Peer Reviewed

Lesser Scaup Spring Nutrient Reserve Dynamics on the Lower Great Lakes

SHANNON S. BADZINSKI,[1] *Long Point Waterfowl and Wetlands Research Fund, Bird Studies Canada, Port Rowan, ON, N0E 1M0, Canada*
SCOTT A. PETRIE, *Long Point Waterfowl and Wetlands Research Fund, Bird Studies Canada, Port Rowan, ON, N0E 1M0, Canada*

Abstract

*The North American lesser scaup (*Aythya affinis*) population has declined since the mid-1980s. The acquisition of nutrient reserves during spring migration may play a role in explaining that trend. We studied nutrient-reserve dynamics of lesser scaup collected during spring at 3 major stopover sites and assessed whether reserves of birds on the lower Great Lakes (LGL) differed from those at other staging (or breeding) areas. At lakes Ontario and St. Clair, males had larger fat reserves than females, but no other substantial sex-related differences were observed in fat, protein, or mineral reserve levels of lesser scaup. Protein in males and mineral reserves of both sexes at lakes Erie and St. Clair did not change throughout spring. Male fat reserves remained constant at Lake Erie and increased at Lake St. Clair, whereas female fat and protein reserves increased at both stopover sites. Patterns of fat and protein dynamics in males partly may be due to energetic costs of courtship and pair-bond maintenance. However, maintenance and accumulation of fat reserves in both sexes while on the LGL is important for impending migration and subsequent reproduction. Female lesser scaup staging on the LGL had fat reserves comparable to, or slightly higher than, those reported in other studies of northern spring-staging and breeding birds. Fat reserves of LGL females, however, were much lower than those reported for birds at another midlatitude stopover site. These comparisons suggest that events occurring on Atlantic Flyway wintering areas or LGL staging areas are potential factors contributing to nutrient-reserve limitation and possibly to observed declines in scaup numbers in North America.*
(WILDLIFE SOCIETY BULLETIN 34(2):395–407; 2006)

Key words

Aythya affinis*, fat, Great Lakes, Lake Erie, Lake Ontario, Lake St. Clair, lesser scaup, Long Point Bay, migration, mineral, nutrient reserves, protein, spring, staging, waterfowl.*

Lesser scaup (*Aythya affinis*) are among the most abundant and widely distributed North American diving ducks (Austin et al. 1998). However, the species is now a conservation concern because of 30-year declines in annual population estimates (Austin et al. 2000). Low recruitment and female survival have been suggested as primary factors causing the long-term population decline (Afton and Anderson 2001). Several hypotheses have been formulated to explain decreased recruitment and female survival, some of which implicate conditions on wintering or spring staging areas as important contributing factors (Austin et al. 2000). Austin et al. (2000), Afton and Anderson (2001), and Anteau and Afton (2004) proposed that the independent or combined effects of contaminants, human disturbance, habitat degradation, and forage quality or availability at spring staging areas, all of which ultimately can affect acquisition of nutrient reserves, may subsequently influence demographic parameters of lesser scaup.

Waterfowl acquire fat, protein, and mineral reserves during spring migration (Alisauskas 1988, Alisauskas and Ankney 1992, Anteau 2002). The amount of reserves accumulated can vary among years (Ebbinge et al. 1982, Davies and Cooke 1983, Hohman et al. 1988), habitats (Gauthier et al. 1984, Tietje and Teer 1988), and individuals depending on their age, sex, and social status (Peterson and Ellarson 1979, Teunissen et al. 1985, Hohman et al. 1988, LaGrange and Dinsmore 1988). Reserves acquired at spring staging areas can be used to offset costs of thermal or nutritional stress, to fuel migratory flight, and as a source of egg nutrients or energy during reproduction (Prince 1979, Afton and Paulus 1992, Alisauskas and Ankney 1992). Thus, in many waterfowl, including lesser scaup, nutrient reserves acquired before arrival at breeding areas are important determinants of reproductive performance and survival (Afton and Ankney 1991, Pace and Afton 1999). Despite several studies of lesser scaup outside of the breeding season (Chappell 1982, Austin and Frederickson 1987, Afton et al. 1989, Gammonley and Heitmeyer 1990, Vest 2002, Herring 2003, Anteau and Afton 2004), little is known about when or where lesser scaup acquire nutrient reserves or to what extent these reserves influence reproductive success (Austin et al. 2000).

The lower Great Lakes (LGL) region has long been recognized as an important spring and fall staging area for several diving duck species, including lesser scaup (Dennis et al. 1984, Prince et al. 1992). Traditionally, lesser scaup ate mainly native gastropods and, to a lesser extent, amphipods while staging on the LGL (Ross et al. 2005). Scaup use of the LGL increased substantially during the mid-1980s in response to the introduction and dramatic increase in zebra mussels (*Dreissena polymorpha*; Wormington and Leach 1992), which is now a major scaup food item (Petrie and Knapton 1999, Badzinski and Petrie 2006). Because lesser scaup reproduction may be limited by food availability, forage quality, and nutrient-reserve acquisition outside of the breeding season (Austin et al. 2000, Afton and Anderson 2001, Anteau and Afton 2004), nutrient-reserve studies on the LGL are needed, especially in light of the major shifts that have occurred in diet, distribution, and abundance of scaup staging there over the past 20 years.

The objectives of this study were to determine if 1) fat, protein, and/or mineral reserves of lesser scaup increased while staging on the LGL, 2) reserves and their rates of acquisition differed between sexes, and 3) midseason reserve levels, particularly that of females, differed among major stopover sites in southern Ontario.

[1] *E-mail: sbadzinski@bsc-eoc.org*

We also compared and discussed our results in relation to those of Anteau and Afton (2004), who evaluated nutrient reserves of lesser scaup staging in the Mississippi Flyway during the 1980s and early 2000s.

Study Area

We conducted this study on the Canadian side of Lake Erie (Long Point Bay), Lake St. Clair (Mitchell's and St. Luke's bays), and eastern Lake Ontario (Bay of Quinte and Wolfe Island area) during spring 2000 (Fig. 1). All study sites were lacustrine wetlands or embayments that were shallow (<3 m) and contained both emergent and submerged aquatic vegetation (Cowardin et al. 1979). More detailed descriptions of these areas are provided by Herdendorf et al. (1986), Petrie and Knapton (1999), and Ball et al. (2003).

