. Smithsonian Inst. Press, Washington, D.C. 295pp.

JONES, J. K., Jr., D. M. ARMSTRONG, R. S. HOFFMAN, and C. JONES. 1983. Mammals of the Northern Great Plains. Univ. Nebraska Press, Lincoln, Nebraska. 379pp.

KANTRUD, H. A. 1985. American coot habitat in North Dakota. Prairie Nat. 17:23-32.

---, and R. E. STEWART. 1984. Ecological distribution and crude density of breeding birds on prairie wetlands. J. Wildl. Manage. 48:426-437.

---, G. L. KRAPU, and G. A. SWANSON. 1989. Prairie basin wetlands of the Dakotas: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85:111pp.

KORSCHGEN, L. J., and H. B. STUART. 1972. Twenty years of avian predator-small mammal relationships in Missouri. J. Wildl. Manage. 36:269-282.

KREBS, J. R. 1973. Behavioral aspects of predation. Pages 73-111 in P. P. G. Bateson and P. H. Klopfer, eds. Perspectives in ethology. Plenum Press, New York.

MARTI, C. D. 1969. Some comparisons of the feeding ecology of four owls in northcentral Colorado. Southwest. Nat. 14:163-170.

---. 1987. Raptor food habits studies. Natl. Wildl. Fed. Sci. Tech. Ser. 10:67-80.

MCINVAILLE, W. B., Jr., and L. B. KEITH. 1974. Predator-prey relations and breeding biology of the great horned owl and red-tailed hawk in central Alberta. Can. Field-Nat. 88:1-20.

NETER, J., W. WASSERMAN, and M. H. KUTNER. 1985. Applied linear statistical models. Irwin, Inc., Homewood, Illinois. 1127pp.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota. 399pp.

OLSSON, V. 1979. Studies on a population of eagle owls, Bubo bubo (L.) in southeast Sweden. Viltrevy 11:99pp.

ORIANS, G., and F. KUHLMAN. 1956. Red-tailed hawk and horned owl populations in Wisconsin. Condor 58:371-385.

ORING, L. W. 1968. Growth, molts and plumages of the gadwall. Auk 85:355-380.

PETERSEN, L. 1979. Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. 111. 63pp.

PETERSEN, L. R., and J. R. KEIR. 1976. Tether platforms - an improved technique for raptor food habits study. Raptor Res. 10:21-28.

PITTMAN, H. H. 1925. The food of the western horned owl. Bird Lore 27:92-96.

PYKE, G. H., H. R. PULLIAM, and E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137-154.

RUDOLPH, S. G. 1978. Predation ecology of coexisting great horned and barn owls. Wilson Bull. 90:134-137.

RUSCH, D. H., E. C. MESLOW, P. D. DOERR, and L. B. KEITH. 1972. Response of great horned owl populations to changing prey densities. J. Wildl. Manage. 36:282-296.

SARGEANT, A. B., and D. G. RAVELING. 1992. Mortality during the breeding season. Pages 396-422 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, eds. Ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

---, S. H. ALLEN, and R. T. EBERHARDT. 1984. Red fox predation on breeding ducks in midcontinent North America. Wildl. Monogr. 89:41pp.

---, R. J. GREENWOOD, M. A. SOVADA, and T. L. SHAFFER. 1993. Distribution and abundance of predators that affect duck production - Prairie Pothole Region. U.S. Fish Wildl. Serv. Resour. Publ. 194. In Press.

SAS INSTITUTE, Inc. 1989. SAS/STAT user's guide, version 6, 4th ed., Vol. 2. SAS Institute, Inc., Cary, NC. 846pp.

SMITH, A. G., J. H. STOUDT, and J. B. GOLLOP. 1964. Prairie potholes and marshes. Pages 39-50 in J. P. Linduska, ed. Waterfowl tommorrow. U.S. Government Printing Office, Washington, D.C.

SNYDER, N. F. R., and J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20. 96pp.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. W.H. Freeman Co., New York, NY. 859pp.

STEELE, R. W. 1977. A demographic study of Microtus pennsylvanicus in relation to habitat structure. M.S. Thesis, Univ. Guelph, Guelph, Ont. 123pp.

STEWART, R. E. 1975. Breeding birds of North Dakota. Tri-college Center for Environmental Studies, Fargo, North Dakota. 295pp.

---, and H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Dep. Inter. Bur. Sport Fish. Wildl. Res. Publ. 92. 57pp.

VOOUS, K. H. 1988. Owls of the Northern Hemisphere. MIT Press, Cambridge, Massachusettes. 320pp.

THESIS SUMMARIZING CONCLUSION

This research contributed to several information needs of raptors as well as of prairie ecology. Documentation of anthropogenic change in a northern prairie plant community and coinciding turnover in species of raptors during the past century, including pioneering and subsequent increases in annual nesting by 2 hawk species, had implications for understanding vegetation structure and raptor foraging habitat requirements in mixed grass prairie (Part I). Long-term nesting data demonstrated high collective abundance of nesting raptors in a northern prairie community and varying degrees of stability in annual nesting density and reproductive output among raptor species, corroborated distinct species habitat affinities and nesting distribution limits, and provided comparative nesting density data from an adjacent area under different land use (Parts II and III). Accounts of diets during breeding season of common, large (>700 g) species of raptors revealed overwhelming importance of avian prey and of wetlands as prey sources, variation in diet among raptor families, influence of nesting area habitat on diet, and rates of use of important prey types (Parts IV, V, and VI).

Kantrud and Kologiski (1983) urged resource personnel in the northern Great Plains to use biogeographic information in their conservation efforts and to preserve communities rather than habitat for individual species. My data on historic and current species composition of a raptor community (Parts I and II) help form a basis for such an approach on Lostwood National Wildlife Refuge (LNWR) in northwestern North Dakota and have direct implications for managing northern mixed grass prairie communities elsewhere. Species composition of the historic raptor assemblage was described; habitat correlates suggested raptors integrated an array of environmental variables and adequately modelled deviation of habitat from its historical condition. Thus, monitoring species composition of breeding raptor assemblages is 1 means of assessing proximity to pristine conditions.

Based on habitat needs of raptors that nested on LNWR about when the area was settled, management for the indigenous wildlife community depends on episodic defoliation to create interspersed grass-forb patches of diverse height and density. Over time, fire creates a mosaic of seral and climax stages (Wright and Bailey 1982) and along with grazing impact is probably the most important determinant of pristine northern mixed grass prairie (Higgins 1986).

Trends in nesting and foraging types of raptors from the historic raptor assemblage on LNWR can be summarized in terms of guilds, a group of species that exploits some class of environmental variables in a similar way without regard to their taxonomic relationship (Phelan and Robertson 1978, Jaksic 1981). The most obvious change was in raptors as part of nesting substrate guilds, from ground- or shrub-nesting to tree-nesting species. A more subtle guild change based on foraging has more significant meaning for understanding the historic wildlife and habitat complex. Ferruginous hawks, Swainson's hawks (B. swainsoni), and burrowing owls (Athene cunicularia) specialized in a foraging substrate guild characterized as open prairie/short vegetation/periodic disturbance and were replaced by red-tailed hawks and great horned owls that were more generalized in forage substrate (and prey type) needs and that depended on elevated hunting perches. Guilds and species are added to a community as vegetation structural complexity increases (Willson 1974); increased woody vegetation especially establishment of trees on LNWR led to additions or replacements rather than an expansion of guilds due to increased environmental patchiness in 3 dimensions, while overall plant diversity declined. Periodic mowing, burning, or grazing of prairie can enhance foraging opportunities for the open prairie/short vegetation/periodic disturbance guild while benefiting plant diversity and a host of indigenous wildlife species (Parts I and II, Ryan 1990).

