

## AMPHIPODS, LAND-USE IMPACTS, AND LESSER SCAUP (*AYTHYA AFFINIS*) DISTRIBUTION IN SASKATCHEWAN WETLANDS

Dorothy H. Lindeman and Robert G. Clark  
*Environment Canada*  
*Canadian Wildlife Service*  
*Prairie & Northern Wildlife Research Centre*  
*115 Perimeter Road*  
*Saskatoon, Saskatchewan, Canada S7N 0X4*

**Abstract:** The abundance and distribution of lesser scaup (*Aythya affinis*) may be influenced by the availability of amphipod crustaceans, since these invertebrates represent an important food source, particularly for immature birds. Another important factor may be degradation of habitat, since scaup nest in wetland margins and adjacent upland habitats. The objective of this study was to evaluate the relative importance of amphipods, wetland features such as area and water depth, and indices of margin/upland habitat, on the distribution and abundance of scaup. A subsample of 108 oligosaline wetlands was chosen on twelve sites located in three eco-regions of southern Saskatchewan, Canada. Data were gathered during 1995 on relative amphipod abundance, wetland area, fall water depth, upland nesting habitat type, wetland margin impacts, and spring numbers of lesser scaup. Scaup use of wetlands was significantly affected by the availability of amphipods, wetland margin impacts, and wetland area. Controlling for the effect of area showed that scaup were most common on ponds with abundant amphipods and minimal margin impacts. In the southernmost mixed grassland eco-region, scaup were affected by amphipod availability only, whereas in the moist mixed grassland and parkland eco-regions, results indicated that both margin impact and amphipod availability were significant factors. Results are consistent with hypotheses that decreases in scaup numbers since the mid-1980s may be due to (1) loss, resulting from both human and climatic factors, of natural wetlands capable of supporting rich amphipod populations and (2) continuing agricultural encroachment on remaining wetlands.

**Key Words:** *Aythya affinis*, amphipods, *Gammarus lacustris*, *Hyaella azteca*, land-use impacts, lesser scaup, Saskatchewan, wetlands, prairie potholes

### INTRODUCTION

In prairie regions of central Canada, lesser scaup (*Aythya affinis* Eyton, hereafter scaup) occupy small seasonal and semi-permanent wetlands and lakes, and they rely exclusively on aquatic foods, mainly aquatic invertebrates (Bartonek and Hickey 1969, Smith 1971, Batt et al. 1989, Austin et al. 1998). Scaup are found throughout Saskatchewan, primarily in boreal forest and parklands (Austin et al. 1998), less commonly in the southern mixed grassland eco-region (see Figure 1), and only in small numbers in the extreme southwestern part of the province (Smith 1996).

Wetland area has been shown to be a factor in scaup use of ponds. Kantrud and Stewart (1977) found that the highest proportion (53%) of breeding pairs in their study site in North Dakota occurred on semi-permanent wetlands (average area 9.3 ha), the next highest (38%) on seasonal wetlands (average area 1.2 ha), and the third highest (5.4%) on permanent wetlands (av-

erage area 32.9 ha). Near Yellowknife, Northwest Territories, breeding pairs showed some preference for larger ponds, while broods (with hens) were even more selective of pond size and strongly preferred large ponds (Toft et al. 1982). However, Kantrud and Stewart (1977) pointed out that semipermanent wetlands are relatively large, and their long shorelines might be occupied simultaneously by numerous breeding pairs. Thus, shoreline length must be taken into account when examining the effect of pond area on scaup numbers.

Amphipods are a predominant food in the diet of scaup (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Bartonek and Murdy 1970, Sugden 1973, Austin 1983, Afton and Ankney 1991). Sugden (1973) found that amphipods averaged 52% of the diet of scaup ducklings. Dirschl (1969) found that amphipods made up a high proportion of the adult scaup diet, especially in spring and fall. *Hyaella azteca* Saussure and *Gammarus lacustris* Sars are the amphipod spe-

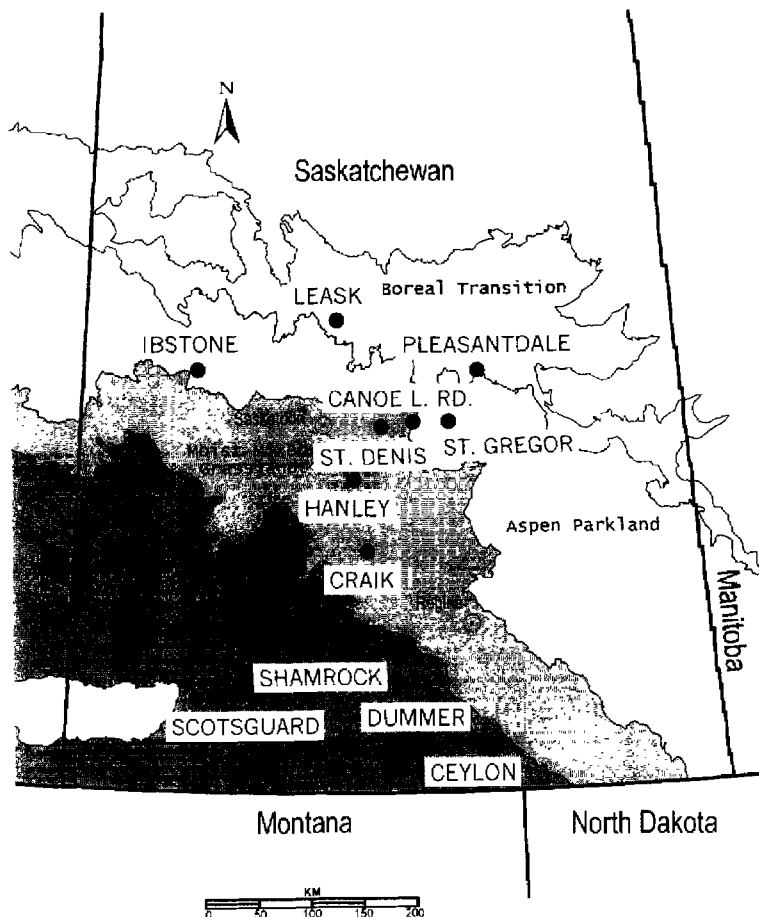


Figure 1. Locations of study sites in Saskatchewan, Canada, with eco-regions after Padbury and Acton (1994).

cies normally found in the Saskatchewan prairies, although *Gammarus* is considerably less common than *Hyaella*, being confined to deeper ponds (Lindeman, pers. comm.). It has been proposed that habitat selection by scaup may be linked with the general density of amphipod prey (Afton and Hier 1991). If so, anthropogenic and/or climatic effects on amphipod populations in prairie wetlands might indirectly affect abundance of lesser scaup.

