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Diets of Nesting Swainson's Hawks in Relation to Land Cover in Northwestern North Dakota

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ABSTRACT Relationships between land use practices and types of prey used by Swainson's hawks (*Buteo swainsoni*) in the Northern Great Plains is of increasing interest as the quantity and quality of habitat in the region declines. I recorded 1,284 prey items at 18 Swainson's hawk nesting areas throughout northwestern North Dakota during summer 1986–1987. After correcting for detectability biases and food needs of adults, I estimated (90% CI) 2,087–2,859 total prey individuals and 138.3–206.7 kg of prey biomass (\bar{X} = 69.8 g/item) were consumed by adult and nestling Swainson's hawks during my study. Major prey (>10% overall frequency or biomass) were small (<50 g) rodents, ground squirrels (*Spermophilus* spp.), juvenile ducks (Anatinae), juvenile galliforms, and amphibians. Wetland-dependent species composed nearly 50% of all identified prey items based on frequency and biomass though wetlands averaged only 18% of land cover in Swainson's hawk nesting areas (i.e., within 1 km of nests). Compared to previous studies in the region, I documented a greater diversity of prey items, with a lower proportion of Richardson's ground squirrels (*S. richardsonii*) and higher proportions of small rodents, avian prey, and amphibians. Relationships between land cover in Swainson's hawk nesting areas and composition of prey items used by nesting pairs indicated that fragments of grazed prairie, hayland, and especially wetland may enhance future conservation efforts for the hawk in intensively farmed landscapes throughout the Northern Great Plains.

KEY WORDS *Buteo swainsoni*, diet, habitat, land use, North Dakota, Northern Great Plains, predator-prey relationships, wetlands

Swainson's hawks (*Buteo swainsoni*) nest mainly throughout the midcontinent prairies and western intermountain grasslands of North America (England et al. 1997). In the Northern Great Plains, distribution of nesting pairs of Swainson's hawks is related mainly to extent of cultivated land. In southeastern Alberta, for example, Swainson's hawks nested most often where cropland for grain production covered a low (11–30%) proportion of the landscape or, to a lesser degree, a high (71–90%) proportion (Schmutz 1984, 1987). Nesting by the species in southeastern Saskatchewan followed a similar bimodal pattern (Groskorth 1995). In southcentral North Dakota, cropland composed less than one-fourth of the land cover within 1 km of Swainson's hawk nests (Gilmer and Stewart 1984).

Knowledge of Swainson's hawk diets remains fundamental to their management and conservation (Giovanni et al. 2007). Influences of land use practices and vegetation conditions on nesting and reproductive success of Swainson's hawks in the Northern Great Plains are of increasing interest as the quantity and quality of habitat in the region declines for this and many other species of grassland birds (Houston and Schmutz 1999, Schmutz et al. 2001, Higgins et al. 2002). Aside from impacts on nest site availability, mechanisms by which rural land use and landscape composition influence types and availability of prey and, ultimately, the reproductive success of Swainson's hawks nesting in the region are poorly understood. Schmutz

(1987) hypothesized the hawk shifted from its main prey, Richardson's ground squirrel (*Spermophilus richardsonii*), to mice and voles (species unspecified) as landscapes changed from grassland to cropland. Schmutz et al. (2001) also hypothesized that Swainson's hawks may broaden their diets in years when Richardson's ground squirrels are scarce. However, published reports of diets of nesting Swainson's hawks in the Northern Great Plains do not address variation in use of prey types among nesting pairs. Such knowledge could elucidate relationships between land cover composition and Swainson's hawk occurrence and reproductive success, and advance its conservation. My primary objective was to assess the relationship between composition of summer diets of the Swainson's hawk and that of land cover surrounding its nest sites in a varied landscape in the Northern Great Plains. My secondary objective was to compare and contrast diversity of Swainson's hawk diets in northwestern North Dakota with diets of Swainson's hawks nesting elsewhere in the region.

STUDY AREA

I studied diets of nesting Swainson's hawks during mid-June to early August 1986–1987 on Lucy Township (93 km²; about 48°40'N;102°35'W) in Burke County, northwestern North Dakota, and on adjoining area of similar land use up to 10 km north, south, and east of the township. The study area was within the Missouri Coteau, a rolling to

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hilly moraine. Annual precipitation was 46 cm in 1986 and 31 cm in 1987 compared to a 42-cm average, and water levels in local wetlands were average and below average in respective years (Murphy 1993:155). Land use was dryland grain farming and cattle ranching. Land cover composition was 41% native (*Stipa-Agropyron*) prairie (approximately 50% grazed heavily by domestic livestock and 50% grazed lightly or idle) with scattered tall shrubs especially hawthorn (*Crataegus* spp.) and chokecherry (*Prunus virginiana*); 31% cropland, a third of which annually was fallow; 19% seasonal, semi-permanent, and permanent wetlands (classification per Cowardin et al. 1979); 5% tame hay; 2% small (< 1 ha), scattered patches of quaking aspen (*Populus tremuloides*) trees, and 2% roads, farmsteads, and tree shelterbelts (Murphy 1993:109). The area was sparsely inhabited by humans (10 farmsteads/100 km²). Common species of nesting raptors were red-tailed hawk (*B. jamaicensis*), Swainson's hawk, northern harrier (*Circus cyaneus*), and great horned owl (*Bubo virginianus*; Murphy 1993:111).

