Transactions of the Illinois State Academy of Science
(1992), Volume 85, 1 and 2, pp. 29 - 40

Habitat Use by the Mississippi Valley Population of Canada Geese

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ABSTRACT

Habitat and refuge use by wintering and migrating Canada geese (*Branta canadensis*) of the Mississippi Valley Population (MVP) were studied October-February 1984-87 at Union County Conservation Area (CA) and Rend Lake in southern Illinois, and October-December and March-April 1984-1986 at Horicon National Wildlife Refuge (NWR) in Wisconsin. Use of refuges increased ($P < 0.05$) during hunting seasons in southern Illinois where hunting was relatively intense, but did not increase ($P = 0.16$) near Horicon NWR where hunting was less intense. Habitat use varied among years and seasons in response to changes in habitat availability, weather, disturbance, physiological needs, and other factors. Use of winter wheat and alfalfa/clover fields was highest ($P < 0.05$) in fall, use of lakes was highest ($P < 0.05$) in winter, and use of lowland pastures was highest ($P < 0.05$) in spring. Lake and winter wheat habitats were used more ($P < 0.01$) than available, while soybean and milo fields were used less ($P < 0.01$) than available in southern Illinois. Near Horicon NWR, proportional use of shallow wetlands exceeded ($P < 0.01$) their availability. Grain, green forage, shallow wetland, and lake habitats should be made available to Canada geese during migration and wintering.

INTRODUCTION

Understanding seasonal patterns of habitat and refuge use is a necessary step toward controlling habitat conditions to influence survival and reproduction of migratory Canada geese. Changes in nutritional needs, disturbance, and weather can affect habitat and refuge use (McLandress and Raveling 1981, Zicus 1981, Frederick and Klaas 1982). Habitat availability influences diet (Alisauskas et al. 1988) which may then affect physiological condition (Delnicki and Reinecke 1986, Gates 1989) and in turn survival (Burnham and Nichols 1985, Haramis et al. 1986, Hepp et al. 1986) and reproduction (Harvey 1971, Ankney and MacInnes 1978, Raveling 1978). Refuge use can also affect survival of Canada geese during hunting (Zicus 1981).

MVP Canada geese depart nesting areas in the Hudson and James Bay lowlands in September and October (Tacha et al. 1991). About 75% stop and remain at or near Horicon NWR in east central Wisconsin until early December when they depart for wintering areas. The remaining 25% bypass Wisconsin and migrate directly to wintering areas in and near southern Illinois (Kennedy and Arthur 1974, Tacha et al. 1991). Geese remain concentrated at Union County CA, Rend Lake Refuge, and other refuges until they depart during late-January or February (Tacha et al. 1991). Horicon NWR and other areas in east central Wisconsin are major spring staging areas; geese are present during March and April (Tacha et al. 1991).

Our goal was to describe seasonal and annual patterns of diurnal habitat and refuge use by MVP Canada geese during migration and wintering, and to identify environmental factors affecting diurnal habitat use. Others (Arthur 1968, Bell and Klimstra 1970, Reed et al. 1977, Paine 1985, Moser and Tacha 1989, Smith 1989) have quantified habitat use of Canada geese at a particular location or season, but drawing generalizations from these studies is difficult because of differences in methods, study sites, and other confounding factors. We describe habitat and refuge use for the entire migration and wintering period at multiple locations and during multiple years.

STUDY AREA

Geese were observed during fall and spring migrations on and adjacent to Horicon NWR (43°30'N, 88°40'W), located in east central Wisconsin. Horicon NWR occupies the northern two-thirds of the 12,550 ha Horicon Marsh. Horicon NWR is closed to goose hunting and currently has no land devoted to agricultural crops. The southern one-third of the marsh is managed by the Wisconsin Department of Natural Resources and includes both hunting and refuge areas. Horicon NWR is a hub to several satellite goose management areas and lakes which receive considerable use by geese (Craven et al. 1985), but were not part of the study area. Areas adjacent to Horicon NWR are intensively managed for dairy cattle; corn, small grains, and hay crops dominate land use.