Methods

We collected lesser scaup staging at Lake St. Clair (9 Mar–9 Apr, $n_{\text{female}} = 32$, $n_{\text{male}} = 28$), Lake Erie (4 Mar–7 May, $n_{\text{female}} = 26$, $n_{\text{male}} = 69$), and Lake Ontario (29 Mar–15 Apr, $n_{\text{female}} = 26$, $n_{\text{male}} = 38$) throughout spring 2000. We collected lesser scaup under the authority of a Canadian Wildlife Service Scientific capture permit (CA 0067) valid from 30 September 1999 to 30 June 2000. All birds we collected likely wintered on or near the Atlantic or Gulf coasts of the United States because shallow bays in all 3 regions typically freeze, and most scaup that overwinter on the LGL are greater scaup (*Aythya marila* [Bellrose 1980; B. Edmonds, Toronto Ornithological Club, Toronto, Ont., Canada, unpublished data]). We began collections as soon as locations at each lake were sufficiently free of near-shore ice to allow safe boating. Arrival of the first migrants slightly preceded that time period, so birds from very early in the season likely are underrepresented in this study. Collections ceased in late April or early May after most scaup had migrated. We shot nearly all birds using decoys and relatively few by pass- or jump shooting. Immediately after collection, a tag (with a unique identification number, sex, collection date, location, and social status–flock size)

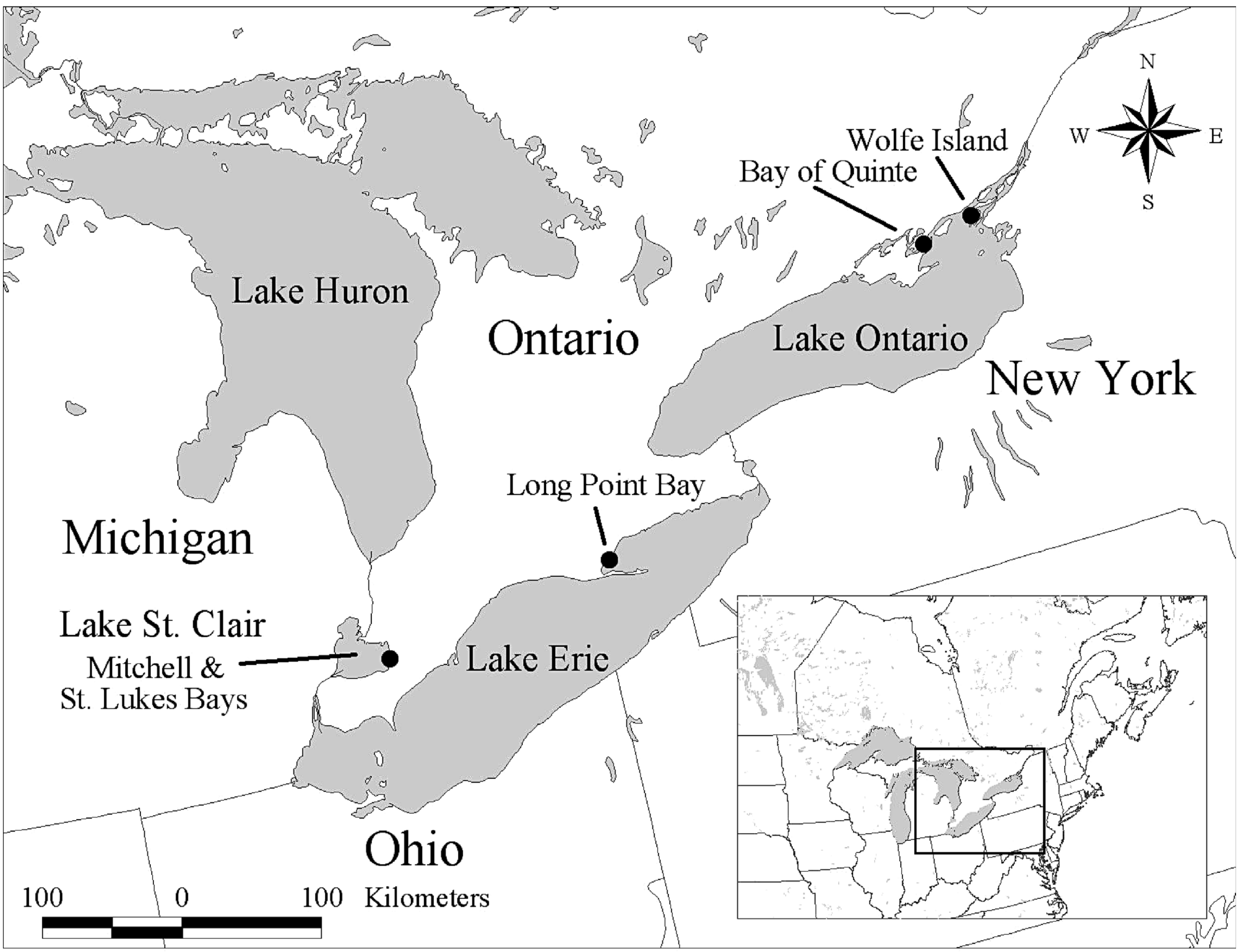


Figure 1. Geographic locations of lesser scaup (*Aythya affinis*) collection sites on the Canadian lower Great Lakes (Mitchell and St. Lukes bays, Lake St. Clair; Long Point Bay, Lake Erie; and Bay of Quinte and Wolfe Island, Lake Ontario) during spring 2000.

was attached to each bird. At the end of each day, we placed each tagged bird individually into a double plastic bag and froze them.

Potential Condition Bias

Some studies found that waterfowl shot during fall, often by hunters using decoys, exhibit relatively low body mass or nutrient reserves and may represent a condition-biased sample (Bain 1980, Dufour et al. 1993, Pace and Afton 1999). Thus, we acknowledge that our sample of spring, decoy-collected lesser scaup might contain a condition bias because lesser scaup in relatively poor condition during fall were more likely to be harvested by hunters (Pace and Afton 1999). We cannot completely dispel an overall condition bias because nearly all our birds were collected using decoys. Preliminary analyses of our data did show, however, that birds shot as singles did not have lower body masses or nutrient reserves than did flocked individuals, and flock size as a continuous variable was not correlated with body mass or fat. So, within our data there is no apparent condition bias and results presented later are not biased by an uneven distribution of single or flocked birds. A potential overall condition bias will not affect comparisons within this study, but could complicate comparisons with studies that have used other collection techniques (Anteau and Afton 2004).