Low mean annual reproductive success of great horned owls and red-tailed hawks during 8 years at LNWR (Part II) suggested recruitment from more productive areas was needed to maintain the relatively stable, high nesting densities observed. Raptors that nest in marginal habitat at edges of their breeding ranges generally experience poor reproductive success and exhibit lower nest site fidelity than raptors in more suitable habitat (Newton 1979). Other than Houston's (1987) note that great horned owls in prairie-agricultural settings of central Saskatchewan experience lower productivity than in nearby parkland habitats, there are no long-term productivity data published on great horned owls and red-tailed hawks from other areas of prairie in the northern Great Plains; such data are needed to corroborate whether patterns I documented pertain to the owl and hawk elsewhere. If such patterns of poor reproduction are more widespread and northern prairies are "sinks" for midcontinent populations of red-tailed hawks and great horned owls, thus unsuited for management to benefit these species, raptor conservation practices that prioritize benefits for historically common species are logical and more strongly justified in addition to other considerations.

I documented moderate rates of use of duck prey by great horned owls in an area of good waterfowl breeding habitat (Part VI), and a survey of red-tailed hawk prey use in early summer on LNWR suggested ducks may be as important to the hawk (Part IV). Although great horned owls probably depredated <4% of the local duck breeding population in late spring in this study (Part VI), the predation occurred at a critical point in the life cycle of ducks. Also, differential mortality between sexes of adult ducks suggested owls contributed to skewed sex ratios of several duck species. Prairie-nesting ducks face increasing predation pressure of many types not confronted historically (Sargeant et al. 1992); predation by great horned owls and red-tailed hawks is another form which ducks in the northern Great Plains rarely experienced under presettlement conditions. This predation may be locally important, should be further quantified, and possibly incorporated as a factor in models for managing prairie ducks (e.g., Cowardin and Johnson 1979) as well as for other migratory birds of special management concern.

However, simply quantifying raptor predation on migratory birds insufficiently addresses consequences of the predation act (Craighead and Craighead 1956, Errington 1967). I used regression analyses to infer some conditions under which ducks may have been vulnerable to raptor predation. Models are helpful for exploring predation and give insight into complex situations (Reynolds et al. 1988), and more definitive work would lead to better habitat management prescriptions.

Optimal foraging models are based on the premise that natural selection favors increased feeding efficiency (Royama 1970, Smith and Sweatman 1974, Pyke et al. 1977). Use of habitat specialist prey such as ducks by great horned owls was difficult to predict based on nesting area habitat (Part VI) compared to Swainson's hawks (Part V), suggesting the owl sought wetlands regardless of their proximity or prevalance in nesting areas.

Swainson's hawk diets were more diverse than other studies in the northern Great Plains have demonstrated (Part V). Predators probably have broader diets when encounter rates for all prey are low (Reynolds et al. 1988) and Swainson's hawks may improve their foraging efficiency by taking a wider variety of prey. This contrasted with great horned owls that tended to focus on juvenile duck prey during June (Part VI); the owl may improve its foraging efficiency by focusing on 1 or 2 prey types at a time, so long as encounter rates remain high (Krebs 1973). At owl tether platforms, I observed runs of duckling prey of same age classes which reinforced my proposal that great horned owls actively distinguished among areas of different prey availability and repeatedly foraged in wetlands that presumably were most profitable patches. Some evidence suggests ducks do not make use of spatial knowledge of their home ranges to avert predation by avoiding places where previously threatened (Curio 1976). Also, a predator's encounter rates of social prey such as ducks may actually increase following an episode of predation, making it profitable for predators to revisit patches (Erwin 1989).

Predation can be managed by altering habitat to increase or decrease hunting efficiency of predators and by dispersing favored habitat (Reynolds et al. 1988). Because predators will abandon search images when encounter rates with prey become too low, wide dispersion of critical habitats (e.g., management for wetland complexes for prairie ducks) is a logical strategy to reduce raptor predation on species of special management concern and should be coupled with management of highly profitable patches of buffer (alternate) prey habitat. Availability of buffer prey will likely emerge as a major factor in predation management in northern prairies (Sargeant and Raveling 1992).

Needs of most species of prairie raptors are modest and can compliment other wildlife management objectives. Based on findings herein, I recommend that where large (>5 km^2) blocks of northern mixed grass prairie are to be managed for an array of indigenous fauna, needs of prairie raptors can be met by alternately defoliating small (<1 km^2) units at least every 5 years through prescribed burning, high intensity/short duration grazing, or mowing and harvesting of hay crops, and by maintaining 1-2 trees or clumps of trees or tall shrubs for nest sites on every km^2. Where possible, these nest sites should be about 0.2-1.0 km from seasonal or semi-permanent wetlands and adjacent to uplands periodically treated by burning, mowing, or grazing, or adjacent to annually cut haylands.

Because raptors maintain large territories and reproduce at relatively slow rates, refuges alone can not provide sufficient breeding habitat area for successful conservation of prairie raptors (Newton 1979). Conservation measures on privately-owned tracts in the northern Great Plains including maintenance of scattered nest sites near haylands, pasture, and wetlands, and preservation of large pastures and wetland complexes will benefit prairie raptors and other wildlife native to the region.

I conclude that raptors nesting on the Missouri Coteau of northwestern North Dakota responded to an array of land use changes in mostly predictable ways. Results of changes generally were unfavorable for the indigenous raptor community, may have marginal net benefit for dominant members of the contemporary raptor community, and potentially pose management conflicts for species native to the region.

Resource personnel must decide on clear missions and objectives for any area to be managed. If the goal is to manage for a natural condition, we must be explicit about what we mean by "natural" and what we want for a natural area (Botkin 1990). I have provided information to assist resource personnel in decision-making for management of both private and public lands in the northern Great Plains.

LITERATURE CITED

BOTKIN, D. B. 1990. Discordant harmonies: a new ecology for the twenty-first century. Oxford Univ. Press, New York. 241pp.

COWARDIN, L. M., and D. H. JOHNSON. 1979. Mathematics and mallard management. J. Wildl. Manage. 43:18-35.

CRAIGHEAD, J. J., and F. C. CRAIGHEAD. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania. 443pp.

CURIO, E. 1976. The ethology of predation. Springer-Verlag, New York. 250pp.

ERRINGTON, P. L. 1967. Of predation and life, 1st ed. University of Iowa Press, Ames, Iowa. 277pp.

ERWIN, R. M. 1989. Predator-prey interactions, resource depression, and patch revisitation. Behav. Processes 18:1-16.