Wintering geese were studied on and near Union County CA and Rend Lake Refuge in southern Illinois. Union County CA (37°35'N, 89°50'W) is located in the Mississippi River bottomlands. Approximately 1,000 ha of the 2,150 ha area is planted in agricultural crops annually. The southern 830 ha of Union County CA is managed for goose hunting; the remainder is Union County Refuge. Most adjacent lands are intensively farmed for soybeans, corn, and winter wheat. Many of these farms are commercial and private (leased) goose hunting clubs.

Rend Lake Refuge (38°10'N, 89°00'W) is along the north shore of Rend Lake and 95 km northeast of Union County CA. The 2,025 ha refuge is composed of about 80% permanent water area and 15% cropland. Rend Lake Wildlife Management Area provides an additional 4,400 ha of land and water open to public use. Most adjacent property is farmed for corn and soybeans. Private and commercial hunting clubs operate along the perimeter of the refuge.

METHODS

Sampling Design

Diurnal habitat use was documented by driving survey routes during October-December, 1984 and 1985, and March-April 1985 and 1986 near Horicon NWR and October-February, 1984-85 to 1986-87 near Rend Lake and Union County CA. Surveys were at weekly intervals except at Rend Lake in 1985-86 and 1986-87 when surveys were conducted twice weekly.

The 92 km survey route near Horicon NWR did not include refuge areas in fall, 1984; in subsequent seasons it was increased 5 km to include a portion of the refuge. Approximately 20% of the 71 km route on and near Union County CA and the 120 km route near Rend Lake included refuge land. All routes extended up to 8 km from refuge areas.

Crop reporting information from the Agricultural Stabilization and Conservation Service (ASCS) indicated that habitat composition in the vicinities of Union County CA and Rend Lake Refuge was very similar to habitat composition along survey routes (Pritchert 1988, Caithamer 1989). An independent survey (Smith 1989) confirmed that habitat composition along the Horicon NWR survey route was representative of the area.

Survey routes were driven 3 times/day: within the first 3 hours after sunrise, midday, and during the last 3 hours before sunset. Habitats within clear viewing distance (usually about 0.5 km) of each route were inventoried and field conditions (unharvested, harvested, or tilled) were recorded weekly. Number of geese, habitat, and land type (refuge or nonrefuge) were recorded for each flock encountered. Precipitation (yes or no), cloud cover (scale of 0-2), snow cover (scale of 0-5), and amount of pond ice (scale of 0-5) were recorded during each survey. Temperature and wind speed data were also obtained for each survey from hourly records at Dane County Airport, Madison, Wisconsin, and Southern Illinois Airport, Carbondale.

Habitat and Season Definitions

Forested, industrial, and residential areas were not considered usable by geese and were excluded from analyses. Remaining areas were categorized into 9 habitat types: corn, soybean, milo, winter wheat (included any field double cropped to winter wheat), alfalfa/clover, other forage (included pastures, fescue [*Festuca pratensis*], and other grass-dominated fields), other crops (included sunflower, clean-tilled agricultural fields, and vegetable crops), shallow wetland (palustrine systems), and lake (lacustrine systems) (Cowardin et al. 1979).

The migrating and wintering period was divided into 5 seasons to facilitate analyses. Season lengths varied slightly each year to correspond with ecological events. Early Fall was defined from arrival of geese in early October to beginning of goose hunting season (early November) in southern Illinois. The goose hunting season closely corresponded with Early Fall near Horicon NWR. Late Fall began with opening of southern Illinois goose hunting season and ended in December after most geese left Wisconsin and arrived in southern Illinois. Nearly all of goose hunting season in southern Illinois occurred during Late Fall. Early Winter ended in mid-January when temperatures moderated. Late Winter ended when large numbers of geese began to migrate north in February. Spring corresponded with major goose use of Horicon NWR area from mid-March to mid-April. We collectively refer to Early and Late Fall as Fall and Early and Late Winter as Winter. Arrival and departure dates of geese were documented by Tacha et al. (1991).