Laboratory Procedures and Carcass Analyses

We thawed birds in the laboratory overnight and then weighed them ($\pm$0.1 g) to determine feathered carcass mass. We also plucked and weighed ($\pm$0.1 g) each bird to determine plucked carcass mass and measured head length ($\pm$0.1 mm), tarsus bone ($\pm$0.1 mm), and total body length ($\pm$1.0 mm; Dzubin and Cooch 1992). We generally followed methods of Afton and Ankney (1991) for dissection of carcasses. We excised the esophagus, proventriculus, gizzard, small and large intestine, and caeca from carcasses and weighed ($\pm$0.1 g) each component separately with and without ingesta. We returned all dissected body parts and organs (including reproductive organs) to plucked carcasses, placed each carcass into its own plastic bag (along with a label), froze, and transported them to the University of Western Ontario (UWO). Body composition (total protein, lipid, and mineral), derived from ingesta-free dry carcass homogenate mass, of each bird was determined at UWO using laboratory protocols and procedures described by Afton and Ankney (1991).

Statistical Analysis

We performed a principal components analysis on the correlation matrix for lengths of head, tarsus, and body of females and males combined (PROC PRINCOMP; SAS Institute 1990). The first principal component (PC1) accounted for 40% of the variation in structural measurements. The coefficients of variables in PC1 ranged from 0.52 to 0.63, indicating positive correlation among measurements, which was interpreted as variation in body size. We used PC1 scores in statistical models to account for variation in nutrient reserves attributable to body size.

Our collection areas were several hundred kilometers apart and at different latitudes (see Fig. 1). Lake Ontario, as compared to the other 2 locations, was further north and ice persisted longer on the bays that birds frequent during spring, which also resulted in later initial arrival dates of migrants at that location. We used information supplied by local bird-watchers to create a new variable ("Day" after arrival) that adjusted collection dates relative to the first day when presumed migrant birds were observed at each collection site. We used this variable in statistical analyses to allow for more meaningful comparisons of nutrient reserves among stopover sites. The ranges and mean adjusted collection dates for females (Erie: 10–69 days, mean = 37 days; Ontario: 19–35 days, mean = 25 days; St. Clair: 14–44 days, mean = 33 days) and males (Erie: 9–72 days, mean = 39 days; Ontario: 19–35 days, mean = 27 days; St. Clair: 14–44 days, mean = 29 days) differed substantially among lakes. Thus, we evaluated sex differences and seasonal changes in nutrient-reserve dynamics separately by lake to avoid extrapolating results beyond the range of our data. To do this, we used lake-specific General Linear Models (PROC GLM; SAS Institute 1990) to evaluate effects of Sex (class), Day (continuous), and PC1 (body size; continuous) on fresh body mass, ingesta-free body mass (with feathers), protein, lipid, and mineral; a Sex $\times$ Day interaction was included to assess if body mass and nutrient reserves changed throughout spring at different rates between sexes. Based on these models, we also estimated midmigration period (35 days after arrival) body mass and nutrient-reserve levels for birds at each stopover site and used those estimates to make comparisons with other lesser scaup nutrient-reserve studies.

To evaluate whether body masses and nutrient-reserve levels differed among lake locations, we combined lake-specific data sets and first tested global models that included all effects in the lake-specific models plus "Lake" main effects and "Lake $\times$ Sex" interactions. When "Lake" main effects were retained in models, we evaluated statistical and biological significance of among-lake contrasts of least squares means (LS means) of body mass or nutrient-reserve levels to assess if differences existed. When "Lake $\times$ Sex" interactions were retained in models, we felt it most appropriate to compare and contrast LS means within sexes among lakes. Comparing LS means provided a study-specific comparison of body mass and nutrient reserves during (or close to) the midmigration periods at each site while controlling for "Day" or other important effects retained in models and ensured that we did not extend interpretation of lake differences beyond the range of our data.

We reduced all initial statistical models using backward elimination by first removing interactions and then main effects ($P \geq 0.10$). We assessed plots of residuals from these reduced models to determine if use of linear models was appropriate or if additional data transformations were necessary (Zar 1996). Residuals from all models approximated a normal distribution and met other model assumptions. For each model, we evaluated Type III sums of squares and considered effects with $P \leq 0.10$ as potentially biologically important and worthy of discussion. We used Tukey-Kramer tests for all tables and text, we report means and parameter estimates $\pm$1 standard error.

Results

Lake Erie

For lesser scaup at Lake Erie, models describing variation in fresh body mass, ingesta-free body mass, protein, and fat reserves each contained effects of Sex, Day, body size (PC1), and interactions

Table 1. Reduced statistical models for body mass and nutrient reserves (grams) based on data for lesser scaup (*Aythya affinis*) staging at Lake Erie, Ontario, Canada, during spring 2000.

Variable	R^2	Model df	Error df	*F*	*P*	Parameter	β	SE	Type III SS	*F*	*P*
Body mass (fresh)	0.25	4	90	7.42	<0.0001	Intercept	728.83	22.44			
						Sex (female)	−73.83	42.17	12,743.19	3.07	0.0834
						Days	−0.12	0.54	16,813.17	4.05	0.0473
						PC1	49.62	11.40	78,795.05	18.96	<0.0001
						Sex × Days	2.31	1.03	20,691.76	4.98	0.0282
Body mass (ingesta-free)	0.26	4	90	7.75	<0.0001	Intercept	639.90	20.82			
						Sex (female)	−67.23	39.12	10,566.02	2.95	0.0891
						Days	0.08	0.50	17,494.69	4.89	0.0295
						PC1	45.05	10.57	64,961.63	18.16	<0.0001
						Sex × Days	1.96	0.96	14,961.68	4.18	0.0438
Fat	0.15	4	90	3.84	0.0063	Intercept	83.83	12.85			
						Sex (female)	−41.34	24.14	3,993.98	2.93	0.0902
						Days	0.35	0.31	11,459.86	8.42	0.0047
						PC1	12.13	6.52	4,709.12	3.46	0.0662
						Sex × Days	1.02	0.59	4,026.71	2.96	0.0889
Protein	0.34	4	90	11.77	<0.0001	Intercept	114.62	2.97			
						Sex (female)	−9.89	5.59	228.68	3.14	0.0799
						Days	−0.01	0.07	166.96	2.29	0.1337
						PC1	7.65	1.51	1,871.58	25.67	<0.0001
						Sex × Days	0.23	0.14	210.08	2.88	0.0931
Mineral	0.15	1	93	16.34	0.0001	Intercept	25.56	0.29			
						PC1	1.57	0.39	122.13	16.34	0.0001

between Sex and Day (Table 1). Specifically, ingesta-free body mass (β = 2.1 ± 1.0 g/day) and protein (β = 0.2 ± 0.1 g/day) and fat (β = 1.3 ± 0.6 g/day) reserves of females tended to increase, whereas males showed little change in body mass (β = 0.1 ± 0.5 g/day), protein (β = −0.1 ± 0.1 g/day), or fat (β = 0.4 ± 0.3 g/day) throughout spring (Fig. 2). Mineral content did not differ between sexes (25.6 ± 0.3 g) and did not change appreciably throughout spring, but it was positively correlated with body size (Table 1; Fig. 2).