Scaup usually nest on dry or moist soil in the wet-meadow zone of wetlands but will also nest away from water in tracts of native prairie, hayfields, or shrub patches (Austin et al. 1998). They are the only North American diving duck to nest on uplands. Scaup typically inhabit regions with relatively stable wetland conditions and tend to use more permanent ponds. However, Dubovsky et al. (1997) noted that scaup populations have decreased over the past decade. It is possible that this decrease may be due to changes in physical and/or biological characteristics of wetlands and associated food sources. Another possible explanation is that scaup decreases are associated with loss of margin or upland nesting habitats. Turner et al. (1987) found that land-use impacts on wetland mar-

gins in the Canadian prairies were severe: 73.9% in 1981, increasing to 84.2% in 1985. Loss of upland habitats is demonstrated by the increase in cultivated land. Millar (1986) indicated that in 1982, grasslands were 78 to 84% cultivated, and parklands were 80% cultivated. The intensification of agriculture, with concomitant destruction of wetlands and upland nesting cover, may be the dominant factor affecting the distribution, abundance and reproductive success of the region's ducks (Batt et al. 1989).

Our objectives were to (1) test whether the distribution and abundance of lesser scaup are correlated with the abundance of amphipods in oligosaline wetlands of Saskatchewan; (2) determine whether the distribution of scaup is related to characteristics of nesting cover immediately adjacent to wetlands; and (3) simultaneously evaluate the relative importance of amphipods, wetland area and depth, and nesting habitat indices on distribution and abundance of scaup.

#### MATERIALS AND METHODS

Wetlands and numbers of waterfowl, including scaup, are routinely monitored along long-term aerial

transects surveyed by the Canadian Wildlife Service of Environment Canada and the U. S. Fish and Wildlife Service. Selected segments of some transects are surveyed by ground crews to provide correction factors for bird visibility (U. S. Fish and Wildlife Service and Canadian Wildlife Service 1987). These air/ground transects are usually 402 m wide and 26–29 km long. In Saskatchewan, both aerial and ground surveys are performed annually each May, typically by the same personnel, when the following are recorded: (1) the number of ducks of each species on each wetland; (2) wetland class; and (3) impacts on wetland margins and land use immediately adjacent to wetlands. Pond class is a qualitative estimate of relative wetland permanency (U. S. Fish and Wildlife Service and Canadian Wildlife Service 1987, Didiuk et al. 1989; see also Batt et al. 1989). Scaup numbers used here are expressed as number of birds per pond.

Sites were chosen to reflect a range of geographic location and long-term scaup data, and included 10 air/ground segments (Figure 1). Four sites were located in each eco-region, although accessibility and local conditions played a role (for example, a promising air/ground segment near the eastern edge of Saskatchewan could not be used due to severe local flooding that spring). It was not possible to find sites with equal numbers of similar ponds on each transect, since pond numbers are a function of landscape and precipitation, not transect. Two other sites for which reliable scaup data are available were included. Duck counts are regularly conducted by trained CWS personnel on the St. Denis National Wildlife Area (NWA) and at another site, called the Canoe Lake Road transect, established by R. G. Clark in 1987 as an alternate area to St. Denis. Hereafter, we collectively refer to these transects and areas as study sites. The Canoe Lake Road transect methods are identical to regular air-ground segments. The St. Denis NWA is surveyed in its entirety, although only a subset of ponds (again, all semipermanent and permanent, plus the largest of the seasonal ponds) on the site were included in this study.

Spring waterfowl-survey data for the 1995 air/ground transects were obtained from raw data files of the Migratory Birds Division at the Prairie and Northern Wildlife Research Centre in Saskatoon. Scaup data for 1995 from St. Denis NWA and Canoe Lake Road were obtained from a single spring survey close to the date of air/ground surveys.

More extensive data from the St. Denis NWA were examined to see if the spring survey data were at all representative of scaup use of ponds throughout the open-water season. Historical data, from 1982 through 1995, were analyzed from 8 surveys, spread as evenly as possible over the open-water season, with survey dates chosen to match as closely as possible so that

each year was comparable to the next. Chi-square tests were performed on these scaup data for 1982–1995, and for the 1995 data only, to compare spring counts on the study ponds to surveys averaged over the entire open-water season.

A subset of the largest, most persistent wetlands (the largest seasonal ponds, plus all semipermanent and permanent ponds) was chosen for study on each site, by examination of the segment aerial photos and maps of St. Denis and Canoe Lake Road. Temporary wetlands, those ponds that persist only about 3 weeks (Didiuk et al. 1989), were excluded after checks of temporary wetlands on all transects revealed no amphipods. Freshwater amphipods have no resting eggs or other mechanisms to survive complete desiccation (Holsinger 1976) when ponds dry out or freeze solid. Pennak and Rosine (1976) state that “the temporary waters of old buffalo wallows and vernal prairie ponds are devoid of amphipods.” While scaup tend to use semipermanent and permanent ponds extensively (Kantrud and Stewart 1977), it was considered important to include a number of seasonal ponds, since there is some evidence that seasonal wetlands are used as well (Hammell 1973, Sugden 1973). Streams and dugouts were excluded from final analyses.

Amphipod sampling was undertaken in spring 1995, just after ice-out, since the presence of large numbers of amphipods at this time should indicate permanent populations. Methods were a modification of the sweep sampling and scoring used by Muck and Newman (1992). At each wetland, five sweep samples were taken at randomly-selected locations. Sweep sampling was performed using a Wildco “Indestructible Triangular Dip Net” (mesh size 800 by 900 micrometers, net mouth 0.3 m wide) by scooping the flat net mouth from the surface across the substrate and back to the surface in a sweeping, digging motion that covered 1.0 to 1.8 m; each sweep therefore sampled an area of 0.3 to 0.5 m<sup>2</sup> as well as passing twice through the water column. The net bag was then dipped into the water and shaken to sieve fine silts out through the mesh, while ensuring that none of the invertebrates or coarser material were lost over the rim. All sweeping was done in 0.5 m of water or less. A sample of several specimens was preserved in 70% ethanol and brought back to the lab to confirm field identifications. Amphipod numbers for each pond were scored as zero, sparse (1 to 2 per sweep, averaged over 5 sweeps), good (3 to 20 per sweep), and rich (>20 per sweep). When amphipods were either absent or considered sparse in the first 5 sweeps, wetlands were subjected to at least 10 more sweeps to confirm the initial scoring and ensure that the amphipods were not simply congregated in another microhabitat. In ponds that scored good or rich in the first 5 sweeps, another 5 sweeps were made to

confirm the initial scoring. Each transect usually took most of a day to sample. However, the early spring tendency of amphipods to congregate in very shallow water in prairie potholes (Lindeman, pers. comm.), their photonegative and thigmotactic behaviour (Holsinger 1976) (amphipods tend to stay on or in the substrate during daylight) plus replicated sweeping, ensured consistency of results within the qualitative ordinal nature of the scoring used.