Analyses

Each survey route was considered one sampling unit to calculate proportional use of each habitat. Proportional use was arc-sine transformed (Sokal and Rohlf 1969) and General Linear Models (GLM) (SAS Inst. 1982) procedures tested effects of year and season on habitat use. Differences ($P \leq 0.05$) among means were detected with Duncan's Multiple Range Tests. Two-tailed Z-tests were used to test null hypotheses that use of a habitat equalled its availability on each route. Risks of committing type I experimental errors were reduced by using an alpha level of 0.01.

Effects of environmental conditions on arc-sine transformations of proportional habitat use were evaluated at each wintering location. Canonical correlation analysis was first used to determine which habitat type accounted for most variation in overall habitat use. Stepwise multiple regression analysis was then used to identify environmental parameters that were associated with use of important habitats identified in canonical correlation analysis. Environmental parameters tested were temperature, wind speed, cloud cover, precipitation, percent snow cover, amount of pond ice, corn stubble availability, soybean stubble availability, and milo stubble availability.

RESULTS

Habitat Availability

Approximately 3,500 ha of habitat on the Union County CA survey route was considered usable by geese. Soybean and corn were the most common habitat types, accounting for 55-67% of available habitat (Caithamer 1989). A total of 166 ha of soybean fields was double-cropped to winter wheat on Union County CA in 1984-85, but no fields were double-cropped on Union County CA in 1985-86 or 1986-87. About half of all corn and soybean fields on the survey route were harvested during Late Fall. Copious rainfall and wet soil conditions prevented nearly all fall tillage at wintering locations in 1984-85. Drier conditions in 1985-86 and 1986-87 permitted tilling of 19-47% of corn and soybean fields.

The Rend Lake survey route included about 6200 ha of usable habitat. Corn and soybean were the most common habitat types, comprising >50% of available habitat (Pritchert 1988). Soybean fields on Rend Lake Refuge were double-cropped to winter wheat in 1986-87, but not in 1984-85 or 1985-86. Approximately 75% of the corn and soybean

fields along the survey route were harvested by Late Fall. Harvest of refuge grain fields was completed by beginning of Late Fall in 1986-87 but was not completed until Early Winter in 1984-85 and 1985-86.

The Horicon NWR survey route included approximately 3,800 ha of usable habitat. Corn was the most abundant, accounting for about 50% of usable habitat (Caithamer 1989). Alfalfa and other forage habitats were also common.

Corn and soybean harvest was early and rapid near Horicon NWR in Fall 1984. Most fields were plowed soon after harvest, so availability of grain stubble habitat never exceeded 50% of area planted to grain in 1984. Snowfall during November and December 1985 prevented harvest of 35% of corn fields. No grain fields were harvested or tilled during Spring.

Refuge Use

Refuge use was highest in Late Fall (hunting season) at wintering locations when >90% of geese remained on-refuge (Table 1). Proportions of geese using refuge areas on the Horicon NWR survey route averaged 34% (SE = 8) and did not vary seasonally ($P = 0.16$) in 1985-86. Concurrent radio telemetry studies (Pritchert 1988, Caithamer 1989) also indicated that refuge use was higher at wintering areas than at Horicon NWR, did not vary seasonally at Horicon NWR, and increased during hunting season at wintering areas.

Habitat Use and Selection at Union County CA

Diurnal habitat use varied seasonally at Union County CA (Table 1). Generally, use of green forage fields was highest in Fall and declined in Winter. Lake use followed an opposite trend with low use in Fall and high use in Winter. Use of corn was constant except for a decline in Late Fall, the hunting season. Milo and other crop fields received little use in all seasons.