Lake Ontario

Models containing only body size (PC1) effects best accounted for variation in fresh body mass and protein and mineral reserves, whereas Sex and PC1 both explained variation in ingesta-free body mass; only Sex was identified as an important source of variation in fat reserves at Lake Ontario (Table 2). Given this result, both female and male lesser scaup did not show any substantial seasonal changes in body masses or in protein, fat, or mineral reserves (Table 2; Fig. 3). Males, however, tended to be slightly heavier than females (ingesta-free body mass = 768.0 ± 8.8 g vs. 653.3 ± 12.5 g, respectively), which was at least partially attributed to their larger (110.4 ± 5.7 g vs. 78.6 ± 6.9 g, respectively) fat reserves, but both sexes had similar amounts of protein and mineral reserves (Table 2; Fig. 3).

Lake St. Clair

Models best describing variation in fresh body mass, ingesta-free body mass, and protein reserves included effects of Sex, Day, PC1, and interactions between Sex and Day (Table 3). Closer inspection of models showed that female ingesta-free body mass increased (β = 3.4 ± 1.7 g/day), whereas body mass of males not change appreciably (β = −0.5 ± 1.4 g/day), throughout spring; females were lighter than males up to 30 days after arrival, but thereafter both sexes had similar body mass (Fig. 4). Females' protein reserves increased (β = 0.5 ± 0.2 g/day) after arrival, but those of males did not noticeably change (β = −0.2 ± 0.2 g/day) throughout spring. Protein reserves of females generally were lower than those of males until 35 days after arrival, but thereafter protein was similar between sexes (Fig. 4).

Models describing variation in fat reserves included effects of Sex, Day, and PC1, but only Sex and PC1 accounted for substantial variation in mineral reserves (Table 3). Fat reserves of both sexes increased at the same rate (1.0 ± 0.5 g/day) throughout spring, but males (111.1 ± 7.0 g) consistently had more fat than did females (94.5 ± 6.5 g). Mineral reserves of both sexes did not change throughout spring, but, after accounting for body size, mineral reserves of males (26.6 ± 0.5 g) were larger than those of females (24.6 ± 0.5; Fig. 4).

Among-Lake Evaluations of Nutrient-Reserve Levels

Evaluations of general models, in which data from all sites were included in analyses, suggested that both sex-specific estimates of body mass and fat reserve levels differed among lakes, whereas differences in protein and mineral reserves depended on both lake and sex (Table 4). Fresh body mass of lesser scaup differed among the 3 lakes; females and males were consistently lightest at Lake Erie, intermediate at Lake St. Clair, and heaviest at Lake Ontario (Table 5). Estimates of ingesta-free body mass of females and males at lakes Ontario and St. Clair were similar, but birds at both of those lakes were heavier than those at Lake Erie (Table 5). Sex-specific fat reserves levels showed the same pattern of among-lake differences reported for ingesta-free body mass (Table 5). Female protein reserves differed among all 3 lakes and were highest at Lake Ontario, intermediate at Lake St. Clair, and lowest at Lake Erie (Table 5). Protein reserves of males at lakes Erie and Ontario were similar, but were lower at both of those locations as compared to Lake St. Clair (Table 5). Females at Lake Ontario had slightly larger mineral reserves than did females at both lakes Erie and St. Clair; mineral reserves of males were similar at all 3 lakes (Table 5).