HIGGINS, K. F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. U.S. Fish Wildl. Serv. Resour. Publ. 161. 39pp.

HOUSTON, C. S. 1987. Nearly synchronous cycles of the great horned owl and snowshoe hare in Saskatchewan. U.S. For. Serv. Gen. Tech. Rep. RM-142:56-58.

JAKSIC, F. M. 1981. Abuse and misuse of the term "guild" in ecological studies. Oikos 37:397-400.

KANTRUD, H. A., and R. L. KOLOGISKI. 1983. Avian associations of the northern Great Plains grassland. J. Biogeogr. 10:331-350.

KREBS, J. R. 1973. Behavioral aspects of predation. Pages 73-111 in P. P. G. Bateson and P. H. Klopfer, eds. Perspectives in ethology. Plenum Press, New York.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota. 399pp.

PHELAN, F. J. S., and R. J. ROBERTSON. 1978. Predatory responses of a raptor guild to changes in prey density. Can. J. Zool. 56:2565-2572.

PYKE, G. H., H. R. PULLIAM, and E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137-154.

REYNOLDS, J. C., P. ANGELSTAM, and S. REDPATH. 1988. Predators, their ecology and impact on gamebird populations. Pages 72-97 in P. J. Hudson and M. R. W. Rands, eds. Ecology and management of gamebirds. Blackwell Professional Books, Oxford, England.

ROYAMA, T. 1970. Factors governing the hunting behaviour and selection of food by the great tit (Parus major L.). J. Anim. Ecol. 39:619-668.

RYAN, M. R. 1990. A dynamic approach to the consevation of the prairie ecosystem in the Midwest. Pages 91-106 in J. M. Sweeney, ed. Management of dynamic ecosystems. North Cent. Sect., The Wildl. Soc., West Lafayette, Ind.

SARGEANT, A. B., and D. G. RAVELING. 1992. Mortality during the breeding season. Pages 396-422 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu, eds. Ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

---, R. J. GREENWOOD, M. A. SOVADA, and T. L. SHAFFER. 1993. Distribution and abundance of predators that affect duck production - Prairie Pothole Region. U.S. Fish Wildl. Serv. Resour. Publ. 194. In Press.

SMITH, J. N. M., and H. P. A. SWEATMAN. 1974. Food-searching behavior of titmice in patchy environments. Ecology 55:1216-1232.

WILLSON, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

WRIGHT, H. A., and A. W. BAILEY. 1982. Fire ecology. J. Wiley and Sons, New York. 501pp.

APPENDIX

Appendix Table 1. Relative abundance[a] of migrant, non-nesting Falconiforms and Strigiforms observed at LNWR during spring (March-May), summer (June-August), fall (September-November), and winter (December-February) 1982-90.[b]

	Season			
Species	Spring	Summer	Fall	Winter
Turkey vulture (*Cathartes aura*)	r	r	r	
Osprey (*Pandion haliaetus*)	r	r	r	
Bald eagle (*Haliaeetus leucocephalus*)	u	r	u	o
Sharp-shinned hawk (*Accipiter striatus*)	u	o	u	
Northern Goshawk (*A. gentilis*)	r		o	o
Broad-winged hawk (*Buteo platypterus*)	o		o	
Rough-legged hawk (*Buteo lagopus*)	o		u	o
Golden eagle (*Aquila chrysaetos*)	u		u	u
Peregrine falcon (*Falco peregrinus*)	o		r	
Gyrfalcon (*F. rusticolis*)	o		o	o
Prairie falcon (*F. mexicanus*)	u	o	u	u
Snowy owl (*Nyctea scandiaca*)	o		o	o
Northern saw-whet owl (*Aegolius funereus*)	r		r	

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[a] Abundance category "r" (rare) = observed only once or twice every 2-5 + years, "o" (occassional) = observed once to several times most years, "u" (uncommon) = encountered infrequently but can be found with moderate search effort.

[b] Includes only species not having nest records for northwestern North Dakota (Stewart and Kantrud 1975).

Appendix Table 2. Prey weights[a] used for estimating relative dietary biomass consumed by Swainson's hawk families, excluding weights of prey species obtained exclusively from published literature.

Species	Weight (g)		Source[b]
	adult	juvenile	
White-tailed jackrabbit			
Lepus townsendii (juvenile; mean hindfoot length 85 mm)		600	1,2
Ground squirrels			
Spermophilus richardsonii	350		1,3
S. tridecemlineatus	175		1,3
S. franklinii	450		1,3
Voles and mice			
Microtus pennsylvanicus	33		1
Peromyscus maniculatus	20		1
Zapus spp.	19		1
Clethrionomys gapperi	18		1
Perognathus fasciatus	11		1,3
Miscellaneous mammals			
Blarina brevicauda	13		1
Ondatra zibethicus (juvenile)		600	1
Rattus norvegicus	250		1
Mustela nivalis	40		1
Ducks			
unidentified juvenile[c]			1,6,7,8,9

Class	Approximate tarsus length	
Ia	23	50
Ib	30	120
Ic	36	180
IIa	38	280
IIb	42	430
IIc	43	600

Galliforms			
Perdix perdix	390		1,4
Tympanchus phasianellus	885		1,4

Appendix Table 2. Continued.

Passeriforms		
Agelaius phoeniceus	53	1,4
Sturnella neglecta	97	1,4
Xanthocephalus xanthocephalus	65	1,4
Euphagus cyanocephalus	62	1,4
Quiscalus quiscula	115	1,4
Molothrus ater	44	1,4
Miscellaneous birds		
Zenaida macroura	120	1,4
Amphibians and Reptiles		
Ambystoma tigrinum	50	1
Rana pipiens	30	1
Thamnophis radix	100[d]	1
Opheodrys vernalis	15	1
Insecta - Orthoptera	1	1

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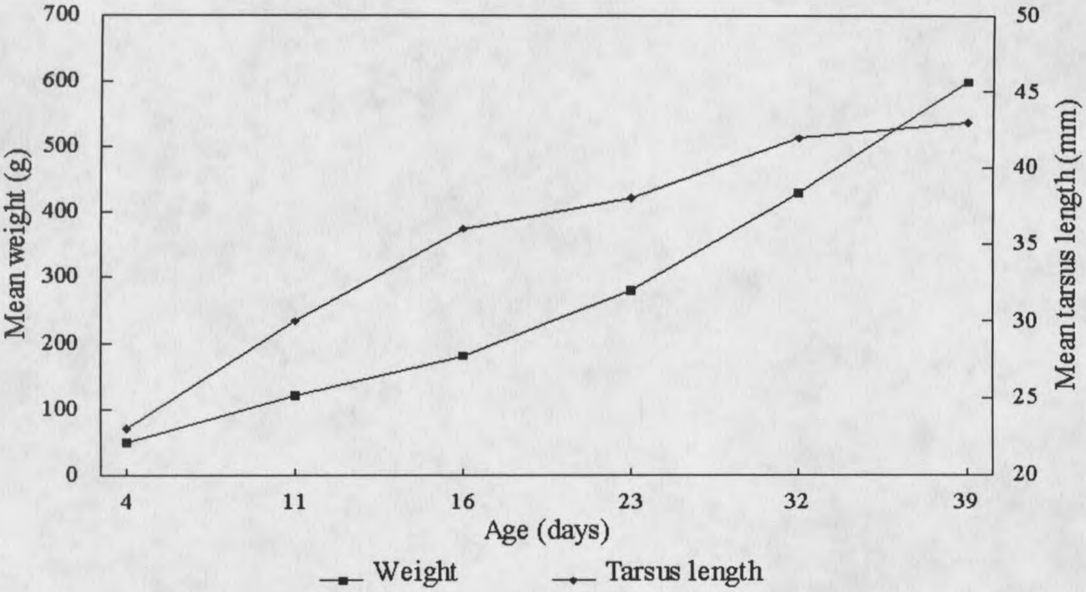
[a] Includes weights of juveniles of specific species; subadults and juveniles of other prey were assigned weights based on their approximate size relative to adults of same species.