METHODS

Data Collection and Interpretation

Each spring I systematically searched the study area and located occupied nests of Swainson's hawks; nearly all were in aspen trees. I visited nests daily to record fresh (i.e., edible) prey items when nestlings were 1–3.5 weeks old. Visits lasted 5–10 min and nest trees were left undisturbed by viewing prey through a mirror on an extendable pole or by using mountaineer's ascenders on fixed ropes to quickly reach tops of nearby trees and look into nests, often with binoculars. When nestling hawks were about 3.5 weeks old, I used falconry jesses and swivels to tether them on platforms 1.5 m above ground in sites sheltered from wind and sun, 0–8 m from nest trees, following published guidelines (Petersen and Keir 1976). My research activities were conducted under the auspices of U.S. Fish and Wildlife Service Master-station banding permit number 5890 and a special purpose salvage permit issued by North Dakota Game and Fish Department to national wildlife refuges in North Dakota; permits for animal care and use in research were unavailable and not required at the time of this work. I visited each tether platform daily for 2.5–3 weeks, weighed all hawks each day to ensure they were maintaining or gaining mass, then released young hawks when they reached fledging age. At each visit, I identified every fresh prey item, marked it by cutting off a foot and subsequently left it on the platform, and identified and removed all discarded (inedible) remains. 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). I excluded regurgitated pellets from my analysis after finding they added negligibly to quantity

of prey used (7.1% increase for small [<50 g] rodents; none for other vertebrate species).

I assessed efficacy of using discarded remains and fresh items to reveal prey delivered by adult Swainson's hawks at 25% of tether platforms by using direct observation from $1 \times 2 \times 1.5$ -m blinds placed 4–8 m away. I stratified the sample based on the number of nestlings, however, the sample was not entirely random because I omitted from consideration 2 sites that were devoid of shrubs to conceal blinds. During my daily visit to a given platform at midday, an assistant entered the blind to observe until approximately 15 min after sunset then returned to the blind just before dawn the next day and remained until my midday visit. Two consecutive half-days of platform observation comprised a period of approximately 15 hr for comparing numbers of prey delivered by adult hawks to those revealed by fresh items and discarded remains on the platform. I used these results to correct data from all platforms for detectability biases.

I report overall dietary makeup in terms of relative (percentage) frequency and biomass. After correcting for detectability bias, I calculated percentage frequency by dividing the number of individuals in each prey species category by the total number of prey items. I estimated percentage biomass by multiplying the number of individuals of each prey category by their respective mean mass, then dividing the subtotal of each prey category by the total prey mass (Marti et al. 2007). For each prey category composing more than 1% frequency of prey pooled from all hawk tether platforms, I estimated the mean biomass (g) of prey killed daily by each nesting pair of Swainson's hawks and defined this as daily biomass consumption rate (DBC). I estimated DBC by multiplying the percentage biomass of each prey category by daily food needs of adults and young combined (Craighead and Craighead 1956:312). I assumed that composition of prey consumed by adults resembled that delivered to their tethered young, and each adult and young Swainson's hawk required a mean of 150 g of prey daily (Craighead and Craighead 1956, Kirkley and Gessaman 1990). My assumption of similar diets was supported by observations from blinds of partially consumed prey delivered by adults. Last, I assumed biomass of prey killed by adult Swainson's hawks approximated that consumed by adults and young.

I assigned mass values to prey from specimens collected from my study area and published literature (Jones et al. 1983, Dunning 1984). I assigned mass values to juvenile prey relative to those of adults of same species: (1) large juvenile (adult mass $\times 0.75$), (2) two-thirds grown ($\times 0.66$), and (3) one-half grown ($\times 0.5$). For prey of undetermined age, I assigned the mean mass of conspecific or congeneric prey for which age could be determined. I estimated mass values of undetermined species of juvenile duck (Anatinae) prey by comparing tarsus lengths to a composite curve of tarsus length versus mass for small, medium, and large species of ducks common on my study area (Murphy

1993:196). I assigned each invertebrate prey (all Orthoptera) a mass of 1 g.