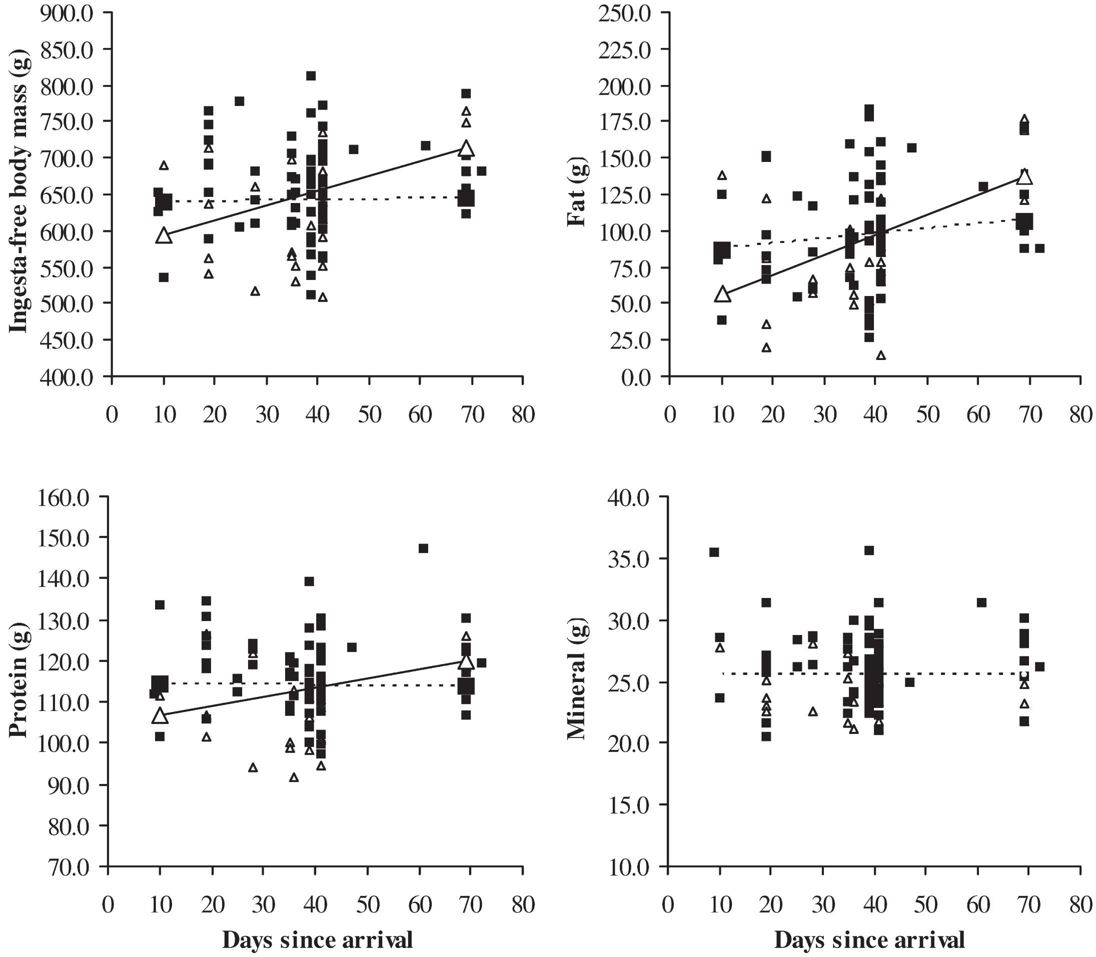


Figure 2. Changes in ingesta-free body mass, fat, protein, and mineral of lesser scaup (*Aythya affinis*) staging Lake Erie, Ont., Canada, from 4 Mar–7 May 2000. Females and males are represented by open triangles and solid squares, respectively.

Discussion

Sources of Variation in Nutrient Reserves of Staging Waterfowl

Several notable patterns of reserve dynamics and sex-related differences were detected in this study, but much variation was left unexplained and likely reduced our ability to detect some among-site and sex-related differences or temporal changes in some reserves throughout spring. Other studies report that factors related to environmental conditions (Whyte and Bolen 1984, Baldassarre et al. 1986, Miller 1986), social status (Peterson and Ellarson 1979, Teunissen et al. 1985, LaGrange and Dinsmore 1988, Afton et al. 1989, Serie and Sharp 1989), and habitat–food (Gauthier et al. 1984, Teunissen et al. 1985, Baldassarre et al. 1986, Tietje and Teer 1988) often explain additional variation in nutrient reserves of waterfowl. We believe much of the unexplained variation in body mass and fat among individual scaup in our study also was due to differences in wintering latitude or areas, arrival time at staging areas, and duration of residence,

Table 2. Reduced statistical models for body mass and nutrient reserves (grams) based on data for lesser scaup (*Aythya affinis*) staging at eastern Lake Ontario, Ont., Canada, during spring 2000.

Variable	R^2	Model df	Error df	*F*	*P*	Parameter	β	SE	Type III SS	*F*	*P*
Body mass (fresh)	0.09	1	62	5.91	0.0179	Intercept	768.03	8.76			
						PC1	13.31	5.47	28,748.39	5.91	0.0179
Body mass (ingesta-free)	0.13	2	61	4.51	0.0149	Intercept	680.31	9.91			
						Sex (female)	–27.00	16.27	10,108.29	2.75	0.1021
						PC1	9.25	5.02	12,477.94	3.40	0.0700
Fat	0.17	1	62	12.73	0.0007	Intercept	110.43	5.69			
						Sex (female)	–31.87	8.93	15,683.65	12.73	0.0007
Protein	0.08	1	62	5.51	0.0221	Intercept	117.43	1.19			
						PC1	1.74	0.74	490.24	5.51	0.0221
Mineral	0.11	1	62	7.47	0.0082	Intercept	26.27	0.36			
						PC1	0.61	0.23	61.10	7.47	0.0082