Uplands (land use within 100 meters of wetland margins) were assigned to habitat types (undisturbed grassland, pasture, cropland, summer fallow, planted cover, "other") by visual inspection during August 1995 duckling surveys and confirmed using the air/ground survey data (where available) and a second set of observations on the ground in September/October. In cases where the upland was composed of more than one habitat type (which occurred relatively rarely in this dataset), scoring was based on the habitat type that constituted 50% or more of the area in question. The uplands around each pond were then classified as suitable or unsuitable nesting areas. We defined suitable as grassland (including shrubs and trees) and dense nesting cover and unsuitable as cultivated or disturbed habitats.

Data on wetland margins and margin impacts were obtained for 1995 from the air/ground survey data where available and from observations following a habitat assessment manual (Didiuk et al. 1989) while at the sites. The area contiguous with and extending 10 m beyond the edge of the wet meadow zone was considered the margin and was assessed in terms of percentage of impacts such as cultivation, burning, haying, grazing, farmyard, clearing or filling, and any wooded cover (U. S. Fish and Wildlife Service and Canadian Wildlife Service 1987, Didiuk et al. 1989). Turner et al. (1987, Figure 2) illustrated how pond margins were scored for impact per cent. After preliminary analyses, margin impact was collapsed into a single binary variable, scoring the presence or absence of a cumulative total of margin impacts 50% or greater.

Sites were re-visited in early August for a duckling survey and again in late September/early October to obtain pond depth to the nearest 0.1 m for the fall low-water mark (a far more accurate indicator of water depth available for overwintering amphipod populations than the spring flood depths). Amphipod relative abundance was again checked in every pond with sweep sampling and each pond re-assessed to confirm margin impact and upland scores.

Wetland areas were calculated by planimetry from aerial photos. In cases where only a part of the wetland was contained within the transect boundaries, only that part of the pond contained within the transect was used to calculate pond size since the surveyors only count

those birds within the transect proper (U. S. Fish and Wildlife Service and Canadian Wildlife Service 1987). While the air photos (from 1990/1991, Jack Smith, CWS Migratory Birds Division, Saskatoon pers. comm.) were not necessarily taken at moisture levels similar to the spring of 1995, it was possible to use ground observations to relate the current water level to vegetation rings on the aerial photos and so correct the comparative water surface area. Sites were also assigned to an eco-region (aspen parkland/boreal transition, moist mixed grassland, or mixed grassland after Padbury and Acton 1994, see also Larson 1995) to evaluate geographic variation in scaup-wetland relationships.

Univariate analyses included Spearman bivariate correlations on raw data (for the continuous and ordinal variables), validated with a sequential Bonferroni test (Rice 1989). T-tests were used for the binary margin and upland variables. Data were  $\log_{10}(x+1)$  transformed where appropriate, checked for normality (Proc Univariate, SAS Institute, Inc. 1990) where appropriate, and used in linear regression analyses to relate scaup numbers to pond area (SPSS Inc. 1993).

Analysis of variance (ANOVA: Proc GLM, SAS Institute, Inc. 1990) was chosen as one multivariate technique that could simultaneously examine the effects of the variables. ANOVA is relatively robust, especially with large sample sizes, and if appropriate transformations are used (Green 1979). Continuous independent variables (area and depth) were categorized for these analyses. Area categories were small (up to 1.4 ha), medium (1.5 to 5 ha), and large (over 5 ha). Fall water depth categories were shallow (up to 0.5 m), medium (0.6 to 1.25 m), and deep (over 1.3 m). The scaup/area residuals obtained from linear regression of transformed data (scaup per pond and pond area) were used as the dependent variable to control for the known effect of wetland area on scaup numbers.

Forward stepwise ordinal logistic regression (Proc Logistic, SAS Institute, Inc. 1990), with a significance level of 0.05 for entry into the model, was chosen as a second multivariate technique. The raw data were a mixture of continuous, ordinal qualitative, and binary categorical variables. Non-parametric tests are most appropriate for these datasets (Green 1979). Scaup numbers were collapsed into four categories for the logistic regression: none (zero), rare (up to 2 scaup per pond), some (over 2 to 5), and common (more than 5). Variables included in the analysis were eco-region, margin impact, suitable nesting upland, fall water depth, and *Hyaella* and were used in their raw form. Area was omitted. This second multivariate technique, using slightly different forms of the variables, provides a check on the validity of the first method and offers further information. "Robustness of decisions reached

by statistical analysis will be increased by the use of several analysis methods based on different assumptions" (Green 1979: 14).

Spearman correlations, Mann-Whitney U tests, and a forward stepwise binary logistic regression (SPSS Inc. 1993) were used to test for any patterns between ducklings and the other variables. Duckling data were expressed for univariate analyses as number of ducklings (not including the hen) seen on each pond and for the logistic regression as presence or absence of ducklings on each pond.

## RESULTS

An examination of data from 1982 to 1995 for the St. Denis ponds used in this study confirmed that the single spring counts, conducted about the same time as the air/ground surveys, adequately represented wetland use by scaup throughout the season during this time period. A  $\chi^2$  test of independence of scaup distribution over the study ponds at this site, between spring surveys and the entire season, indicated that there was no difference ( $\chi^2 = 9.07$ , d.f. = 15,  $P > 0.05$ ). The May survey for 1995 included an obvious outlier: a group of 12 scaup were counted on pond 70 that particular day. Pond 70 is not a pond where scaup were normally seen in any other year for which records were available. With this outlier removed, the  $\chi^2$  test also indicated that for the 1995 data alone, the pattern of scaup sightings was not significantly different between the single spring survey and the entire open-water season ( $\chi^2 = 18.88$ , d.f. = 12,  $P > 0.05$ ).

Table 1 lists eco-region and transect summaries for site sizes, numbers of ponds, and means and ranges of the final forms of all pond variables. Univariate analyses (Spearman correlations on ordinal and continuous variables) showed that the number of scaup per pond increased with pond area, relative *Hyaella* abundance, and fall maximum water depth (Table 2), although none of the  $r$  values were particularly high. *Gammarus* abundance was correlated with scaup numbers, but the significance level was rejected when the sequential Bonferroni technique was applied. T-tests on the margin impact and suitable nesting upland variables showed that scaup numbers per pond decreased with the presence of (50% or greater) margin impact ( $T = 4.13$ , d.f. = 72,  $P < 0.05$ ). There was no apparent relationship between scaup numbers and presence or absence of large-scale suitable upland nesting cover ( $T = -1.63$ , d.f. = 106,  $P > 0.05$ ).

Regression analysis indicated a positive, although relatively unimportant, relationship (overall model:  $F = 19.68$ , d.f. = 1,106,  $P < 0.001$ ) between numbers of scaup and wetland area ( $\log(x+1)$  transformed data). Residuals from this regression were used to rep-

resent scaup numbers, corrected for area effect, in the analyses of variance.