Land Cover Measurements

I defined nesting area as the land within 1 km of a Swainson's hawk nest; 1 km was approximately 50% of the mean distance between Swainson's hawk nests on my study area and in most studies reviewed by England et al. (1997). I classified land cover within each nesting area using 8 categories: aspen tree patch, seasonal wetland, semi-permanent wetland, cropland, hayland (tame hay), grazed native prairie (moderate to heavy annual grazing), idle prairie (infrequent or light grazing to no grazing), or miscellaneous (farmstead, road right-of-way; Murphy 1997). I measured area (ha) of each land cover type using aerial photographs (1:15,840). Within every nesting area I also measured area of each land cover type within 100 m of a tall (>6 m high) perch because Swainson's hawks sometimes hunt from elevated perches (Janes 1984). I also measured distance (m) from a given nest to nearest seasonal wetland, semi-permanent wetland, cropland, hayland, grazed prairie, idle prairie, and to the next nearest aspen patch (hereafter referred to as e.g., distance or proximity to cropland).

Statistical Analyses

I assessed relationships between Swainson's hawk diets and land cover using ANOVA (Sokal and Rohlf 1981). I tested frequency and biomass data for normality and homogeneity of variances using the Kolmogorov-Smirnov and F -tests in BMDP statistical software (Dixon 1992). I used multivariate ANOVA to test for between-year differences in frequency proportions of prey used by Swainson's hawks. I used linear regression models (Neter et al. 1985) to explore variation in DBC of important prey categories among Swainson's hawk families. I used biomass in this analysis because it may better convey relative importance of prey to raptors than frequency of occurrence (Marti et al. 2007). To maintain independence, I randomly omitted 1 season's data for each of 2 nesting areas monitored in 1986 and 1987. I used an index of the local abundance of meadow voles (Murphy 1993) as an independent variable to account for a possible year effect. Number of tethered young also was included as an independent variable. I used the stepwise regression procedure in BMDP (Dixon 1992) with DBC of prey as the dependent variable to select 5 to 8 biologically meaningful independent variables then explored all possible 2- and 3-variable models to find the most parsimonious (Neter et al. 1985). Additionally, I log transformed all independent variables not normally distributed. I referenced correlation matrices to avoid multicollinearity among independent variables and examined residual plots to meet an assumption

of homogeneity of variance (Neter et al. 1985). To convey the relative importance and validity of independent variables in each model, I reported standardized regression coefficients and associated P -values (probability of t in a reduced model test for coefficient; Neter et al. 1985). Throughout, I conveyed exact probability levels for test results where $P > 0.001$ and considered $P < 0.1$ to indicate statistical significance.

RESULTS

Detectability Corrections

I obtained 15 observation periods from 4 tether platforms, during which 141 prey were delivered ($\bar{X} \pm SD = 0.66 \pm 0.33$ items/hr; Table 1). Differences in handling by tethered young of 2 prey types led to a contrast in detectability between types. Excluding avian prey, I detected 43% of small (<50 g) prey items delivered to platforms (Table 1). Young Swainson's hawks swallowed these prey items whole or otherwise consumed them entirely, leaving minimal discarded remains. This low detectability (LD) group included meadow voles, deer mice, tiger salamanders, and northern leopard frogs, and comprised 91% of prey delivered to platforms during observations. In contrast, I detected 79% of birds and large (≥ 50 g) mammals (Table 1). Juvenile passeriforms, juvenile ducks, Richardson's ground squirrels, and thirteen-lined ground squirrels comprised this high detectability (HD) group. Based on mean detectability of LD prey and HD prey, I used correction factors of $1/0.43 = 2.3$ for LD prey and $1/0.79 = 1.3$ for HD prey.

Generalized Diet of Swainson's Hawks

During July through mid-August 1986 and 1987, I recorded 1,284 prey items (fresh and discarded remains) at 20 Swainson's hawk tether platforms (10 platform sites each year). Eighteen nesting areas were represented in this sample; 2 nesting areas were sampled both years. I tethered 29 young on platforms ($\bar{X} = 1.5$ and 1.4 in 1986 and 1987, range = 1–3 young/platform each year), 1 of which was killed by a raccoon (*Procyon lotor*) despite erecting metal guards to deter mammalian predators, and another was killed by a great horned owl. After correcting for detectability and food needs of adults, food items I recorded at daily visits to tether platforms represented 2,087–2,859 (90% CI) total prey individuals and 138.3–206.7 kg of prey biomass consumed by Swainson's hawk families. Mean prey mass was 69.8 g. I detected no overall year effect in prey use by Swainson's hawks ($F_{1,17} = 1.14$, $P = 0.42$), although numbers of meadow voles killed daily by hawk pairs seemed greater in 1987 (3.6 ± 1.5) than in 1986 (1.5 ± 1.1).

Table 1. Numbers of low detectability (LD) and high detectability (HD) prey items noted during daily visits to 4 Swainson's hawk nest sites at which juvenile hawks were placed on tether platforms to determine diet composition. Numbers of prey represented by fresh and discarded remains noted on platforms are compared with total numbers of prey delivered by adult hawks, based on direct observation from blinds.