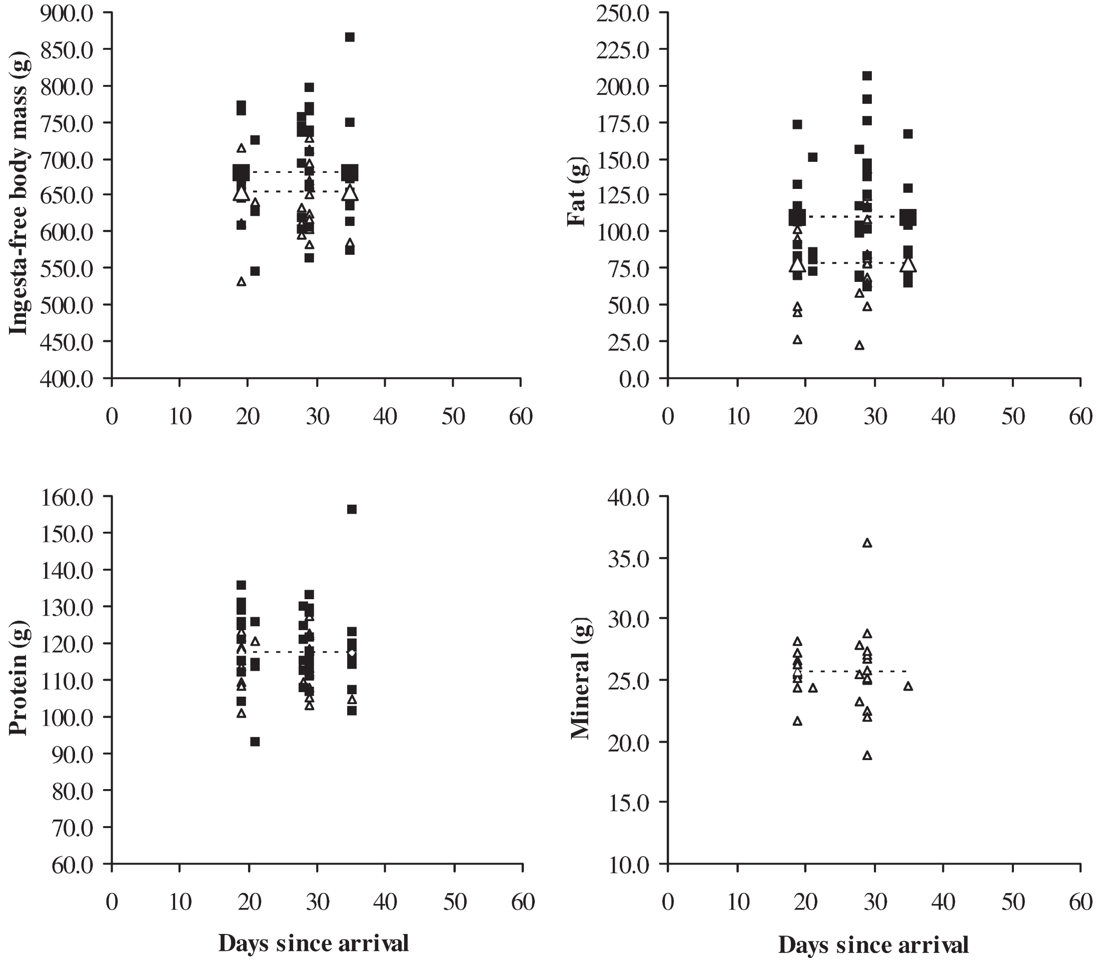


Figure 3. Changes in ingesta-free body mass, fat, protein, and mineral of lesser scaup (*Aythya affinis*) staging at eastern Lake Ontario, Ont., Canada, from 29 Mar–15 Apr 2000. Females and males are represented by open triangles and solid squares, respectively.

thus feeding, at staging areas (Serie and Sharp 1989). This argument seems reasonable given the potential physiological limitations for energy storage in scaup (Lovvorn and Jones 1994, Herring 2003) and the protracted nature of spring migration in this species (Austin et al. 1998).

Sex Differences in Nutrient Reserves

Male lesser scaup staging at eastern lakes Ontario and St. Clair consistently had larger fat reserves (i.e., were in better condition) than females, but similar sex-related differences were not consistent throughout spring at Lake Erie. Protein reserves of both sexes, with the exception of Lake St. Clair where males had larger reserves than females, generally were similar throughout spring. These patterns of sex-related differences, both among and within sites, for fat and protein reserves and their seasonal dynamics (see below) may be partly due to extent of collection periods (Ontario = 16 days, St. Clair = 30 days, and Erie = 60 days) and distribution of sampling effort during spring at each site (Ontario: days [after arrival] 19–35; St. Clair: days 14–44; and Erie: days 9–69).

Because lesser scaup form pairs during spring migration (Austin et al. 1998), relatively larger fat (or protein) reserves of males may be adaptive if they allow for reductions in foraging so that time spent developing or maintaining pair-bonds with females can be maximized. Mate defense by males also may increase female foraging time, which could allow more rapid acquisition of nutrient reserves at initial spring stopover sites, such as those of the LGL, and facilitate departure with optimal fat and protein reserves. Birds that have relatively lower lipid (or protein) reserves may have less resistance to thermal or nutritional stresses occurring at staging areas, and departing with low reserves could put those birds at an energetic disadvantage at subsequent stopover areas or their breeding grounds (Prince 1979, Hohman 1986, Hohman et al. 1988, Hipes and Hepp 1995). Currently there are no sex-specific survival estimates for lesser scaup at LGL or other spring stopover sites, but this would be interesting to determine given that females at lakes St. Clair and Ontario had lower fat reserves, thus potentially lower survival, than males.

Nutrient-Reserve Dynamics of Lesser Scaup

Patterns of nutrient-reserve dynamics differed substantially among stopover sites. Because we were interested in the changes in reserves throughout spring, birds from the early, mid-, and late-staging periods should have been better represented at each site. Our collections were, however, biased more toward mid- (and late-) season birds, which was most apparent at Lake Ontario. Thus, lack of seasonal changes in nutrient reserves at Lake Ontario was not unexpected because birds also were only collected

Table 3. Reduced statistical models for body mass and nutrient reserves (grams) based on data for lesser scaup (*Aythya affinis*) staging at Lake St. Clair, Ont., Canada, during spring 2000.

Variable	R^2	Model df	Error df	F	P	Parameter	β	SE	Type III SS	F	P
Body mass (fresh)	0.39	4	55	8.67	<0.0001	Intercept	807.99	51.27			
						Sex (female)	−199.36	65.99	44,338.01	9.13	0.0038
						Days	−1.55	1.71	6,447.65	1.33	0.2543
						PC1	40.53	11.27	62,828.36	12.93	0.0007
						Sex × Days	5.51	2.08	33,927.94	6.98	0.0107
Body mass (ingesta-free)	0.42	4	55	10.01	<0.0001	Intercept	696.89	42.89			
						Sex (female)	−157.23	55.20	27,579.44	8.11	0.0062
						Days	−0.53	1.43	9,075.20	2.67	0.1080
						PC1	34.43	9.43	45,323.47	13.33	0.0006
						Sex × Days	3.90	1.74	17,037.23	5.01	0.0292
Fat	0.26	3	56	6.61	0.0007	Intercept	79.70	15.48			
						Sex (female)	−16.60	10.19	3,128.77	2.65	0.1090
						Days	1.04	0.48	5,525.97	4.68	0.0347
						PC1	15.11	5.55	8,737.18	7.41	0.0086
Protein	0.55	4	55	16.45	<0.0001	Intercept	127.06	5.48			
						Sex (female)	−28.35	7.05	896.70	16.17	0.0002
						Days	−0.19	0.18	89.50	1.61	0.2093
						PC1	4.87	1.20	905.92	16.34	0.0002
						Sex × Days	0.66	0.22	486.84	8.78	0.0045
Mineral	0.42	2	57	20.32	<0.0001	Intercept	26.64	0.49			
						Sex	−2.02	0.72	47.97	7.81	0.0071
						PC1	1.52	0.40	88.69	14.43	0.0004

over a short (16-day) time period. Collections occurred over a much longer time at lakes Erie (60 days) and St. Clair (30 days), so data from those sites likely were more representative of bird reserves throughout spring. Discussion of seasonal changes in lesser scaup reserves will be based on results from those 2 stopover sites.