Analysis of variance to simultaneously assess the effects of all variables showed that scaup (adjusted for wetland area) were more abundant ( $F = 2.72$ , d.f. = 33, 107,  $P < 0.01$ ) on wetlands with greater relative numbers of *Hyaella* (partial  $F = 3.79$ , d.f. = 3,  $P = 0.014$ ). No two-way interactions were significant ( $P > 0.10$ ) in this model except eco-region\**Hyaella* (partial  $F = 2.16$ , d.f. = 5,  $P = 0.068$ ), so all other interactions were dropped and the model was re-run with main effects and the eco-region\**Hyaella* interaction (Table 3). Scaup were more common on wetlands with greater relative numbers of *Hyaella* and little or no land-use impacts on wetland margins, but the relationship between scaup and *Hyaella* showed possible variation with eco-region. Therefore, we analyzed each eco-region separately.

In the parkland/boreal transition eco-region ANOVA model (Table 4), *Hyaella* was the only variable having a significant effect on scaup at the 0.1 probability level. The model for the moist grassland region (Table 5) included *Hyaella* and margin impact ( $P < 0.1$ ). However, in the grassland eco-region ( $n = 29$  wetlands, 4 sites), the model was not significant ( $F = 1.88$ , d.f. = 6,22,  $P > 0.1$ ).

Forward stepwise ordinal logistic regression of categorized scaup counts against eco-region, *Hyaella*, *Gammarus*, fall water depth, suitable nesting upland, and margin impact, for all sites, provided a model that included the variables *Hyaella* and margin impact (Tables 6 and 7). Results for each step are not included here, but the variables are listed in the order they entered the models. Individual eco-region logistic models  $-2 \log L$  probabilities were all significant (Table 6) but differed slightly in the individual variables selected (Table 7). In the parkland/boreal transition region, the model selected margin impact as the first variable to be entered into the model, then *Hyaella*; in the moist grassland region, *Hyaella* was selected first, then margin impact; and in the southern grassland region, *Hyaella* alone was selected as the significant predictor.

In the August survey of all sites, only 12 of 108 (11%) natural ponds had scaup ducklings. All broods were on semi-permanent or permanent ponds, except one brood on the Hanley transect, which was seen on a large seasonal pond. One brood was encountered on a dugout (73 dugouts were originally included in the spring field work). Spearman correlations showed that duckling numbers increased with wetland area ( $P < 0.05$ ), fall water depth ( $P < 0.001$ ), *Gammarus* abundance ( $P < 0.001$ ), and *Hyaella* abundance ( $P < 0.001$ ) and showed no relationship to eco-region ( $P > 0.1$ ), although all correlations were weak ( $R = 0.228$ , 0.378, 0.290, 0.364, and 0.025 respectively). The

Table 1. Summary information on study sites, plus eco-regions (see Figure 1). All variables are in the form used in the multivariate analyses. Note that the unit of analysis was the individual pond, not transect averages. N—number of wetlands in subsample at that site; Area—individual pond area; Depth—wetland depth at centre; Margin Impact—presence/absence of margin impact 50% or greater; Suitable upland—presence/absence of 50% or more suitable nesting cover in upland; *hya*—score for *Hyalella* abundance; Scaup—number of scaup per pond; Eco-region 1—aspens parkland/boreal transition; Eco-region 2—moist mixed grassland; Eco-region 3—mixed grassland.

Site	Site Size (ha)	N	Av. Area (ha)	Area Range (ha)	Av. Depth (m)	Depth Range (m)	Av. Margin Impact	Margin Impact Range	Av. Suitable Upland	Suitable Upland Range	Av. Hya	Hya Range	Av. Scaup	Scaup Range
Ibstone	582	12	2.2	0.1-10.2	0.0	0-0.2	0.2	0-1	0.2	0-1	0.2	0-3	3.4	0-39
Leask	388	6	3.7	0.2-9.6	0.9	0.5-1.8	0.0	0-0	0.3	0-1	0.7	0-2	3.8	0-17
Pleasantdale	1294	6	2.9	0.5-8.1	1.0	0.3-2.1	0.0	0-0	0.7	0-1	1.3	1-3	6.3	0-17
St. Gregor	582	12	1.0	0.1-2.2	1.1	0.2-2.5	0.8	0-1	0.0	0-0	1.2	0-3	0.4	0-5
Eco-region 1		36	2.1	0.1-10.2	0.71	0-2.5	0.4	0-1	0.2	0-1	0.8	0-3	3.0	0-39
Canoe L. Rd.	302	10	1.2	0.03-3.4	1.0	0.4-2.2	0.2	0-1	0.1	0-1	1.5	0-3	5.7	0-20
St. Denis	385	15	1.6	0.7-6.2	0.7	0.2-2.2	0.1	0-1	0.7	0-1	0.7	0-3	2.1	0-12
Hanley	712	12	0.5	0.1-1.2	0.4	0-1.0	0.9	0-1	0.2	0-1	0.0	0-0	0.2	0-2
Craik	906	6	0.4	0.2-0.7	0.0	0-0	0.7	0-1	0.3	0-1	0.0	0-0	0.0	0-0
Eco-region 2		43	1.1	0.03-6.2	0.6	0-2.2	0.4	0-1	0.4	0-1	0.6	0-3	2.1	0-20
Scotsguard	776	3	3.3	1.6-5.0	0.7	0-1.2	1.0	1-1	0.3	0-1	0.3	0-1	6.7	0-20
Shamrock	582	5	1.0	0.4-2.0	0.4	0-1.8	0.6	0-1	0.0	0-0	0.4	0-2	0.2	0-1
Dummer	518	10	2.9	0.2-7.4	0.6	0-3.8	0.9	0-1	0.2	0-1	0.6	0-2	1.8	0-18
Ceylon	776	11	2.1	0.1-7.0	0.1	0.0-0.5	1.0	1-1	0.0	0-0	0.1	0-1	0.3	0-3
Eco-region 3		29	2.3	0.1-7.3	0.4	0-3.8	0.9	0-1	0.1	0-1	0.3	0-2	1.4	0-20

Table 2. Spearman correlations between scaup numbers and the original variables (raw data). N = 108 ponds. \*\* indicates correlation probabilities still significant at the 0.05 level, after application of the sequential Bonferroni technique (Rice 1989).

	Area	Fall Depth	<i>Hyaella</i>	<i>Gamma-rus</i>	Eco-region
R	0.354	0.399	0.468	0.256	-0.129
p	0.000**	0.000**	0.000**	0.008	0.183

duckling/area correlation was rejected as non-significant when the sequential Bonferroni technique was used to validate the correlations.