Site	Young	Observation periods (hr)	LD ^a items		HD ^b items	
			Detected/delivered	Detected (%)	Detected/delivered	Detected ^d (%)
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	
Total		15 (214.3)	58/127	43.4 ± 8.2 ^c	11/14	78.6

^a Low detectability items included meadow vole, deer mouse (*Peromyscus maniculatus*), tiger salamander (*Ambystoma tigrinum*), and northern leopard frog (*Rana pipiens*); ^b High detectability items included juvenile passeriforms, juvenile ducks, Richardson's ground squirrel, and thirteen-lined ground squirrel (*S. tridecemlineatus*); ^c $\bar{X} \pm SD$; ^d Number of HD items from individual sites insufficient to warrant percentage breakdown and variance estimate; overall percentage for HD items based on total derived from all sites.

Major prey (>10% frequency or biomass) were Richardson's and thirteen-lined ground squirrels, small rodents (nearly all of which were meadow voles and deer mice), juvenile ducks, juvenile galliforms (sharp-tailed grouse [*Tympanuchus phasianellus*] and gray partridge [*Perdix perdix*]), and amphibians (tiger salamander and northern leopard frog). Mammals and birds dominated dietary biomass of Swainson's hawks (55% and 36%) and mammals were the most frequently delivered prey (Table 2). Richardson's ground squirrel contributed 18.2% of dietary biomass, more than any other single species. Overall, 49% frequency and 42% biomass of prey items represented species associated directly with wetlands (muskrat [*Ondatra zibethicus*], American coot, [*Fulica americana*], sora [*Porzana carolina*], juvenile ducks, wetland-dwelling species of shorebirds, yellow-headed blackbird [*Xanthocephalus xanthocephalus*], red-winged blackbird [*Aegialius phoeniceus*], and amphibians), even though wetlands averaged only 18.1% (SD = 5.2%) of land cover within nesting areas. Amphibians were detected at all but 1 tether platform (Table 2). Tiger salamanders comprised 77% frequency and 86% biomass of this prey type.

I noted 207 fresh prey at visits to 27 Swainson's hawk nests during mid-June through early July, 1986 and 1987. Compared to data from tether platforms, frequency of occurrence of major groups of prey based on nest visits suggested greater use of ground squirrels (6.5% at platforms and 20.8% at nest visits) and birds (12.8% and 29.4%) and

less use of small rodents (63.3% and 48.8%). Amphibians composed 15.3% of prey at tether platforms but I did not detect them among fresh prey at nests.

Variation in Diet among Hawk Families

Composition of land cover and prey items varied among individual nesting areas (Fig. 1, Fig. 2). I did not detect each major prey species or species group at 1 to 5 nesting areas except for voles and mice (Table 2), which comprised >50% of all prey delivered at each of 13 (72%) nesting areas. Richardson's and thirteen-lined ground squirrels were primary ground squirrel prey (Fig. 2). Two models with 2 and 3 variables, respectively, explained approximately 50% of the variation in DBC of Richardson's ground squirrels among Swainson's hawk nesting areas (Table 3). Both models indicated greater use of Richardson's ground squirrels when nests were closer to grazed prairie and, to a lesser extent, with increased cropland area within 100 m of hunting perches. Best supported models for DBC of meadow voles (Table 3) suggested Swainson's hawks preyed more on voles as area covered by hayland increased and area covered by semi-permanent wetland decreased. A contrast in local abundance of voles between 1986 and 1987 (0.1 and 12.4 captures per 100 trap-nights; Murphy 1993) and idle prairie near perches also helped explain variation in use of this prey (Table 3).