[b] Source: 1 = data collected from study area; 2 = James and Seabloom 1969; 3 = Jones et al. 1983; 4 = Dunning 1984; 5 = Bellrose 1976; 6 = Greenwood 1975; 7 = Oring 1968; 8 = Dane 1965; 9 = Northern Prairie Wildlife Research Center, unpubl. manuscripts.

[c] Duckling classification according to Gollop and Marshall (1954). Biomass estimates derived from averages in Appendix D.

[d] Weight for an adult of length 43 cm.



Appendix Figure 1. Composite age-growth curve for juvenile mallard (Anas platyrhynchos), gadwall (A. strepera), and blue-winged teal (A. discors) used to estimate biomass of unidentified species of juvenile duck prey items recorded at Swainson's hawk and great horned owl tether platforms.

Appendix Table 3. Composition (percentage frequency) of Swainson's hawk diets based on prey recorded by observation of fresh (edible) prey items and discarded (inedible) remains at tether platforms during late nestling to early fledgling periods, and on fresh prey noted at nests during early to mid-nestling periods of the hawks on the Missouri Coteau in Burke County, North Dakota, summer 1986 and 1987.[a]

Prey category	Tether platform visits %	Nest visits %
Mammals[b]		
Ground squirrels	6.5	20.8
Voles and mice	63.3	48.8
Misc. mammals	0.8	0.5
Birds[c]		
Galliforms	2.3	2.4
Anseriforms	4.2	8.7
Passeriforms	4.9	13.0
Misc. birds	1.4	5.3[c]
Amphibians[d]	15.3	0
Reptiles[e]	0.5	0.5
Insects[f]	0.8	0
Total %	100.0	100.0
<u>N</u>	2473[g]	207

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[a] Based on 10 tether platforms in 1986 and 10 in 1987 at a total of 18 nesting areas, and nests at respective platform sites plus a total of 7 other nests at which no young reached tetherable age.

[b] Mammalian prey not specifically identified in table were (1) ground squirrel: mainly Richardson's (<u>Spermophilus richardsonii</u>) and thirteen-lined (<u>S. tridecemlineatus</u>), also (<5 individual prey) Franklin's (<u>S. franklini</u>); (2) vole and mouse: mainly meadow vole (<u>Microtus pennsylvanicus</u>) and deer mouse (<u>Peromyscus maniculatus</u>), also southern red-backed vole (<u>Clethrionomys gapperi</u>), olive-backed pocket mouse (<u>Perognathus fasciatus</u>), jumping mouse (<u>Zapus</u> spp.); (3) miscellaneous: short-tailed shrew (<u>Blarina brevicauda</u>), white-tailed jackrabbit (<u>Lepus townsendii</u>), muskrat (<u>Ondatra zibethicus</u>), Norway rat (<u>Rattus norvegicus</u>), least weasel (<u>Mustela nivalis</u>).

Appendix Table 3. Continued.

[c] Bird species were (1) Galliform: sharp-tailed grouse (*Tympanuchus phasianellus*) and gray partridge (*Perdix perdix*); (2) duck: mallard (*Anas platyrhynchos*), northern pintail (*A. acuta*), blue-winged teal (*A. discors*), American wigeon (*A. americana*), lesser scaup (*Aythya affinis*); (3) Passeriform: mainly unknown sparrows and unknown blackbirds (Emberizinae and Icterinae), also western kingbird (*Tyrannus verticalis*), eastern kingbird (*T. tyrannus*), horned lark (*Eremophila alpestris*), tree swallow (*Tachycineta bicolor*), black-billed magpie (*Pica pica*), Sprague's pipit (*Anthus spragueii*), vesper sparrow (*Pooecetes gramineus*), savannah sparrow (*Passerculus sandwichensis*), red-winged blackbird (*Agelaius phoeniceus*), western meadowlark (*Sturnella neglecta*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), Brewer's blackbird (*Euphagus cyanocephalus*), common grackle (*Quiscalus quiscula*), brown-headed cowbird (*Molothrus ater*); (4) miscellaneous: sora (*Porzana carolina*), American coot (*Fulica americana*), killdeer (*Charadrius vociferous*), lesser yellowlegs (*Tringa flavipes*), willet (*Catoptrophorus semipalmatus*), upland sandpiper (*Bartramia longicauda*), marbled godwit (*Limosa fedoa*) mourning dove (*Zenaida macroura*), short-eared owl (*Asio flammeus*), northern flicker (*Colaptes auratus*).

[d] Includes tiger salamander (*Ambystoma tigrinum*) and northern leopard frog (*Rana pipiens*).

[e] Includes plains garter snake (*Thamnophis radix*) and smooth green snake (*Opheodrys vernalis*).

[f] Insects all were grasshoppers or crickets (Orthoptera: Oedipodinae).

[g] Point estimate based on corrections for size-related biases for 1284 prey items actually recorded.

Appendix Table 4. Two crude estimates of duckling density near Swainson's hawk diet study area on the Missouri Coteau in Burke County, North Dakota, mid-July, 1987.

	Duckling survey or count	
Survey attribute	Segment 11[a]	Lostwood National Wildlife Refuge[b]
Distance from hawk diet study area	Traverses north end study area[c]	Adjacent (southeast)
Similarity of waterfowl breeding habitat to that around Swainson's hawk nest areas	about same; mixed land use	Similar wetland base, but twice as much nesting cover
Survey or count type	0.4 x 28.8 km plot, aerial count	Simple random sample, 5.4% of area; ground (foot) survey
Biases and validity	Visibility error, ≥50-80% ducklings overlooked; no variance estimate	Unknown accuracy; wide confidence intervals
Density estimate	35/km^2 (minimum count)	37-152/km^2 (90% confidence interval)

[a] Segment 11 is part of transect 2, stratum 45 of the North American Waterfowl Breeding Population Survey (U.S. Fish Wildl. Serv., unpubl.).
[b] U.S. Fish Wildl. Serv., unpubl. refuge files.
[c] Transect was 1.6 km north of and extended from 13 km west to 6 km east of Lucy Township in Burke County.

Appendix Table 5. Prey weights[a] used for estimating relative dietary biomass consumed by great horned owl families, excluding weights of prey species obtained exclusively from published literature.