A binary forward stepwise logistic model (SPSS Inc. 1993), with duckling presence/absence as the dependent variable, indicated that pond area and fall water depth were the strongest factors explaining duckling occurrence (predicted model accuracy 90%). When area was excluded from the variable list, on the basis of the Bonferroni results given above, fall water depth was the selected predictor ( $-2 \text{ Log L } \chi^2 = 12.6$ , 1 df,  $P < 0.001$ , model concordance 89%). The strong correlation of fall water depth with any amphipod indicator suggested that it should be removed from the analysis; the model then defaulted to *Hyaella* ( $-2 \text{ Log L } \chi^2 = 12.5$ , d.f. = 1,  $P < 0.001$ , model concordance 89%).

## DISCUSSION

Populations of most prairie-nesting waterfowl typically fluctuate in response to variations in the abundance and distribution of wetlands (Batt et al. 1989). During the dry years of the late 1980s, for example, most species decreased in abundance. However, populations of lesser scaup have decreased steadily over the past 15 to 20 years (except for 1983/84), apparently regardless of wet or dry conditions. Furthermore,

Table 4. ANOVA table for main effects of *Hyaella*, margin impact, fall water depth category and suitable nesting upland on scaup in the Parkland/Boreal Transition eco-region (n = 36 ponds; overall  $R^2 = 0.34$ ). Margin impact—50% or greater margin impact; Suitable upland—50% or greater suitable nesting habitat in pond upland.

Source	df	Sum of Squares	Mean Square	F	p
Total	35	4.460			
Model	7	1.499	0.214	2.03	0.0871
<i>Hyaella</i>	3	0.928	0.309	2.93	0.0511
Depth category	2	0.103	0.051	0.49	0.6205
Suitable upland	1	0.139	0.140	1.32	0.2604
Margin impact	1	0.092	0.092	0.87	0.3577
Error	28	2.961	0.106		

in 1997, despite several consecutive years of remarkably good wetland conditions, prairie scaup populations remained about 25% below the long-term (1955–1997) average, unlike other species such as mallard (*Anas platyrhynchos* Linnaeus), which were showing population upturns (Dubovsky et al. 1997). Degradation of food resources or nesting cover may be particularly important to scaup, given this marked long-term decline.

Since air/ground surveys may be taken at times when some scaup are still migrating (Austin et al. 1998) and the single spring data point for each pond might therefore not necessarily reflect scaup distributions at other times, it was considered important to check the spring survey against more extensive data. The comparison of a spring survey chosen to match the regular air/ground survey dates against surveys spread throughout the open-water season at St. Denis showed that, at least at this site, scaup tended to be seen on much the same ponds in May as over the rest of the season. While an analysis such as this does not necessarily take into account the potentially complicated movements of female scaup with their broods,

Table 3. ANOVA table for effects of the main variables, and the two-way interaction between eco-region and *Hyaella*, on scaup (n = 108 ponds; overall  $R^2 = 0.40$ ). Margin impact—50% or greater cumulative margin impact; Suitable upland—50% or greater suitable nesting habitat in pond upland.

Source	df	Sum of Squares	Mean Square	F	p
Total	107	14.810			
Model	14	5.852	0.418	4.34	0.0001
Eco-region	2	0.162	0.081	0.84	0.4335
<i>Hyaella</i>	3	2.078	0.693	7.19	0.0002
Depth category	2	0.488	0.244	2.53	0.0848
Suitable upland	1	0.054	0.054	0.56	0.4577
Margin impact	1	0.589	0.589	6.12	0.0152
Eco-region* <i>Hyaella</i>	5	0.924	0.185	1.92	0.0986
Error	93	8.958	0.096		

Table 5. ANOVA table for main effects of *Hyaella*, margin impact, fall water depth category and suitable nesting upland on scaup in the Moist Mixed Grassland eco-region (n = 43 ponds; overall  $R^2 = 0.51$ ). Margin impact—50% or greater margin impact; Suitable upland—50% or greater suitable nesting habitat in pond upland.

Source	df	Sum of Squares	Mean Square	F	p
Total	42	5.670			
Model	7	2.891	0.413	5.20	0.0004
<i>Hyaella</i>	3	1.228	0.409	5.16	0.0047
Depth category	2	0.297	0.148	1.87	0.1691
Suitable upland	1	0.163	0.163	2.06	0.1603
Margin impact	1	0.465	0.465	5.86	0.0208
Error	35	2.778	0.079		

molting migrations, etc., it was interpreted to mean that the spring survey data could indeed be used to relate scaup use of ponds to the indices examined here.

The importance of *Hyaella* in these results supports the Afton-Hier (1991) hypothesis that the abundance of amphipods may be an important determining factor in scaup use of wetlands. Although pond area was correlated with scaup, the fact that a larger water body can physically accommodate more birds (Kantrud and Stewart 1977) means that this relationship is not necessarily the most important one and may be masking other effects. Any analyses with area removed or corrected for area (by use of scaup/area residuals) consistently indicated that *Hyaella* and margin impact were important factors affecting scaup. Nonetheless, experimental manipulations of amphipod numbers would be useful to verify the relative importance of wetland depth, area, and amphipod abundance. Scaup will use and raise broods on (Sugden 1973) ponds that have no amphipods.

The relationship between scaup and pond area may also reflect a tendency of scaup to choose ponds on the basis of size and open water, as well as philopatry. Kantrud and Stewart (1977) showed that, in North Dakota, scaup used semipermanent and permanent wetlands most heavily. Near Yellowknife, NWT, scaup abundance increased with pond size, although Toft et al. (1982) found that perimeter had a closer association

with numbers of pairs and broods than area. The relatively weak correlation herein of scaup with area (Table 2) may reflect this as well. Larger ponds may tend to have reliably dense amphipod populations, partly because larger size often (but not necessarily) means deeper water, and water depth seems to be the crucial factor to amphipods (Lindeman, pers. comm.). The birds could be using area, or possibly the relative area of open water, as a visual cue to the potential for a good food base. Turner et al. (1987) emphasized that a very high overall proportion of pond margins were degraded and that this proportion increased every year. It is possible that heavily degraded margins could be another visual cue used by scaup when assessing a pond for use.

Scaup nests in pond margins are often located on dry or moist soil in the wet-meadow zone of wetlands (Smith 1971, Austin et al. 1998). Hines (1977) found 75% of nests in Saskatchewan parkland within 10 m of water (i.e., within the margin as defined here). In contrast, Hammell (1973) found 61% of nests in southwest Manitoba to be over water on floating mats and the mean distance between nest and water for upland nests to be 13 m. If many scaup nest in or near wetland margins, heavy impacts on that vegetation zone could cause female scaup to avoid those ponds. However, it must be noted that even though scaup may avoid nesting on ponds with degraded margins, it would not necessarily affect their potential use for foraging (Austin, pers. comm., see also discussion of dugouts, below). The spring count data used herein do not distinguish between use types.