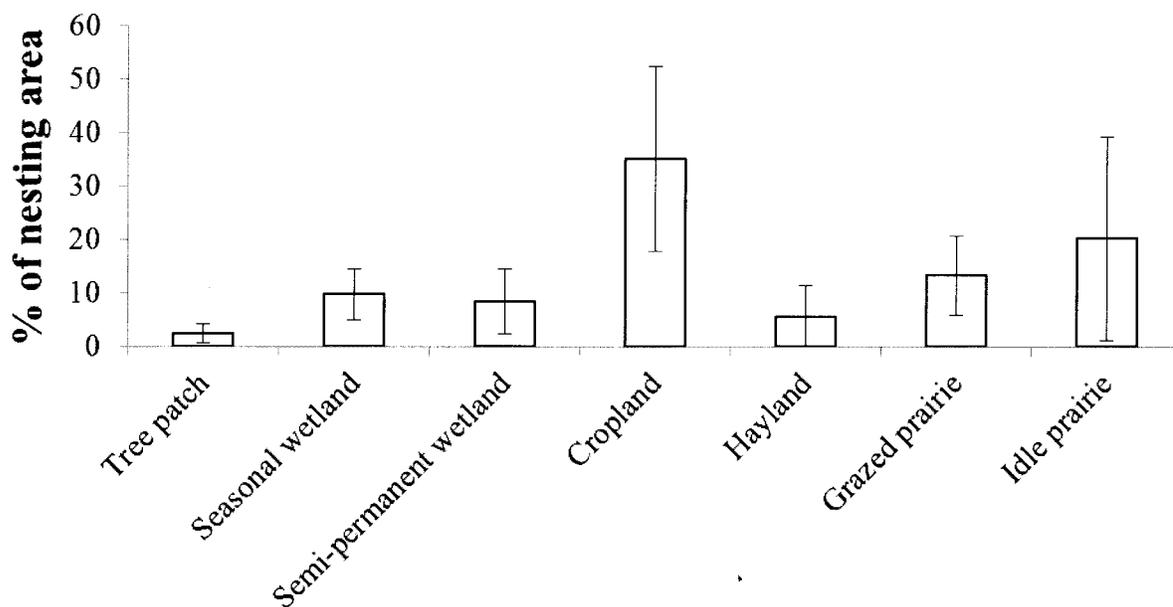


Figure 1. Variation (± 1 SD) in land cover within 1 km of Swainson’s hawk nests during summer 1986 and 1987 in northwestern North Dakota. Data are from 18 nesting areas; nests examined 1 year are exclusive (>2 km from) of those in the other year.

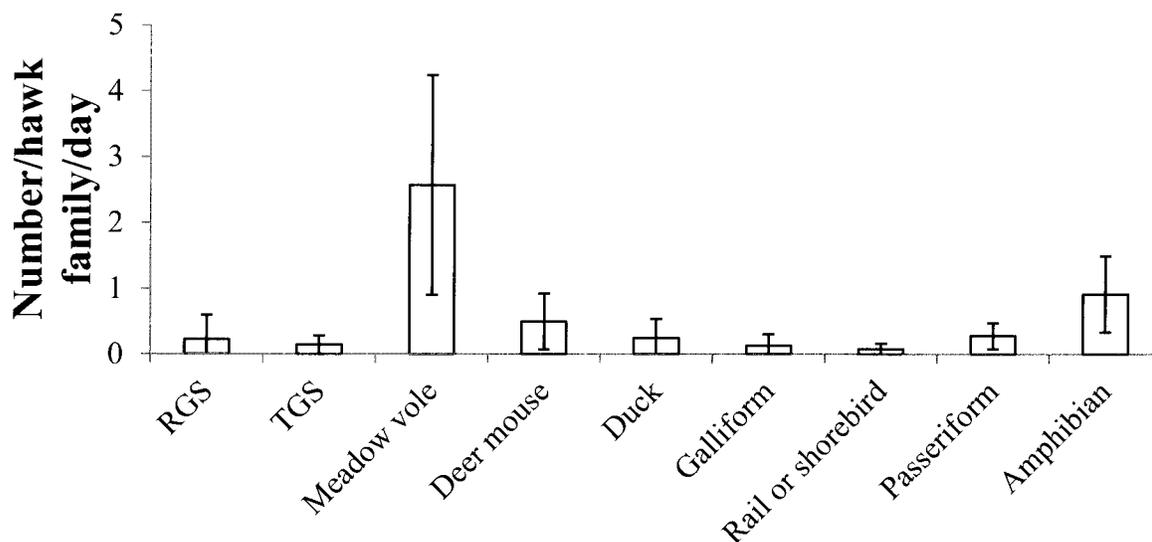


Figure 2. Variation (± 1 SD) in estimated mean daily intake of numbers of prey among Swainson’s hawk nests, i.e., families, during summer 1986 and 1987 in northwestern North Dakota. Excludes prey species or prey species groups that composed less than 1% of dietary composition by frequency. Data are from 18 nesting areas; nests examined 1 year are exclusive (>2 km from) of those in the other year. RGS = Richardson’s ground squirrel and TGS = thirteen-lined ground squirrel.

Several 2- and 3-variable models explained most (65–69%) of the variation in DBC of juvenile ducks among Swainson’s hawk nesting areas. Hawks preyed on ducks in proportion to amount (ha) or proximity of brood-rearing habitat (e.g., seasonal or semi-permanent wetland cover) surrounding hawk nests (Table 3). Models also suggested predation on ducks increased with greater area of wetland near tall perches and with area of idle prairie, and decreased in a year with elevated vole abundance. Nearly all (97.5%)

duck remains were of juveniles, most less than 2.5 weeks old; 2 female blue-winged teal (*Anas discors*) were the only adult ducks represented. I estimate Swainson’s hawk pairs preyed on about 2.6 and 1.5 juvenile ducks/week/nesting area in 1986 and 1987. Adjusting for local Swainson’s hawk breeding density (7.5 occupied nests/100 km²), this translates to a predation loss of 0.1–0.2 juvenile ducks/week/km².