Species	Approximate length (mm)		Weight (g)		Source[b]
	hind foot	radius/ulna	adult	juvenile	
White-tailed jackrabbit					
Lepus townsendii (juvenile)					1,2
	40	26		115	
	50	33		160	
	60	40		210	
	70	46		285	
	80	53		375	
	90	60		500	
	100	66		650	
	110	73		900	
Ground squirrels					
Spermophilus richardsonii			350		1,3
S. tridecemlineatus			175		1,3
S. franklinii			450		1,3
Voles and mice					
Microtus pennsylvanicus			33		1
Peromyscus maniculatus			20		1
Zapus spp.			19		1
Clethrionomys gapperi			18		1
Onychomys leucogaster			40		1,3
Perognathus fasciatus			11		1,3
Mus musculus			20		1
Miscellaneous mammals					
Blarina brevicauda			13		1
Sorex cinereus or *Sorex* spp.			4		1
Ondatra zibethicus			1200		1
Rattus norvegicus			250		1
Mustela nivalis			40		1
Mephitis mephitis			1240[c]		1

Appendix Table 5. Continued.

Ducks		
unidentified juvenile[d]		1,6,7,8,9

Class	Approximate tarsus length	
Ia	23	50
Ib	30	120
Ic	36	180
IIa	38	280
IIb	42	430
IIc	43	600

Galliforms		
Perdix perdix	390	1,4
Tympanchus phasianellus	885	1,4
Agelaius phoeniceus	53	1,4
Sturnella neglecta	97	1,4
Xanthocephalus xanthocephalus	65	1,4
Euphagus cyanocephalus	62	1,4
Quiscalus quiscula	115	1,4
Molothrus ater	44	1,4
Miscellaneous birds		
Zenaida macroura	120	1,4
Amphibians and Reptiles		
Ambystoma tigrinum	50	1
Rana pipiens	30	1
Thamnophis radix	100[e]	1
Opheodrys vernalis	15	1
Insecta - Orthoptera	1	1

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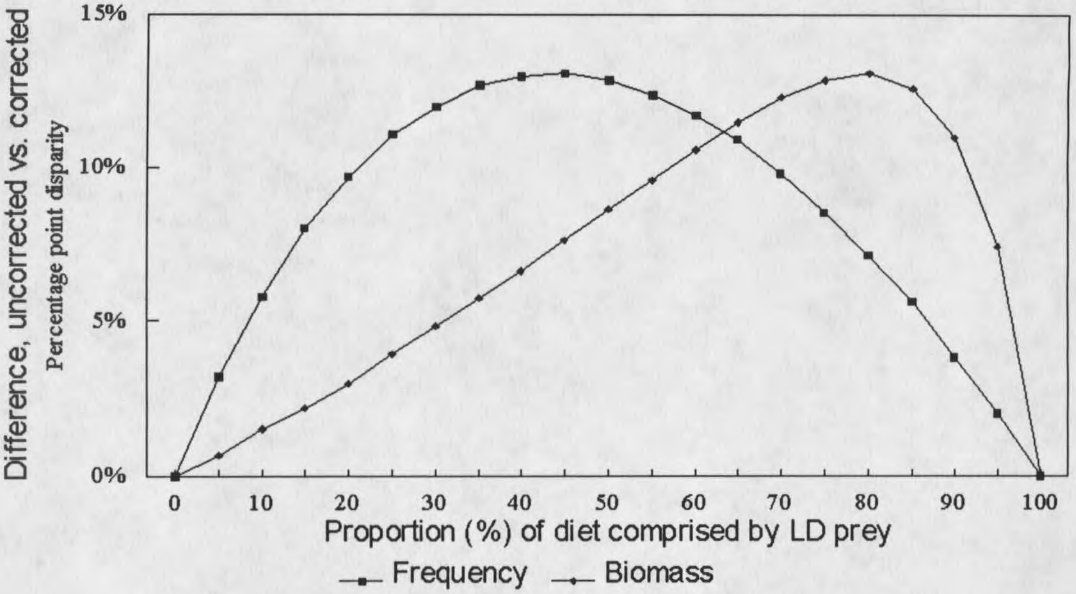
[a] Includes weights of juveniles of specific species; subadults or juveniles of other prey were assigned weights based on their approximate size relative to adults of same species.

[b] Source: 1 = data collected from study area; 2 = James and Seabloom 1969; 3 = Jones et al. 1983; 4 = Dunning 1984; 5 = Bellrose 1976; 6 = Greenwood 1975; 7 = Oring 1968; 8 = Dane 1965; 9 = Northern Prairie Wildlife Research Center, unpubl. manuscripts.

[c] Estimated biomass contributed by 1 striped skunk to a family of 2 adult and 2 juvenile owls.

[d] Duckling classification according to Gollop and Marshall (1954). Weights used for unidentified ducklings also were used for ducklings identified to species except weight was multiplied by 1.3 for mallard (*A. platyrhynchos*) and northern pintail (*A. acuta*) and by 0.5 for blue-winged teal. Estimates are from Appendix D.

[e] Weight for an adult of length 43 cm.



Appendix Figure 2. Hypothetical model of significance of bias correction on reported relative frequency and biomass of diet for varying proportions of low and high detectability (LD and HD) prey observed at Swainson's hawk tether platforms, based on correction factors 2.3x and 1.3x and mean prey weights of 25 g and 125 g for LD and HD prey. Percentage composition (frequency, uncorrected) of HD prey = 100 - %LD prey.

Appendix Table 6. Occupancy and success of red-tailed hawk nesting areas on Lostwood National Wildlife Refuge during 1983-90.

Nesting area no.[b]	Nesting area status by year[a]								Total years	
	1983	1984	1985	1986	1987	1988	1989	1990	occupied	successful[d]
1[c]	s	s	s	s	x	o		o	7	4
2	s	o	s	s	x	s	s	s	8	6
3	o		o	s	x	s	o	s	7	3
4[c]	s	o	x	s	x	s	o	o	8	3
5	s	s	s	s	x		s	o	7	5
6	o	s	s	s	x	o	s	o	8	4
7	s		o	o			o	o	5	1
8			s	o	x	s			4	2
9	s	o		s	x	o			5	2
10				s	x		o	o	4	1
11		o		o		o		s	4	1
12			s	o	x	s	o		4	2
13	o	o	s	o	x	o	s	o	8	2
14	s		s					s	3	3
15	s	o			x		o	o	5	1
16			s	s	x	o	o	o	6	2
17	o	s	s	s	x	s	s		7	5
18	s	s	s	s	x	s	s	s	8	7
19	o	o							2	0
20		o					o		2	0
21	o	o	s	s	x	o	s	s	8	4
22[c]		s	o	x	x	o	s	s	7	3
23	o	o	s	s	x	o	o	o	8	2
24	s	o	s	s	x	s	o	o	8	4
25			o	o					2	0
26	s	s	s	s	x	s	s	o	8	6

Appendix Table 6. Continued.