The lack of any evident pattern between scaup and uplands suggests that distance between ponds and upland nests reduces dependence on adjacent upland habitat. Hammell (1973) found nests up to 146 m from water. Females and duckling are reported to walk up to 0.8 km from upland nests to water or from pond to pond (Austin et al. 1998). Much of what they walk across could be cultivated land. In extensive habitat studies, Millar (1989, 1992) found that the relative proportion of total upland as annual crops and summerfallow was 79% for the parklands and 86% in mixed grass prairie. These figures, although for 1985,

Table 6. Forward stepwise ordinal logistic regression  $-2 \text{ Log L } \chi^2$  scores and probabilities for overall final model of categorized scaup counts on all wetlands, and in each of three eco-regions in Saskatchewan.

Region	No. of Ponds	$-2 \text{ Log L } \chi^2$	df	$-2 \text{ Log L } \text{Probability}$	Model Concordance
All Sites	108	37.38	2	0.0001	73%
Aspen Parkland/Boreal Transition	36	12.29	2	0.0021	72%
Moist Mixed Grassland	43	21.08	2	0.0001	72%
Mixed Grassland	29	5.50	1	0.0190	67%



Table 7. Forward stepwise ordinal logistic regression  $\chi^2$  scores and probabilities for variables meeting the 0.05 significance level for entry into the final models of categorized scaup counts on wetlands, for all sites, and in each of three eco-regions in Saskatchewan. Variables are in the order they entered the model.

Region	No. of Ponds	Final Variables in Model	Variable $\chi^2$ Score	Variable $\chi^2$ Probability
All Sites	108	<i>Hyaella</i>	22.53	0.0001
		margin impact	15.88	0.0001
Aspen Parkland/Boreal Transition	36	margin impact	5.01	0.0252
		<i>Hyaella</i>	6.59	0.0103
Moist Mixed Grassland	43	<i>Hyaella</i>	12.20	0.0005
		margin impact	8.31	0.0039
Mixed Grassland	29	<i>Hyaella</i>	7.53	0.0061

agree with the presence of suitable nesting upland for each eco-region given in Table 1. It may be that with such consistently high levels of upland cultivation, any pattern is overwhelmed. Also, the birds could be using very small refugia of suitable habitat when nesting in uplands.

When the potential effects of all variables on scaup were simultaneously assessed using ANOVA, uplands again showed no apparent effect, either alone or in two-way interactions. The overall model for all ponds over all sites indicated that *Hyaella* and margin impact (50% or more) were apparently the most important factors to scaup (adjusted for pond area). Differences among eco-regions might be explainable by differences in the relative proportions and availability of large ponds and lakes. The collapse of the model for the mixed grasslands eco-region may be the result of a relatively small sample size and a large proportion of ponds with degraded margins, poor or no amphipods, and no scaup (see Table 1). Scaup are not common in the southernmost part of Saskatchewan (Smith 1996).

Differences among the logistic regression models (the second simultaneous assessment of all variables) for the three eco-regions indicate that the factors affecting scaup use of ponds may vary from region to region within Saskatchewan. This could be due to regional differences in the availability of good ponds. Larson (1995) indicated that wetland density is highest in the parklands but did not discuss pond types. In this study, the proportion of semipermanent and permanent ponds was higher in parklands than grasslands. The cumulative percentage of semipermanent and permanent ponds in the subsamples was 72.3% in the parklands/boreal transition, 55.8% in the moist grasslands, and 34.4% in the mixed grassland. The availability of large numbers of good quality ponds and lakes in the parklands/boreal transition may give scaup sufficient options that ponds with margin impacts can be avoided, at least for nesting. Extensive margin impact usually means the upland has been affected as well, so

that nesting opportunities both close to the water and farther away may be diminished.

A lower density of permanent, deep wetland basins in the grasslands may bring limiting factors of food base and margin impact into play. There may be relatively more ponds in the grasslands that are so saline and/or shallow that amphipods are excluded. This could result in fewer choices of alternate ponds. Land use may also be an important factor when the wetland density is lower. Virtually all ponds in the mixed grassland had heavy margin impact. This lack of variability may have caused the removal of margin impact from the logistic regression model for this eco-region. Millar also found that margin impacts were greater in the mixed grass prairie than in the parklands; cropping, haying and grazing impacts affected 64.6% of wetlands in mixed grass prairie (Millar 1992, Table 9) as opposed to 35.5% of wetlands in the parkland region (Millar 1989, Table 9).

Indirect, margin-impact effects on the pond itself are possible. Nutrients and agricultural chemicals, including pesticides (Leonard 1988), can run off into wetlands, along with erosional sediment deposits, which can even lead to the infill of pond basins over time (Dieter 1991). Many pesticides are toxic to amphipods and/or other macroinvertebrate food resources important for waterfowl foraging (Sheehan et al. 1987). Higher levels of phosphorus and nitrogen in ponds due to agricultural runoff could increase bacterial, algal, and/or macrophyte productivity (Wetzel 1983), which could lead to an increase in severe winterkill conditions in the pond due to decomposition of senescent biomass. The effects of burning and mowing pond margins upon invertebrates were studied by de Szalay and Resh (1997), but invertebrate responses were difficult to assess, with little response to mowing treatment and different responses to burning among different taxa. Further studies of this sort may be a fruitful line of inquiry.

The very low incidence (11%) of scaup ducklings found in this study suggests that interpretation of the

duckling results should be made with caution. The duckling survey was undertaken in early August when most hatchlings should have been very young and, hence, on their natal ponds (Sugden 1973). However, there may have been movement between ponds by this date. While the duckling results generally agreed with the adult (spring survey) results, fall water depth persisted in the duckling logistic regression model. It was not a significant variable in the adult model, despite the strong association of water depth with amphipods. These results suggest that scaup ducklings are more likely to be found on larger, deeper ponds, which are generally those that tend to have good amphipod food resources. However, the location of all but one brood on semi-permanent and permanent ponds may be partially an artifact of the duckling survey timing.

Female scaup often move their broods to the largest and most permanent ponds in the vicinity (Sugden 1973, Afton 1984). However, Sugden (1973) noted that newly-hatched scaup were often found on very small ponds, where they were feeding on chironomids, while older ducklings were seldom found on small ponds, and when they were, the pond was invariably deeper than average. He also discussed the fact that bills of newly-hatched ducklings are relatively unspecialized and undergo a change in morphology as the duckling grows. The change in food selection by scaup ducklings from bottom larvae to amphipods (Sugden 1973, Figure 4) was assumed to be related to movements of the broods to larger ponds. This could be not only to avoid predation and harassment on small ponds (Sugden 1973), which often dry up, but also as part of the ontogeny of the birds as their beaks become more specialized (and capable of processing amphipods and other macrobenthic food) and their bodies become more capable of sustained diving. Moving to larger, deeper ponds as these changes begin would guarantee that the growing young have the best available food supply, which would be particularly critical for later-hatched broods. Sugden (1973) also noted that there is a peak in food intake at 5 to 7 weeks, which accompanies the latter stages of exponential growth. This timing would correspond to the increase in amphipod biomass, as young-of-the-year begin to enter the larger instars (Lindeman and Momot 1983, Wen 1992).