Body Mass and Lipid and Protein Reserves

Lesser scaup incur many energetic costs, such as diving for food, feather molt, courtship activities, maintenance activities, local flight, and thermoregulation, while at spring staging areas (Chappell 1982, Stephenson 1994, Austin et al. 1998). Ultimately staging birds must meet or exceed those costs to maintain or increase their energy and nutrient reserves (Wypkema and Ankney 1979, Chappell 1982, Gauthier et al. 1984, LaGrange and Dinsmore 1988). Because migratory flight for waterfowl requires substantial energy (Prince 1979), we expected that body mass and fat of male and female lesser scaup would not decrease during their spring residence on the LGL. Our results met those expectations because body mass, fat, and protein of females increased at lakes Erie and St. Clair, and body mass and protein reserves of males generally did not change throughout spring at those 2 sites. Fat reserves of males at Lake St. Clair also increased, but not enough to affect spring body mass; at Lake Erie, the slope for the relationship between fat and days since arrival was positive (0.4 ± 0.3 g/day), but fat reserves and body mass of males basically remained constant throughout spring. The male pattern of limited body mass and fat acquisition at these LGL stopover sites was different from that reported for a small sample of males staging on the St. Lawrence River in Quebec, Canada, because body mass and fat of those birds increased substantially throughout spring (Chappell 1982).

Lesser scaup begin to form pair-bonds during spring migration (Austin et al. 1998). The sex ratio in this species favors males, and many single males actively pursue females and engage in courtship displays while at stopover sites (Austin et al. 1998; S. Badzinski, Bird Studies Canada, Port Rowan, Ont., Canada, personal observation). Paired males maintain pair-bonds through displays and incur other energetic burdens such as mate or feeding territory defense (Austin et al. 1998). Many of the males we collected likely were paired, but a large number of unpaired males undoubtedly also were shot. Thus, energetic costs of courtship and pair-bond maintenance may partly explain why large seasonal gains in male body mass or nutrient reserves generally were not observed in this study. Most of the females we collected also were paired, so mate-guarding activities by males may facilitate fat and protein storage while staging on the LGL.

Little is known about spring migration chronology and strategies of lesser scaup (Austin et al. 1998). Their protracted spring migration suggests they may make a series of flights northward, using several stopover sites between their winter and breeding grounds. Using very simple flight range calculations (see Vangilder et al. 1986 and references therein), we calculated that birds could theoretically travel about 1,300–1,600 km nonstop if they exhausted fat reserves they acquired by the end of their residence on the LGL. Covering those distances would allow birds to reach other major stopover sites further north and west in the United States and Canada as well as the eastern portion of the species' breeding range (Bellrose 1980). Energy stored (or maintained) on the LGL must be used to fuel migration, but given that females use endogenous reserves for breeding (Afton and Ankney 1991, Esler et al. 2001), some amount of the reserves acquired there could also contribute to reproduction. The LGL region may be very important for breeding females because if birds depart in poor condition they would have to overcome much steeper nutrient accumulation gradients later in migration to attain breeding threshold levels, especially if staging habitat or

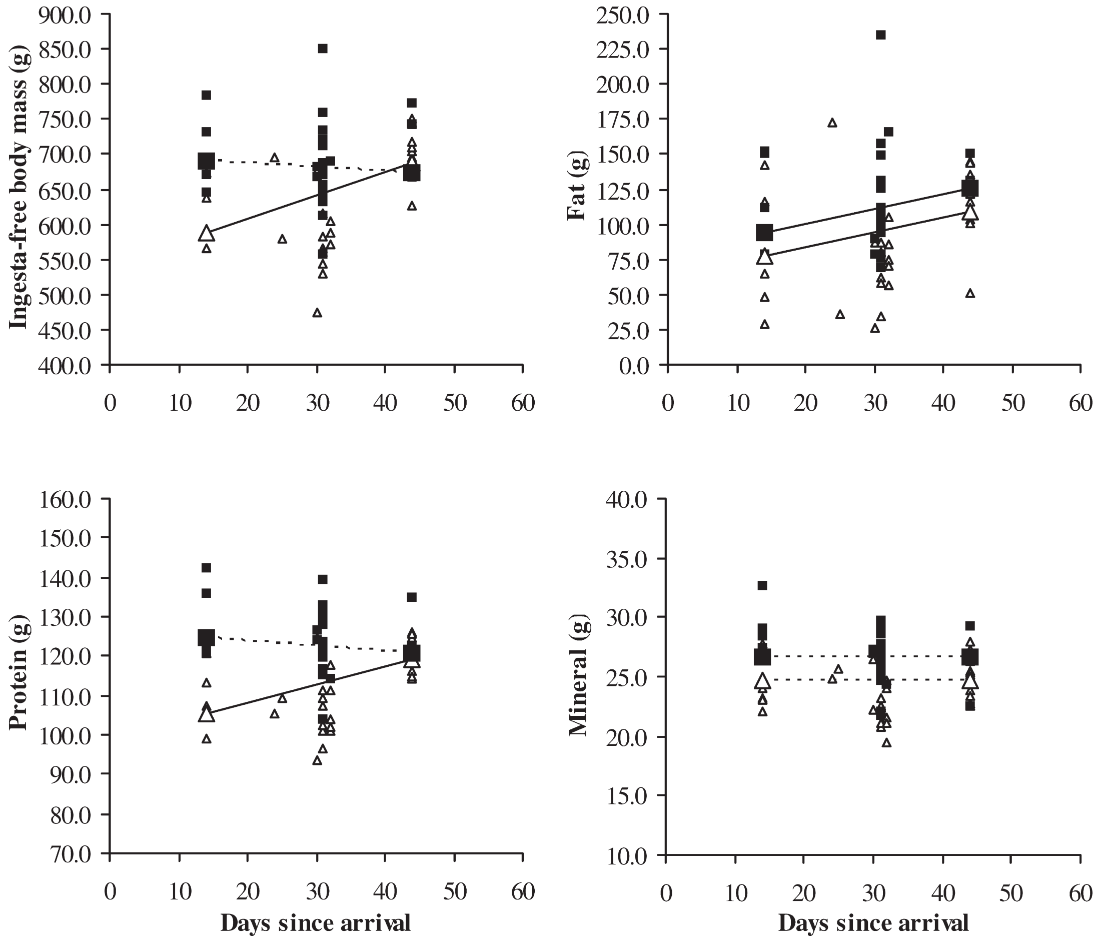


Figure 4. Changes in ingesta-free body mass, fat, protein, and mineral of lesser scaup (*Aythya affinis*) staging at Lake St. Clair, Ont., Canada, from 9 Mar–9 Apr 2000. Females and males are represented by open triangles and solid squares, respectively.

food quality is (or becomes) limiting further north and west (see Anteau and Afton 2004).