Use of lake, corn, and other forage habitats did not vary annually at Union County CA. Winter wheat use was lowest in 1986-87 and soybean use was highest in 1984-85.

Habitat selection varied on the Union County CA survey route (Table 1) with use of alfalfa/clover fields, lakes, and shallow wetlands exceeding availability. Conversely, grain fields were either used less than or equal to their availability.

Habitat Use and Selection at Rend Lake

Diurnal use of all habitats except corn varied seasonally at Rend Lake (Table 1). Soybean use was lowest in Early Fall when winter wheat use was highest. Lake use was higher in Winter than Early Fall. Alfalfa/clover use was highest in Late Fall. Milo and other forage habitats had relatively low use in all seasons.

Use of soybean and alfalfa/clover habitats varied between years at Rend Lake. Alfalfa/clover was not used in 1984-85, but received 20% (SE = 2.8) of goose-use in 1986-87. Conversely, use of soybeans averaged 17% (SE = 3.5) and was highest in 1984-85, but averaged 5% (SE = 3.5) and was lowest in 1986-87.

Lake and winter wheat habitats were used more than available, while soybean and milo habitats tended to be used less than available on the Rend Lake survey route (Table 1). Use of alfalfa/clover exceeded its availability in 1986-87 when it was available on Rend Lake Refuge, but not in 1984-85 when none was available on the refuge.

Habitat Use and Selection at Horicon NWR

Goose use of upland habitats near Horicon NWR varied seasonally (Table 1). Alfalfa use was highest in Early Fall when other forage use was lowest. Corn use was lower in Spring than in Late Fall. Soybeans and winter wheat received relatively low use in all seasons.

Total wetland use on the Horicon survey route did not vary seasonally (Table 1), but the type and location of wetlands used did vary seasonally. Nearly all wetland use during Fall was on-refuge, while small wetlands scattered to the west and north of Horicon NWR received considerable use in Spring. Small, off-refuge wetlands were probably attractive in Spring because they were often inundated with meltwater from creeks and provided the first snow-free habitat. As temperatures continued to moderate, lowland grass pastures (other forage habitat) adjacent to creeks and shallow wetlands were also used extensively. Radio telemetry data showed some geese roosted on small private wetlands and remained in adjacent lowland areas throughout the day during Spring (Caithamer 1989).

Most habitats on and near Horicon NWR showed no change in use between 1984-85 and 1985-86. However, use of other forage habitat was higher ($P = 0.03$) in 1985-86 than in 1984-85.

Most upland habitats were used in approximately the same proportion as available along the Horicon NWR survey route (Table 1). Proportional use of shallow wetlands exceeded availability ($P < 0.01$).

Effects of Environmental Variables

Changes in use of lakes accounted for the greatest change in overall habitat use at Union County CA. The first canonical correlation was 0.83 ($P < 0.001$), and lakes had the largest standardized canonical coefficient (-0.99). Stepwise regression indicated 50% of variation in lake use could be accounted for by variations in the environmental parameters studied. Temperature was negatively correlated with and uniquely explained 41% of variation in lake use. Amount of pond ice, amount of cloud cover, and corn stubble availability together accounted for the remaining 9% of variation in lake use.

Similar to Union County CA, changes in lake use accounted for the greatest change in overall habitat use on the Rend Lake survey route. The first canonical correlation was 0.72 ($P < 0.001$), and lake use had the largest standardized canonical coefficient (-1.01). Environmental parameters explained 25% of variation in lake use. Temperature was negatively correlated with and uniquely explained 17% of variation in use of lakes. Precipitation and percent snow cover accounted for approximately 8% of variation in lake use.