The dietary differences noted by Bartonek and Murdy (1970) among scaup ducklings over time near Yellowknife, NWT can also be explained by amphipod life history: the low per cent volume of amphipods in the oesophagi of Classes Ia–IIa scaup juveniles (late July, early August) corresponds to relatively small numbers of amphipods in the benthic and pelagic invertebrate samples (Bartonek and Murdy 1970, Figure 1). This is the portion of the summer when most adult

amphipods have disappeared and the young-of-the-year are still in the smallest size classes (Lindeman and Momot 1983, Wen 1992, Pickard and Benke 1996). As the birds grow, so do the amphipods, until by September, young-of-the-year are reaching adult size and again provide a rich food resource for the young scaup. Bartonek and Murdy's (1970) samples from early September showed amphipods to comprise 57% of the average oesophageal volume. Dirschl (1969) also found that amphipods made up a large proportion of the adult scaup diet in May/June, and again in October.

*Gammarus* is apparently not an important factor affecting the distribution of scaup in Saskatchewan prairie potholes. Austin (1983) also did not find a clear relationship between the abundance of *Gammarus* and scaup. Afton et al. (1991) and Afton and Hier (1991) list *Gammarus* as a higher percentage of food items than *Hyaella*, but this may simply reflect the relative amphipod populations in those waterbodies on which the studied birds were collected. Bartonek and Murdy (1970) did not find that one species of amphipod appeared to be selected over the other in subarctic taiga ponds. The results obtained in this study may be a consequence of the paucity of *Gammarus* in the smaller, shallower wetlands that were sampled. Observations of scaup broods on ponds at St. Denis that had *Hyaella* but no *Gammarus*, suggests that *Hyaella* may be a suitable crustacean resource in wetlands where *Gammarus* is not available. Also, the potential for scaup to use ponds with no amphipods, at least when broods are newly hatched, (Sugden 1973) must not be discounted.

*Gammarus* is extremely abundant in dugouts, borrow pits, and other manmade depressions, and in larger, deeper water bodies in Saskatchewan, particularly those with no fish (Lindeman pers. comm.). It may provide optimal food for scaup at these sites. Scaup have been seen visiting dugouts (Afton pers. comm.) and may fly in for brief feeding visits to take advantage of the rich resource, but they may prefer to breed on less restrictive ponds. One scaup female and her two ducklings were found on a dugout at the Pleasantdale site (see Figure 1). This particular dugout was unusual in that it was neither in an active pasture nor near a human dwelling (as is more common for these artificial water bodies). Such relatively undisturbed dugouts may therefore be valuable for providing food resources to breeding and migrating scaup.

Management activities such as wetland excavation could be beneficial to scaup and other diving ducks in areas where there are few deep ponds, particularly in cases where there are ponds with large surface areas (which may attract exploring birds to land) but very shallow depths (insufficient to maintain rich amphipod

populations). Creighton et al. (1997) found that excavating shallow wetlands filled with emergent vegetation increased both invertebrate biomass and the use of these wetlands by most species of dabbling and diving ducks. Climate change models predict loss of numbers and quality of wetlands with increased temperatures, particularly in the parkland region (Larson 1995). Pond excavation could be a viable management tool where needed to maintain a mix of wetland types at the landscape level and retain sufficient water in certain basins to provide the depth needed to maintain rich amphipod resources. Land-use practices that avoid pond margin disruption, particularly on larger, deeper ponds, would also help to provide the nesting habitat needed for prairie scaup to take advantage of these food resources.

Old-time hunters in Minnesota commonly associated good scaup hunting with the presence of "blue-bill bugs," a local name for amphipods (Bartonek and Murdy 1970). This study validates these hunters' observations. While pond area does come into play, a good amphipod food source and relatively undisturbed margins appear to be the major factors in scaup use of Saskatchewan prairie potholes.

#### ACKNOWLEDGMENTS

We acknowledge the assistance and cooperation of the Migratory Birds Division, particularly Jack Smith and Andrew Didiuk, in providing access to, and help with, the annual waterfowl breeding survey data and transect aerial photos. David Donald, Cameron Teichroeb, Bruce Holliday, Steve Leach, Vance Lester, Jim Syrgiannis, Dallard Legault, Bob Crosley, and Geoff Wilson assisted at various times on the amphipod and duckling surveys. Vance Lester helped with data entry and proofing. Figure 1 was prepared by Gary Weiss, GIS Section, Environment Canada, Regina. Al Afton provided input on the research proposal. Jane Austin and David Donald provided information and advice during the course of the study. Eric Woodsworth was extremely generous with his time and statistical expertise. We thank our internal reviewers, Kevin Cash, Kathy Meeres, and Eric Woodsworth, and the journal reviewers for their helpful comments on the manuscript.