Table 2. Percentage composition of prey used by nesting Swainson's Hawks in northwestern North Dakota during summer 1986–1987, based on prey items pooled from all hawk families^a.

Prey category	Frequency		Biomass		% nesting areas where recorded ^e
	<i>n</i> ^b	%	kg ^b	%	
Mammals					
White-tailed jackrabbit ^c	12	0.5	7	4.1	33.3
Ground squirrel ^d	160	6.5	42.1	24.4	88.9
Vole and mouse ^e	1566	63.3	44	25.5	100
Miscellaneous ^f	8	0.3	1.5	0.9	
Subtotal		70.6		54.9	
Birds					
Duck ^g	103	4.2	27.3	15.8	88.9
Galliform ^h	57	2.3	20.5	11.9	38.9
Rail and shorebird ⁱ	30	1.2	7.9	4.6	38.9
Passeriform ^j	122	4.9	5	2.9	88.9
Miscellaneous ^k	5	0.2	0.9	0.5	
Subtotal		12.8		35.7	
Amphibians ^l	378	15.3	15.4	8.9	94.4
Reptiles ^m	12	0.5	0.9	0.5	16.6
Insects ⁿ	20	0.8	<0.1	<0.1	22.2
Total	2473	100	172.5	100	

^a Ten nesting areas monitored in 1986 and 1987, 2 of the nesting areas were monitored both years; ^b Sample and biomass are point estimates based on corrections for size-related biases; ^c *Lepus townsendii*; ^d Richardson's, thirteen-lined, and Franklin's (*S. franklinii*) ground squirrels; ^e Meadow and southern red-backed voles (*Clethrionomys gapperi*), deer, western or meadow jumping (*Zapus* spp.), and olive-backed pocket mice (*Perognathus fasciatus*); ^f Muskrat, Norway rat (*Rattus norvegicus*), short-tailed shrew (*Blarina brevicauda*), least weasel (*Mustela nivalis*); ^g Mallard, northern pintail (*A. acuta*), blue-winged teal, American wigeon (*A. americana*), lesser scaup (*Aythya affinis*), unknown duck species; ^h Sharp-tailed grouse, gray partridge; ⁱ American coot, sora, killdeer (*Charadrius vociferus*), lesser yellowlegs (*Tringa flavipes*), upland sandpiper (*Bartramia longicauda*), willet (*Catoptrophorus semipalmatus*), marbled godwit (*Limosa fedoa*); ^j Eastern (*Tyrannus tyrannus*) and western kingbird (*T. verticalis*), horned lark (*Eremophila alpestris*), tree swallow (*Tachycineta bicolor*), black-billed magpie (*Pica pica*), Sprague's pipit (*Anthus spragueii*), vesper (*Pooecetes gramineus*), Savannah (*Passerculus sandwichensis*) and unknown sparrows (Emberizinae), red-winged blackbird, western meadowlark (*Sturnella neglecta*), yellow-headed blackbird, Brewer's blackbird (*Euphagus cyanocephalus*), common grackle (*Quiscalus quiscula*), brown-headed cowbird (*Molothrus ater*), unknown blackbird (Icterinae); ^k Mourning dove (*Zenaida macroura*), short-eared owl (*Asio flammeus*), yellow-shafted flicker (*Colaptes auratus*); ^l Tiger salamander, northern leopard frog; ^m Plains garter snake (*Thamnophis radix*), smooth green snake (*Opheodrys vernalis*); ⁿ Grasshopper (Orthoptera: Oedipodinae).

Table 3. Most parsimonious linear regression models that best explain variation in daily biomass consumption (g/day) of major prey items by nesting Swainson's hawks in northwestern North Dakota, summer 1986 and 1987.

Model and independent variables ^a	Coefficient		Model fit		
	β	P^b	R^2	F	P
RGS I			0.425	5.55	0.016
Distance to grazed prairie	-0.48	0.027			
Cropland near perches	0.37	0.080			
RGS II			0.556	5.85	0.008
Distance to grazed prairie	-0.52	0.012			
Distance to hayland	0.37	0.062			
Cropland near perches ^c	0.32	0.100			
Vole I			0.466	6.55	0.009
Year (vole abundance)	0.54	0.013			
Idle prairie near perches	0.48	0.022			
Vole II			0.569	6.17	0.007
% semi-permanent wetland	-0.55	0.012			
% hayland	0.55	0.011			
Idle prairie near perches	0.39	0.053			
Duck I ^e			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			
Duck II			0.651	8.72	0.002
% semi-permanent wetland	0.93	<0.001			
Seasonal wetland near perches ^d	0.48	0.031			
Year (vole abundance)	-0.34	0.058			

^a RGS = Richardson's ground squirrels; ^b Probability of t in reduced model test for coefficient; ^c Total area (ha) within 1 km of nest that was ≤ 100 m from any perch > 6 m tall (e.g., utility poles, trees); ^d Year effect: 1986 and 1987 vole abundance index, 0.1 and 12.4 captures/100 trap-nights (Murphy 1993); ^e Approximately 98% of duck prey were juveniles ≤ 6 weeks old.