27	o	o	s	s	x	o	o	o	7	2
28		s	s	s	x	o		o	6	3
29	s	o	s	s	x	s	o	s	8	5
30						o	s	o	3	1
31[c]	o	o	s	s	x	o	x	x	8	2
32	s	o	s	s	x			s	6	4
33			s		x	s	s	s	5	4
34[c]			o	s	x	s	x	o	6	2
35[c]				o	x	x	s	o	5	2
36	s	s	s						3	3
37[c]			s	x	x		o	o	5	1

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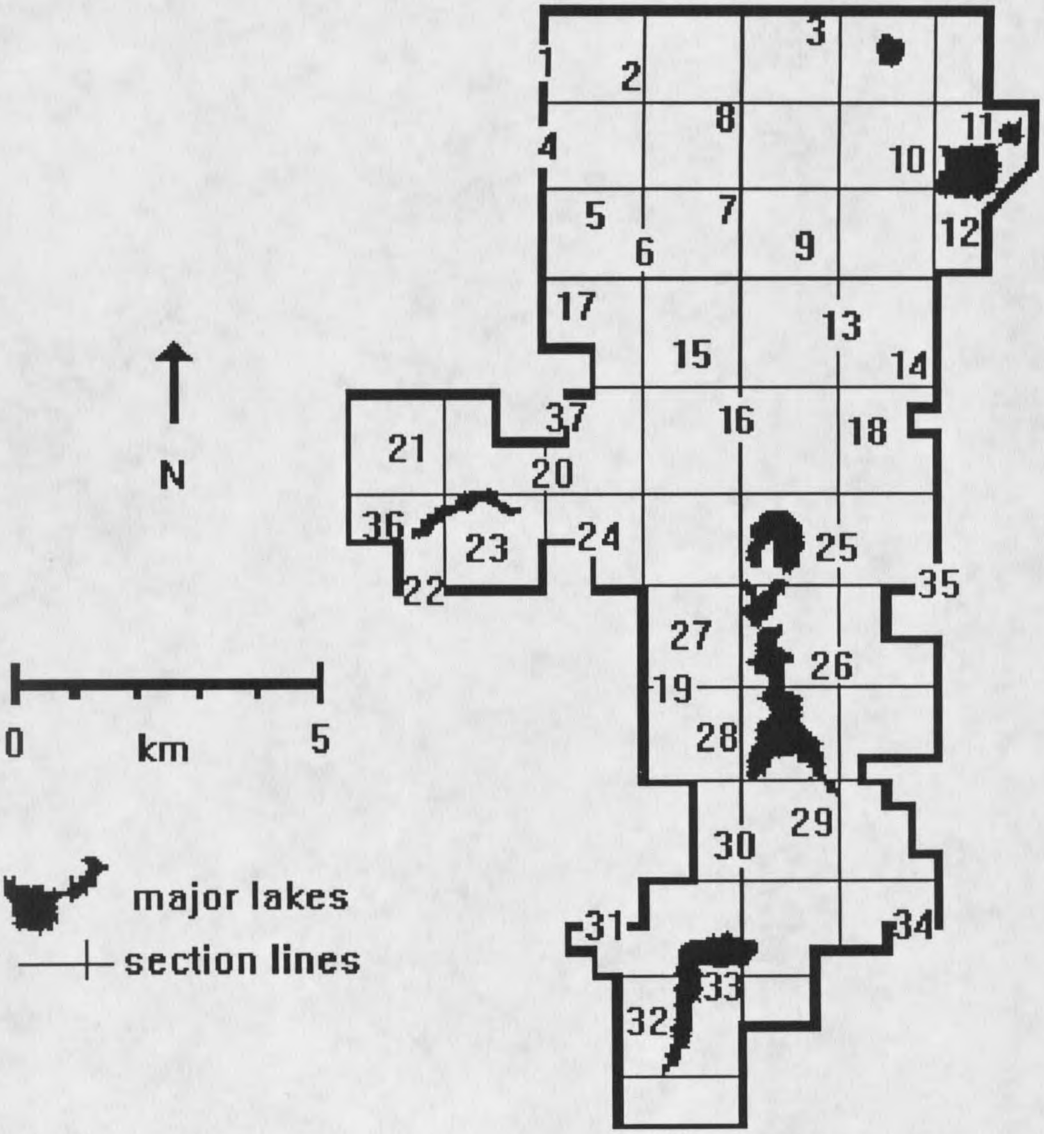
[a] Nesting area status: o = occupied but not successful; s = occupied and successful; x = occupied but success undetermined; blank = unoccupied.

[b] Location of each nesting area indicated in Appendix Fig. 4; a nesting area was considered reoccupied if a nest occupancy occurred within 1 km of a nest that had been occupied during or after 1983.

[c] Nesting area includes nest sites on adjacent private lands some years.

[d] Out of years during which success was determined.



Appendix Figure 3. Location of red-tailed hawk nesting area centers on Lostwood National Wildlife Refuge during 1983-90; nesting area numbers are referenced in Appendix Table 6.

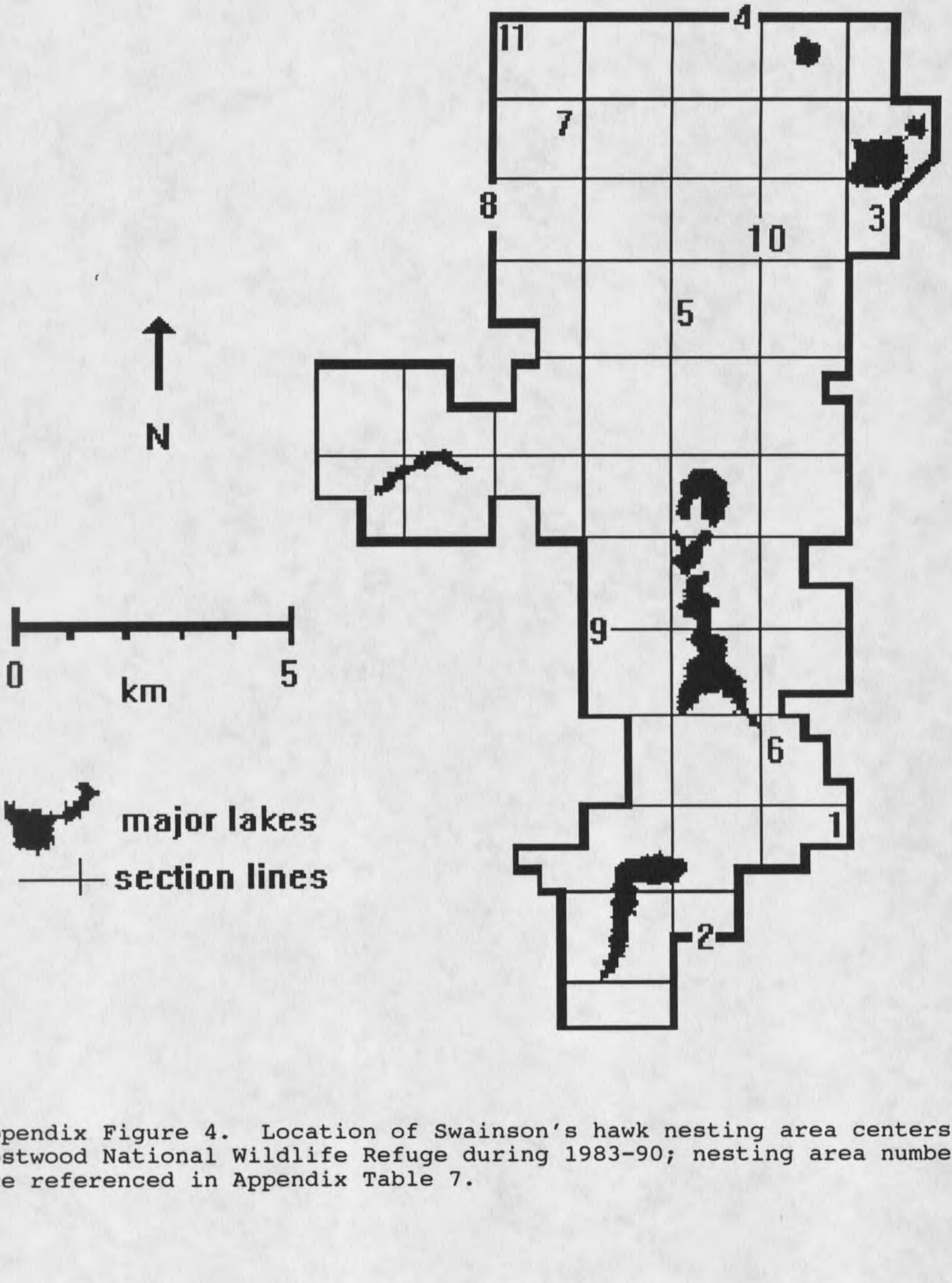
Appendix Table 7. Occupancy and success of Swainson's hawk nesting areas on Lostwood National Wildlife Refuge during 1983-90.