DISCUSSION

Seasonal Patterns of Habitat Use

Comparisons of habitat use information from this and other studies on the MVP (Sauer 1983, Paine 1985, Moser and Tacha 1988, Smith 1989) with information on other populations in the Atlantic (Addy and Heyland 1968, Reed et al. 1977) and Mississippi flyways (Gulden and Johnson 1968, McLandress and Raveling 1981, Austin 1988) suggest consistent patterns of habitat use during migration and wintering throughout eastern North America. Agricultural crops, especially corn, are important during all seasons and at all latitudes. Use of corn shows no consistent seasonal high or low. Shallow wetlands are important except during the coldest periods when lakes and other open waters are used. Use of green forage crops, such as wheat, is highest in fall. During spring at mid-latitudes, geese use lowland pastures and other grassy habitats bordering creeks and wetlands extensively for feeding.

High variability in habitat use indicates that MVP geese are very adapatable. The MVP is currently at record high levels due in part to the birds' ability to utilize various agricultural and wetland habitats during migration and wintering.

Importance of Various Habitats

Nutritional value of different foods eaten by geese varies. Corn and milo seeds are excellent sources of energy (approximately 4 kcal/g dry weight), but relatively poor sources of protein (approximately 9% dry weight) (Joyner et al. 1987). Green forage foods, including winter wheat, alfalfa, red clover, fescue, and blue grass, contain relatively high amounts of protein (12-29% dry weight), but relatively little energy (approximately 2 kcal/g dry weight) (Ensminger and Olentine 1978, Maynard et al. 1979, McLandress and Raveling 1981, Buchsbaum et al. 1986, Caithamer 1989). Soybean seeds contain both high amounts of protein (43% dry weight) and energy (approximately 3 kcal/g dry weight) (Storey and Allen 1982, Ensminger and Olentine 1978, Caithamer 1989).

The value of soybean seeds to geese is reduced because they can cause mortality through impaction (Jarvis 1976). No impaction was observed in this study, probably because weather conditions following harvest were not dry and because many soybean fields were double-cropped to winter wheat (Jarvis 1976). Double-cropped fields provided both soybean seeds and newly sprouted wheat to feeding geese (Gates 1989).

Milo appears relatively unimportant to Canada geese. It had low use and/or low selection in this study and others in southern Illinois (Arthur 1968, Sauer 1983, Paine 1985) and Missouri (Austin 1988). Low use and selection of milo may be related to greater abundance of more palatable foods, difficulty that geese appeared to have in walking through milo stubble because of relatively high stem density and height, or other factors.

Fall tillage impacts habitat quality for geese. Waste grain availability is reduced $\geq$80% by fall tilling (Warner et al. 1985, 1989). Smith (1989) suggested that reduction in fall tilling of corn fields near Horicon NWR would alleviate goose depredation on alfalfa and other crops. However, geese may benefit from tilling of soybean fields during dry falls since this reduces risk of impaction (Jarvis 1976).

Dairy farming seems compatible with habitat needs of migrating geese. Lowland pastures, alfalfa, and high-moisture corn fields were frequently used by geese and common on dairy farms near Horicon NWR. High-moisture corn fields, typically mowed in Early Fall as a silage crop, provided substantial waste grain (Caithamer 1989) and were among the first available grain stubble fields. Cow manure spread on fields contains undigested grain that geese consumed (Gates 1989). Food value of manure may be most important to geese in spring (Hunt and Hanson 1975).

Lakes provide a secure resting environment (Raveling et al. 1972) that is most important during cold weather. Energy expenditures for activities are reduced on lakes (Caithamer 1989) allowing geese to endure prolonged periods of cold weather with minimal catabolism of energy reserves.