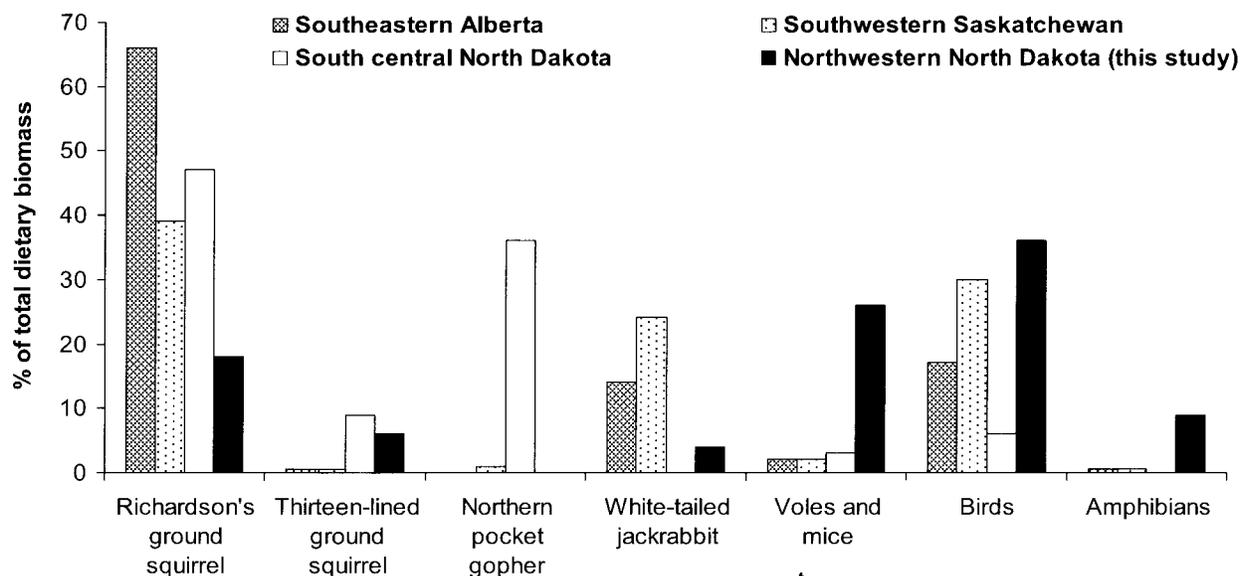


Figure 3. Percentage composition of diets of nesting Swainson's hawks in 4 areas of the Northern Great Plains in terms of biomass of major categories of prey (e.g., excludes prey groups that comprised <1% frequency in all studies). Biomass percentages for southeastern Alberta and southeastern Saskatchewan are approximated from 1983–1996 data presented in Appendix 1 of Schmutz et al. (2001) and those for south central North Dakota are from Gilmer and Stewart (1984). Data for these 3 areas were collected by noting prey items in nests. Percentages for northwestern North Dakota (this study) are based on items observed at tether platforms corrected for detectability biases via direct observation.

DISCUSSION

Tethering of Young

For several decades, which include this study, large nestling raptors sometimes were tethered on the ground (Craighead and Craighead 1956) or on raised platforms (Peterson and Keir 1976) beneath nests often beyond the normal fledging period, so prey delivered to them by adults could be recorded. When tethered, however, young raptors could be more vulnerable to predators, be fed or protected less by adults, or exhibit delayed physical and behavioral development (Marti et al. 2007). Depredation of 2 young Swainson's hawks on tether platforms in this study may have been less likely had they been in their respective nests. Except in unusual circumstances, use of tether platforms is no longer warranted with recent advances in videography for study of raptor diets (Giovanni et al. 2006, Marti et al. 2007) and may be considered unacceptable by modern institutional animal care and use committees.

Relationships Between Land Cover and Diet

Variation in avian diets is of greater ecological interest than what the average bird eats (Wiens 1989). My models performed well in predicting influences of land cover attributes on Swainson's hawk use of species with specialized habitat needs (e.g., juvenile ducks versus ha of semi-permanent wetland). The extent that Richardson's

ground squirrels occur in Swainson's hawk diets was explained in my models mostly by proximity to grazed prairie, the preferred habitat of this rodent (Jones et al. 1983). Richardson's ground squirrels also use annually tilled cropland; my models suggested vulnerability of the ground squirrel to Swainson's hawk predation increases when it inhabits growing grain near elevated perches. Swainson's hawks generally underuse croplands until harvest (Bechard 1982), but might exploit rodents in croplands earlier when suitable hunting perches are present.