Nesting area no.[b]	Nesting area status by year[a]								Total years	
	1983	1984	1985	1986	1987	1988	1989	1990	occupied	successful
1[c]	s	s	o	s	s		o	o	7	4
2[c]	o			o	s	s		o	5	2
3	o	s	s	s	o				5	3
4[c]	o	s	s	s					4	3
5		s		o		s		s	4	3
6	o								1	0
7		o	o						2	0
8[c]		s	o		s		o		4	2
9		o							1	0
10				s	s		o		3	2
11				s					1	1

[a] Nesting area status: o = occupied but not successful; s = occupied and successful; blank = unoccupied.

[b] Location of each nesting area indicated in Appendix Fig. 4; a nesting area was considered reoccupied if a nest occupancy occurred within 1 km of a nest that had been occupied during or after 1983.

[c] Nesting area includes nest sites on adjacent private lands some years.



Appendix Figure 4. Location of Swainson's hawk nesting area centers on Lostwood National Wildlife Refuge during 1983-90; nesting area numbers are referenced in Appendix Table 7.

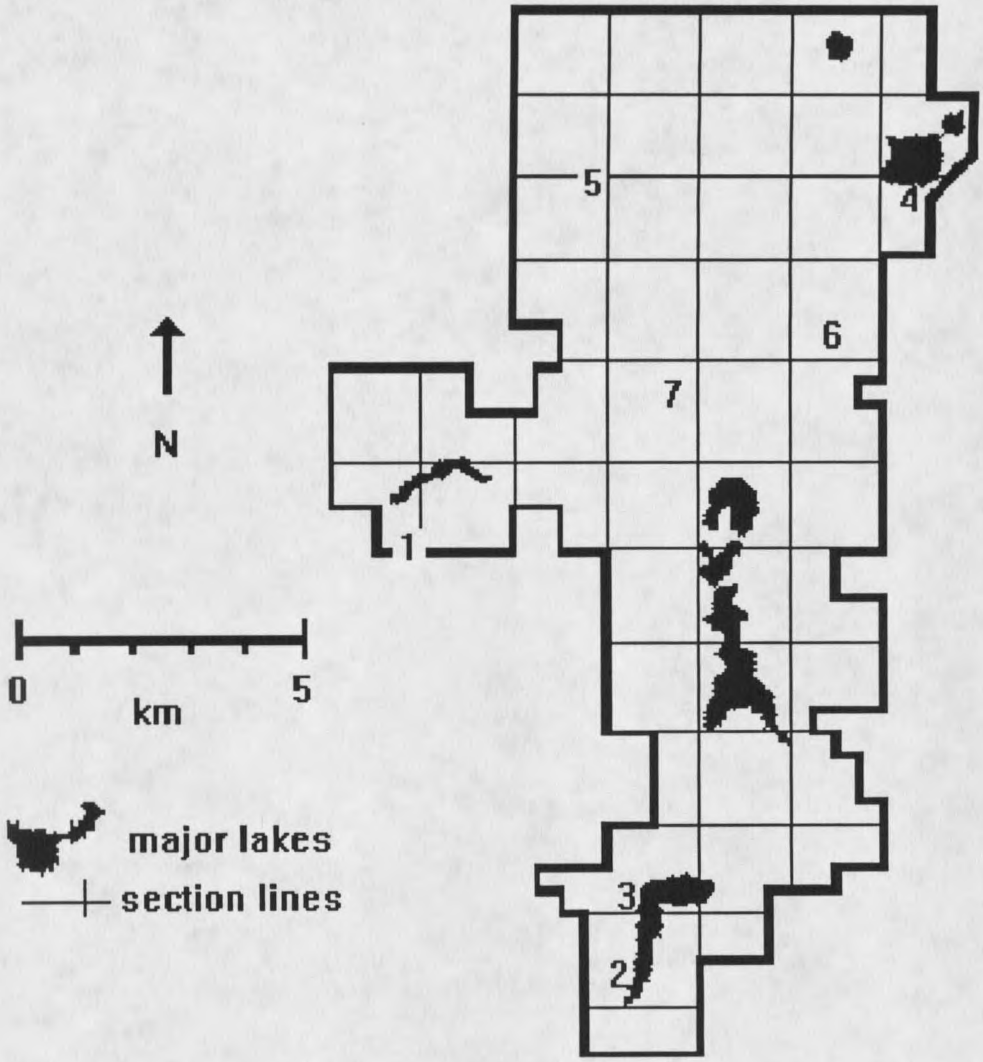
Appendix Table 8. Occupancy and success of Cooper's hawk nesting areas on Lostwood National Wildlife Refuge during 1983-90.

Nesting area no.[b]	Nesting area status by year[a]								Total years	
	1983	1984	1985	1986	1987	1988	1989	1990	occupied	successful
1[c]	o	s	s	s	s	o	o	s	8	6
2				s		o	s	s	4	3
3					s				1	1
4					o	o	s	o	4	1
5							s	s	2	2
6							s	s	2	2
7								s	1	1

[a] Nesting area status: o = occupied but not successful; s = occupied and successful; blank = unoccupied.

[b] Location of each nesting area indicated in Appendix Fig. 4; a nesting area was considered reoccupied if a nest occupancy occurred within 0.5 km of a nest that had been occupied during or after 1983.

[c] Nesting area includes nest sites on adjacent private lands some years.