Roles of Hunting and Refuges

Intensity of hunting pressure and availability of agricultural crops influenced refuge use. No agricultural crops were available on Horicon NWR during this study, while farming was extensive on southern Illinois refuges. Geese in Illinois functionally restricted their activity to refuges during hunting season, while geese near Horicon NWR exhibited no detectable change in refuge use associated with hunting. These differing responses were probably due to different intensities of hunting pressure. Hunting pressure was intense on both public and private lands on and adjacent to Union County CA and Rend Lake. Permanent hunting blinds and large (>100) spreads of goose decoys were common in southern Illinois. Conversely, hunting pressure was relatively low near Horicon NWR. No adjacent property was managed intensively for goose hunting as in southern Illinois, although some landowners constructed temporary blinds that were rented to hunters.

Habitat composition and quality on wintering refuges influenced habitat use. Soybean habitat on Union County Refuge was available only in 1984-85; soybean use on the Union County survey route that year was higher than other years when none was available on the refuge. Low wheat use along the Union County CA survey route in 1986-87 was associated with tall (>25 cm) winter wheat on the refuge. Younger, shorter wheat has more crude protein and soluble carbohydrates and less crude fiber than older, taller wheat (Comm. on Anim. Nutr., U.S.A. and Natl. Comm. on Anim. Nutr., Can. 1964). Use of alfalfa/clover habitat was lowest in 1984-85 at Rend Lake when none of the habitat was available on the refuge. Similarly, use of soybean habitat at Rend Lake was lowest in 1986-87 when none of the habitat was available on the refuge.

Impact of Environmental Conditions

Wintering geese responded to changing temperature primarily by varying their use of lakes. Cold temperatures led to increased use of lakes where geese minimized energy expenditures by resting more and expending less energy than while on uplands (Caithamer 1989). Geese remained on roosting lakes for extended periods at temperatures <-9°C (Raveling et al. 1972). At more moderate temperatures, wintering geese left roosting lakes to feed in various upland habitats. Energy expenditures increased when geese were on uplands (Caithamer 1989).

Influence of Nutritional Requirements on Habitat Use

High use of green forage fields in Early Fall may reflect high protein needs of geese and not low availability of grain stubble as suggested by Bell and Klimstra (1970) and Sauer (1983). Grain stubble seemed adequately available as an average of 69% and 29% of corn and soybean fields on the Rend Lake and Union County survey routes, respectively, were harvested in Early Fall (Pritchert 1988, Caithamer 1989). Body feather replacement in Canada geese peaks in September and steadily declines through spring (Gates 1989). Canada geese and other waterfowl meet protein needs for feather growth through diet and not mobilization of internal body reserves (Ankney 1979, 1984; Raveling 1979, Heitmeyer 1988). The diets of MVP geese in Early Fall contained more protein than during Late Fall or Winter periods (Gates 1989).

Canada geese acquire fat and protein reserves essential for reproduction during spring migration and staging (Hanson 1962, Raveling 1979, McLandress and Raveling 1981, Gates 1989). These needs are met by intensive feeding in corn, grass, and wetland habitats while staging during mid-migration. MVP geese observed near Horicon NWR in this study selectively used lowland pastures and shallow wetlands in Spring. Their use of corn fields remained high but less than in Fall. Diets of MVP geese were most varied in Spring, yet corn still constituted approximately 50% of food ingested (Gates 1989).

MANAGEMENT RECOMMENDATIONS

A complex of grain, green forage, shallow wetland, and lake habitats should be made available to Canada geese during migration and wintering. Each habitat provides specific needs not furnished by the other habitats. Corn should be provided in place of milo since corn had consistent high use while milo had consistent low use. The value of soybeans to geese can be enhanced by management practices (such as disking or over-seeding to winter wheat) that reduce risk of impaction. Fall tilling of corn stubble and green forage fields should be discouraged as this reduces food availability.

Habitat management on refuges is most important in regions where hunting restricts geese to refuges. In these regions, all habitat needs during hunting should be provided by refuge resources if the goal is to reduce movements of geese and/or to maintain them in the best possible condition. However, if the goal is to increase movements of geese off refuge to increase harvest, then refuge crops should be made less available through smaller acreages and/or mowing and harvesting should be delayed until after hunting. Prolonged or delayed hunting seasons increase the importance of refuges (Caithamer 1989).