Use of meadow voles by Swainson's hawks related directly to spatial extent of hayfield within nesting areas, which likely related to altered vulnerability of voles during cutting of hay in midsummer. Swainson's hawks characteristically catch prey flushed by hay-harvesters and other farm machinery (Schmutz 1987, England et al. 1997), and such vegetation disturbance may be an important aspect of the hawk's foraging and evolutionary ecology (Bechard 1982, Janes 1985, Murphy and Smith 2007). Additionally, Swainson's hawks may have used voles less as wetland cover in nesting areas increased, in part because wetland-associated prey items (such as juvenile ducks and amphibians) were readily available.

Use of juvenile ducks by Swainson's hawks related mostly to extent of semi-permanent wetlands within nesting areas. Other land cover variables such as percentage cropland or hayland could be important because, even if relatively few juvenile ducks occurred, they may have been particularly vulnerable in these habitats. This hypothesis

was not supported by my models, although juvenile ducks (e.g., their brood hens) may have avoided these areas. In 1987, all seasonal wetlands and small (<1 ha) semi-permanent wetlands were dry by late July. This likely triggered extensive overland movement by duck broods, making them more vulnerable to predation and other causes of mortality (Rotella and Ratti 1992). The role of raptors in mortality of nesting ducks and their young in the northern Great Plains is poorly understood (Sargeant and Raveling 1992). This study occurred during the nesting season in good waterfowl habitat, yet Swainson's hawks preyed on relatively few juvenile ducks/km² and rarely preyed on adult ducks.

Comparison to Swainson's Hawks Elsewhere

My data indicate diets of Swainson's hawks in northwestern North Dakota are more diverse and include a greater proportion of wetland-dependent prey species than reported elsewhere in the Northern Great Plains. I found biomass contributed by small rodents and amphibians more important and biomass by Richardson's ground squirrel less important than previous researchers in the region (Fig. 3). Avian prey also were more important to Swainson's hawks I studied. However, I assessed Swainson's hawk diets during what likely was a period of low abundance of Richardson's ground squirrels in much of the region. In southeastern Alberta and southern Saskatchewan, a substantial decline in Richardson's ground squirrel abundance was apparent in the late 1980s and early 1990s and coincided with poor reproductive success among Swainson's hawks (Houston and Schmutz 1995, Houston and Zazelenchuk 2004). Scarcity of Richardson's ground squirrel in my study likely explained, in part, increased use of alternative prey items by Swainson's hawks as noted in Alberta and Saskatchewan (Schmutz et al. 2001). Northern pocket gopher (*Thomomys talpoides*), a major, widespread prey species of Swainson's hawks in southcentral North Dakota (Gilmer and Stewart 1984), did not occur on my study area.

Greater dietary diversity of Swainson's hawks relative to reports elsewhere in the Northern Great Plains also may have been influenced by differences in diet study methods. Gilmer and Stewart (1984) relied solely on fresh prey items observed in nests. Schmutz et al. (2001) apparently also used fresh remains of prey at nests. I increased detection rates of small rodents and amphibians by using tether platforms combined with direct observation to correct for biases, an assertion supported by comparing data from tether platforms with those based on fresh prey observed at nests just before I tethered young. At nests I observed no amphibian prey but amphibians comprised 15% of the total number of prey items at platforms, whereas ground squirrels occurred 3 times more frequently at nests than at platforms. Some differences between composition of fresh prey at nests and of prey at tether platforms could be related to time of data collection, although time periods overlapped (mid-

June through early July versus July through mid-August).

Wetland-dependent species represented nearly 50% of the frequency and biomass of prey used by hawk families. In contrast, at least 90% of the frequency and biomass of prey used by Swainson's hawks in other areas of the Northern Great Plains were associated with uplands (Gilmer and Stewart 1984, and calculated from 1983–1996 data in Appendix 1 of Schmutz et al. 2001). Relatively high importance of amphibians in diets of nesting Swainson's hawks in my study has not been reported previously (England et al. 1997), perhaps in part because of biases discussed above (e.g., see relevant note in Gilmer and Stewart [1984]). Most amphibian prey items in my study were tiger salamanders, despite noxious secretions from skin granular glands being exuded by this species (Hamning et al. 2000).

MANAGEMENT IMPLICATIONS

I found relationships between components of Swainson's hawk diets and variation in land cover attributes that characterized northwestern North Dakota. Though prairie wetland habitats comprised a relatively small portion (19%) of the study area, wetland-dependent prey items were an important food source for Swainson's hawks. To help facilitate adequate reproductive success by Swainson's hawks, maintenance of seasonal and semipermanent wetlands is recommended, particularly given the increasing emergence of agricultural monotypes throughout the Northern Great Plains.

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