Appendix Figure 5. Location of Cooper's hawk nesting area centers on Lostwood National Wildlife Refuge during 1983-90; nesting area numbers are referenced in Appendix Table 8.

Appendix Table 9. Occupancy and success of great horned owl nesting areas on Lostwood National Wildlife Refuge during 1985-90.

Nesting area no.[b]	Nesting area status by year[a]						Total years	
	1985	1986	1987	1988	1989	1990	occupied	successful
1[c]			s	o			2	1
2[c]	s	o	s	o	o	o	6	2
3[c]	s	o	s	o	o	o	6	2
4[c]	s	o	o	s	o	o	6	2
5	s	s	s	o	o		5	3
6	s	o	o	o		o	5	1
7[c]	s	o			o	o	4	1
8		o	s		s	o	4	2
9	s	o	s	o	o	o	6	2
10	s		s		o		3	2
11	s	o	o	o	o	o	6	1
12					s		1	
13	s	o	s	s	o	s	6	4
14	s	s	s	o	s	o	6	4
15	s	o	s	s	o	s	6	4
16	s		s				2	2
17[c]	s		o			s	3	2
18[c]	o		s		o		3	1
19	o	s	o	o	o	s	6	2
21	s	s	s	s	s	o	6	5
22[c]	o	o	s			s	4	2

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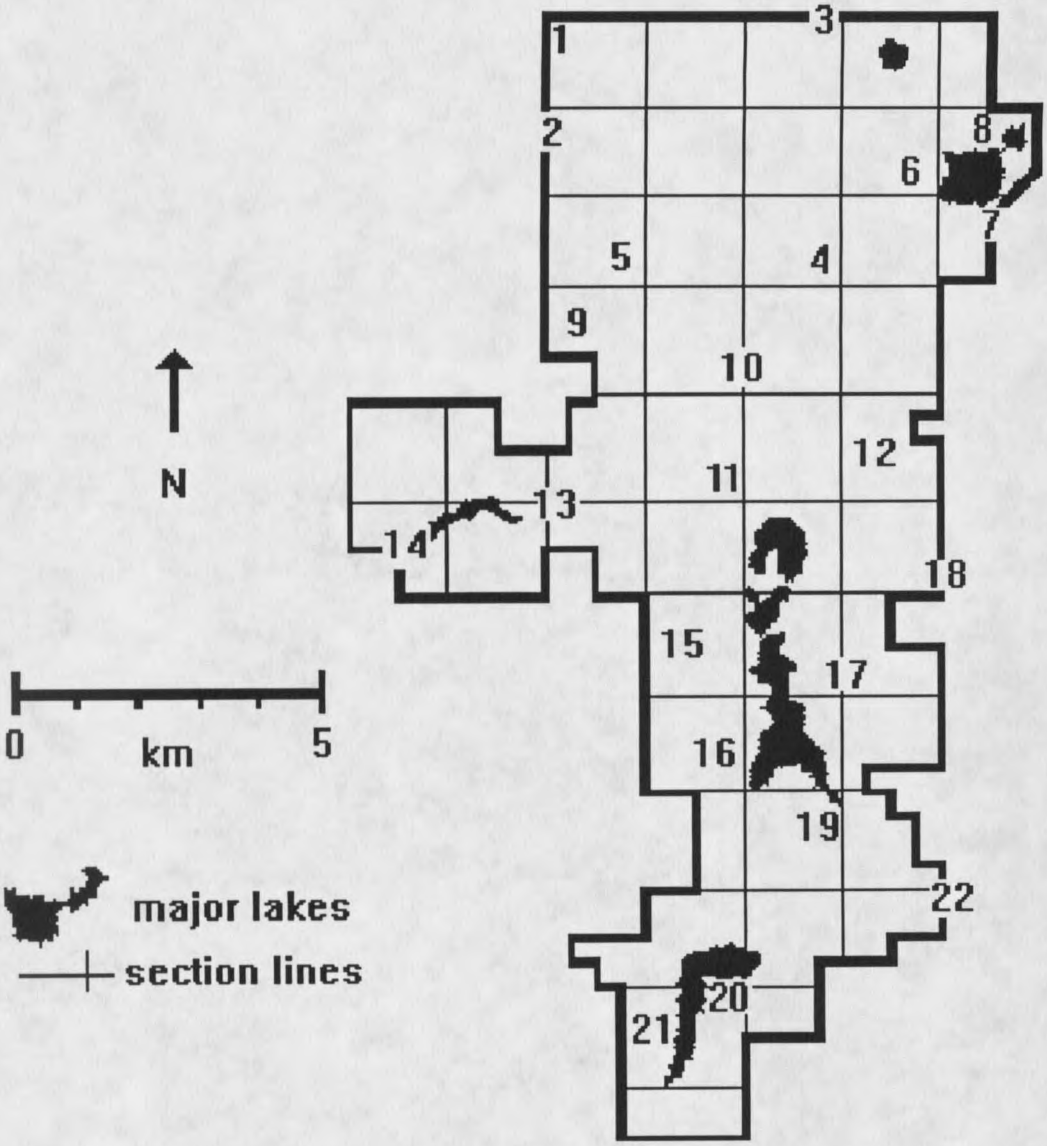
[a] Nesting area status: o = occupied but not successful; s = occupied and successful; blank = unoccupied or apparently occupied by single owl.

[b] Location of each nesting area indicated in Appendix Fig. 4; a nesting area was considered reoccupied if a nest occupancy occurred within 1 km of a nest that had been occupied during or after 1983.

[c] Nesting area includes nest sites on adjacent private lands some years.



Appendix Figure 6. Location of great horned owl nesting area centers on Lostwood National Wildlife Refuge during 1983-90; nesting area numbers are referenced in Appendix Table 9.

Appendix Table 10. Hatching dates (Julian calendar) and dates of unusually early and late observations of eggs and young of raptors nesting on and within 10 km of Lostwood National Wildlife Refuge, northwestern North Dakota, during 1981-90.

					Extreme dates of direct observation of viable eggs or young			
	Estimated hatching date[a]				eggs		nestlings	
Species	n nests	mean	SD	range	early	late	early	late
Red-tailed hawk	99	151.9	7.3	139-177[b]	--	177	--	221
Swainson's hawk	45	177.5	6.7	166-201	--	190	--	232
Ferruginous hawk	7	144.0	1.9	141-147	--	--	--	--
Cooper's hawk	15	174.9	4.4	165-182	--	--	--	--
Northern harrier	37	170.3	10.9	151-202	130	186	151	223
Great horned owl	70	107.2	8.4	93-131[b]	--	131	--	166
Long-eared owl	4	152.8	10.9	150-160	102	--	--	--
Short-eared owl[c]	6	159.5	23.1	122-197	116	--	125	--

[a] Hatching date for each nest calculated by backdating from mean age of brood estimated based on primary remige measurement and plumage development, except exact hatching dates were known for extremely late nests.

[b] Includes 2 late nests where renesting probably occurred; excluding these late nests, mean estimated hatching dates were 151.1 for red-tailed hawk and 106.5 for great horned owl.

[c] From A. Kruse and B. Bowen, unpubl. data.