#### LITERATURE CITED

- Afton, A. D. 1984. Influence of age and time on reproductive performance of female lesser scaup. *Auk* 101:255-265.
- Afton, A. D. and C. D. Ankney. 1991. Nutrient-reserve dynamics of breeding lesser scaup: a test of competing hypotheses. *Condor* 93:89-97.
- Afton, A. D. and R. H. Hier. 1991. Diets of lesser scaup breeding in Manitoba. *Journal of Field Ornithology* 62:325-334.
- Afton, A. D., R. H. Hier, and S. L. Paulus. 1991. Lesser scaup diets during migration and winter in the Mississippi flyway. *Canadian Journal of Zoology* 69:328-333.
- Austin, J. E. 1983. Postbreeding ecology of female lesser scaup. M.S. Thesis. University of Missouri, Columbia, MO, USA.
- Austin, J. E., C. M. Custer, and A. D. Afton. 1998. Lesser scaup (*Aythya affinis*). p. 1-32. In A. Poole and F. Gill (eds.) *The Birds of North America*, No. 338. *The Birds of North America, Inc.* Philadelphia, PA, USA.
- Bartonek, J. C. and J. J. Hickey. 1969. Food habits of canvasbacks, redheads and lesser scaup in Manitoba. *Condor* 71:280-290.
- Bartonek, J. C. and H. W. Murdy. 1970. Summer foods of lesser scaup in subarctic taiga. *Arctic* 23:35-44.
- Batt, B. D. J., M. G. Anderson, C. D. Anderson, and F. D. Caswell. 1989. The use of prairie potholes by North American ducks. p. 204-227. In A. van der Valk (ed.) *Northern Prairie Wetlands*. Iowa State University Press, Ames, IA, USA.
- Creighton, J. H., R. D. Sayler, J. E. Tabor, and M. J. Monda. 1997. Effects of wetland excavation on avian communities in eastern Washington. *Wetlands* 17:216-227.
- de Szalay, F. A. and V. H. Resh. 1997. Responses of wetland invertebrates and plants important in waterfowl diets to burning and mowing of emergent vegetation. *Wetlands* 17:149-156.
- Didiuk, A. B., F. D. Caswell, and G. Hochbaum. 1989. A preliminary manual for habitat assessment procedures during spring air/ground waterfowl surveys in prairie Canada. Canadian Wildlife Service, Winnipeg, MB, Canada.
- Dieter, C. D. 1991. Water turbidity in tilled and untilled prairie wetlands. *Journal of Freshwater Ecology* 6:185-189.
- Dirschl, H. J. 1969. Foods of lesser scaup and blue-winged teal in the Saskatchewan River delta. *Journal of Wildlife Management* 33:77-87.
- Dubovsky, J. A., C. T. Moore, J. P. Bladen, G. W. Smith, and P. D. Keywood. 1997. Trends in duck breeding populations, 1955-97. U. S. Fish and Wildlife Report. Migratory Bird Management, Laurel, MD, USA.
- Green, R. H. 1979. *Sampling Design and Statistical Methods for Environmental Biologists*. John Wiley and Sons, New York, NY, USA.
- Hammell, G. S. 1973. The ecology of lesser scaup (*Aythya affinis* Eyton) in southwestern Manitoba. M.S. Thesis. University of Guelph, Guelph, ON, Canada.
- Hines, J. E. 1977. Nesting and brood ecology of lesser scaup at Waterhen Marsh, Saskatchewan. *Canadian Field-Naturalist* 91:248-255.
- Holsinger, J. R. 1976. The freshwater amphipod crustaceans (Gammaridae) of North America. U.S. Environmental Protection Agency, Office of Research and Development, Cincinnati, OH, USA. ELD04/72.
- Kantrud, H. A. and R. E. Stewart. 1977. Use of natural basin wetlands by breeding waterfowl in North Dakota. *Journal of Wildlife Management* 41:243-253.
- Larson, D. L. 1995. Effects of climate on numbers of northern prairie wetlands. *Climate Change* 30:169-180.
- Leonard, R. A. 1988. Herbicides in surface waters. p. 45-87. In R. Grover (ed.) *Environmental Chemistry of Herbicides Volume 1*. CRC Press, Boca Raton, FL, USA.
- Lindeman, D. H. and W. T. Momot. 1983. Production of the amphipod *Hyalella azteca* (Saussure) in a northern Ontario lake. *Canadian Journal of Zoology* 61:2051-2059.
- Millar, J. B. 1986. Estimates of habitat distribution in the settled portions of the prairie provinces in 1982. Canadian Wildlife Service unpublished report, Saskatoon, SK, Canada.
- Millar, J. B. 1989. Baseline (1985) habitat estimates for the settled portions of the prairie provinces Report no. 3: Saskatchewan parkland. Canadian Wildlife Service unpublished report, Saskatoon, SK, Canada.
- Millar, J. B. 1992. Baseline (1985) habitat estimates for the settled portions of the prairie provinces Report no. 8: Saskatchewan mixed grass prairie. Canadian Wildlife Service unpublished report, Saskatoon, SK, Canada.
- Muck, J. A. and R. M. Newman. 1992. The distribution of amphipod

- Pods in southeastern Minnesota and their relation to water quality and land use. *Journal of the Iowa Academy of Science* 99:34-39.
- Padbury, G. A. and D. F. Acton. 1994. Ecoregions of Saskatchewan. Map scale at 1:2000000. Minister of Supply and Services Canada and Saskatchewan Property Management Corporation, Regina, SK, Canada.
- Pennak, R. W. and W. N. Rosine. 1976. Distribution and ecology of Amphipoda (Crustacea) in Colorado. *American Midland Naturalist* 96:324-331.
- Pickard, D. P. and A. C. Benke. 1996. Production dynamics of *Hyalella azteca* (Amphipoda) among different habitats in a small wetland in the southeastern USA. *Journal of the North American Benthological Society* 15:537-550.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.
- Rogers, J. P. and L. J. Korschgen. 1966. Foods of lesser scaups on breeding, migration, and wintering areas. *Journal of Wildlife Management* 30:258-264.
- SAS Institute Inc. 1990. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2. SAS Institute Inc., Cary, NC, USA.
- Sheehan, P. J., A. Baril, P. Mineau, D. K. Smith, A. Harfenist, and W. K. Marshall. 1987. The impact of pesticides on the ecology of prairie nesting ducks. Canadian Wildlife Service, Ottawa, ON, Canada. Technical Report Series No. 19.
- Smith, A. G. 1971. Ecological factors affecting waterfowl production in the Alberta parklands. U. S. Department of the Interior, Fish and Wildlife Service, Washington, DC, USA. Resource Publication 98.
- Smith, A. R. 1996. Atlas of Saskatchewan Birds. Saskatchewan Natural History Society, Regina, SK, Canada. Special Publication No. 22.
- SPSS Inc. 1993. SPSS for Windows: Advanced Statistics, Release 6.0. SPSS Inc., Chicago, IL, USA.
- Sugden, L. G. 1973. Feeding ecology of pintail, gadwall, american widgeon and lesser scaup ducklings in southern Alberta. Canadian Wildlife Service, Ottawa, ON, Canada. Report Series Number 24.
- Toft, C. A., D. L. Trauger, and H. W. Murdy. 1982. Tests for species interactions: breeding phenology and habitat use in subarctic ducks. *The American Naturalist* 120:586-613.
- Turner, B. C., G. S. Hochbaum, F. D. Caswell, and D. J. Neiman. 1987. Agricultural impacts on wetland habitats on the Canadian prairies, 1981-85. *Transactions of the North American Conference on Wildlife and Natural Resources* 52:206-215.
- U. S. Fish and Wildlife Service and Canadian Wildlife Service. 1987. Standard operating procedures for aerial waterfowl breeding ground population and habitat surveys in North America. U.S. Fish and Wildlife Service unpublished report, Laurel, MD, USA.
- Wen, Y. H. 1992. Life history and production of *Hyalella azteca* (Crustacea: Amphipoda) in a hypereutrophic prairie pond in southern Alberta. *Canadian Journal of Zoology* 70:1417-1424.
- Wetzel, R. G. 1983. *Limnology*, 2nd ed. Saunders College Publishing, Fort Worth, TX, USA.

Manuscript received 20 October 1998; revision received 11 March 1999; accepted 2 June 1999.