Shallow wetlands should be protected and developed throughout the migrating and wintering range of the MVP. Small, privately owned wetlands to the north and west of Horicon NWR appeared particularly important in spring. Agricultural habitats currently need not be developed on Horicon NWR since important agricultural habitats were adequately available on private land and geese did not appear restricted to Horicon NWR. Managers of refuges on wintering areas of the MVP should continue to provide a complex of habitats and recognize that refuge resources are most important during hunting. Alfalfa/clover, winter wheat, and lake habitats may be inadequately available on southern Illinois refuges as use of these habitats exceeded their availability.

ACKNOWLEDGEMENTS

We thank W. D. Klimstra and A. Woolf for providing administrative support and advice. R. M. Birger, R. A. Hunt, J. R. Lennartson, M. S. Nelson, J. T. Pohlman, D. D. Thornburg, and W. A. Wheeler provided valuable assistance. A. Woolf reviewed early drafts of the manuscript. Research project W-95-R(SI), Ecology of Canada Geese, was conducted with funding from the Federal Aid in Wildlife Restoration Act -- a cooperative program between the states and the U. S. Fish and Wildlife Service. The project was sponsored by the Illinois Department of Conservation in cooperation with the Cooperative Wildlife Research Laboratory, Southern Illinois University at Carbondale (SIUC). The form, content, and interpretations of data are the responsibility of the authors, and not of the Illinois Department of Conservation or other cooperating agencies/organizations. Additional support was provided by the Department of Zoology and the Graduate School at SIUC.

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Table 1. Refuge use and habitat use and selection on and near Union County Conservation Area, Rend Lake, and Horicon National Wildlife Refuge, 1984-1987.

Location	Variable	$\bar{x}$ %[b]	SE	Seasonal high[c]	Seasonal low[c]	Selection[a] 1984-85	1985-86	1986-87
Union County	Refuge	75	2	L. Fall				
	Corn	14	1		L. Fall	0	0	0
	Soybean	9	1	E. Fall	L. Fall	-	-	-
	Milo	2	<1			0	-	0
	Winter wheat	20	2	E. Fall		+	0	0
	Alfalfa/clover	12	2	L. Fall	L. Winter	0	+	+
	Other forage	5	1	L. Fall	E. Fall	0	0	0
	Other crops	1	<1			-	0	0
	Wetland	14	1	L. Fall	E. Fall	+	+	+
	Lake	24	2	E. Winter	E. Fall	+	+	+
Rend Lake	Refuge	73	2	L. Fall	L. Winter			
	Corn	16	2			0	0	0
	Soybean	10	1		E. Fall	0	-	-
	Milo	2	1			-	-	0
	Winter wheat	24	2	E. Fall		+	+	+
	Alfalfa/clover	10	1		L. Fall	0	0	+
	Other forage	<1	<1	L. Winter		0	0	-
	Wetland	3	1		L. Winter	0	0	0
	Lake	35	2	E. Fall	Winter	+	+	+
Horicon[d]	Refuge	34	3			0	-	
	Corn	26	2	L. Fall	Spring	0	0	
	Soybean	2	1			0	0	
	Winter wheat	3	1	E. Fall		0	0	
	Alfalfa	17	2	E. Fall		0	0	
	Other forage	19	2		E. Fall	0	0	
	Wetland	34	2			+	+	

[a] "+" indicates use exceeded ($P < 0.01$) availability, "-" indicates use was less ($P < 0.01$) than availability, and "0" indicates use equalled ($P \geq 0.01$) availability.

[b] Within a location all years and seasons combined; n=171 at Union County Conservation Area, n=222 at Rend Lake, and n=69 at Horicon National Wildlife Refuge.

[c] $P < 0.05$, "E." indicates Early, and "L." indicates Late.

[d] No data were collected in 1986-87.