Mineral Reserves

Despite high availability and consumption of mineral-rich mussels and gastropods by scaup on the LGL (Petrie and Knapton 1999, Badzinski and Petrie 2006), female lesser scaup apparently did not store appreciable amounts of minerals during time spent on LGL stopover sites. Afton and Ankney (1991) and Anteau and Afton (2004) suggest that, at least historically, northern staging and breeding areas were important locations for mineral storage. Our results suggest that females either were not prepared physiologically to store mineral at this stage of spring migration or they generally have sufficient time and resources available to do so later and closer to the breeding grounds. This reasoning seems logical, because lesser scaup do use some endogenous minerals (Afton and Ankney 1991, Esler et al. 2001), but to a large extent rely on exogenous sources of mineral obtained near or on their breeding grounds (Esler et al. 2001) for egg production.

Nutrient-Reserve Comparisons among Stopover Sites

Some nutrient-reserve levels, particularly fat, of female and male lesser scaup differed among LGL stopover sites. Female protein (Erie < St. Clair < Ontario) and mineral (Erie and St. Clair < Ontario) reserves and male protein reserves (Erie and Ontario < St. Clair) differed among some stopover sites, but these relatively small differences (3–8%) in LS means likely were not biologically meaningful. However, females at Lake Erie had, on average, 11 g (13%) and 14 g (15%) less fat than did females at lakes Ontario and St. Clair, respectively, and males at Lake Erie also had 11 g (10%) and 14 g (12%), respectively, less fat on average than did males at both lakes Ontario and St. Clair. These differences in fat reserves were not clearly related to among-site variation in diet observed in lesser scaup staging at these 3 stopover sites (Badzinski and Petrie 2006) or to contaminant, specifically selenium, burdens since they generally did not differ among these 3 stopover sites during spring 2000 (S. Petrie, S. Badzinski, Bird Studies Canada, Port Rowan, Ont., Canada, and K. Drouillard, University of Windsor, Windsor, Ont., Canada, unpublished data). Much larger among-site variations in spring fat reserves have been documented in another study of lesser scaup nutrient reserves (Anteau and Afton 2004). Site-specific food availability estimates combined with behavioral observation and study of sex-specific food intake and preferences at stopover sites would help to explain among-site variability in nutrient reserves in lesser scaup.

Comparing female fat reserves during midmigration (35 days postarrival) in this study with levels reported in other spring staging and breeding studies allows determination of the relative condition of birds staging on the LGL. Despite the potential for a

Table 4. Reduced statistical models evaluating among-lake differences in body mass and nutrient reserves (grams) of lesser scaup (*Aythya affinis*) staging on the Canadian lower Great Lakes during spring 2000.

Variable	R^2	Model df	Error df	F	P	Parameter	Type III SS	F	P
Body mass (fresh)	0.21	6	212	9.48	<0.0001	Lake	75,646.77	7.82	0.0005
						Sex	55,636.46	44.50	0.0008
						Days	27,336.90	5.65	0.0183
						PC1	107,104.83	22.15	<0.0001
						Sex × Days	38,686.70	8.00	0.0051
Body mass (ingesta-free)	0.22	6	212	10.00	<0.0001	Lake	46,010.48	6.10	0.0026
						Sex	43,892.53	11.65	0.0008
						Days	32,523.92	8.63	0.0037
						PC1	79,652.56	21.13	<0.0001
						Sex × Days	24,276.34	6.44	0.0119
Fat	0.15	5	213	7.36	<0.0001	Lake	7,384.11	2.83	0.0612
						Sex	17,480.66	13.40	0.0003
						Days	18,073.31	13.85	0.0003
						Sex × Days	6,163.17	4.72	0.0308
Protein	0.29	8	210	10.57	<0.0001	Lake	1,255.46	8.04	0.0004
						Sex	1,238.01	15.85	<0.0001
						Days	446.51	5.72	0.0177
						Sex × Days	576.69	7.39	0.0071
						Lake × Sex	734.80	4.70	0.0100
Mineral	0.21	6	212	9.48	<0.0001	Lake	30.72	2.06	0.1295
						Sex	61.74	8.30	0.0044
						PC1	160.30	21.54	<0.0001
						Lake × Sex	52.18	3.51	0.0318

condition bias in our data, such comparisons are noteworthy given that Anteau and Afton (2004) recently reported that fat reserves of female lesser scaup have declined substantially: 1) on northern staging areas in Minnesota, USA, since the late 1980s, 2) on breeding areas in Manitoba, Canada, since the late 1970s–early 1980s, and 3) between a major midlatitude staging area (Pool 19 on the Mississippi River) in Illinois, USA, and more northern staging (Minnesota) and breeding areas (Manitoba) during the early 2000s. These findings led them to propose that females were arriving in poor condition on the breeding grounds during the early 2000s and in the upper midwestern United States staging areas were critical for females to acquire nutrient reserves (Anteau and Afton 2004).

Unfortunately, we did not have historic body mass or fat reserve levels for females on the LGL to test if birds collected in spring 2000 were in poorer condition than in the past. Our data showed that female body mass, fat, and protein did not decline, but rather increased, at LGL stopover sites. Based on comparisons with Anteau and Afton's (2004) data, it seems that females on the LGL 35 days after arrival generally were in relatively "good" condition. Lower Great Lakes females had, on average, 23% larger fat reserves than females staging further north in Minnesota and 22%

Table 5. Among-lake differences and site-specific estimates 35 days after arrival for body mass and nutrient reserves of female and male lesser scaup (*Aythya affinis*) at major stopover sites on the Canadian side of the lower Great Lakes during spring 2000.

		Least squares means (±SE)[a]		Estimates 35 days postarrival (±SE)[b]	
Variable (g)	Lake	Female	Male	Female	Male
Body mass (fresh)	Erie	715.3 ± 10.8 a	734.6 ± 8.2 a	731.6 ± 14.2	724.7 ± 9.2
	Ontario	764.6 ± 11.4 b	783.9 ± 10.1 b	768.0 ± 8.8	768.0 ± 8.8
	St. Clair	739.7 ± 10.4 c	759.0 ± 10.7 c	747.0 ± 13.6	753.6 ± 17.4
Body mass (ingesta-free)	Erie	626.9 ± 9.5 a	651.3 ± 7.2 a	644.0 ± 13.2	642.5 ± 8.5
	Ontario	663.8 ± 10.1 b	688.1 ± 8.9 b	653.3 ± 12.5	680.3 ± 9.9
	St. Clair	653.2 ± 9.2 b	677.6 ± 9.5 b	657.8 ± 11.3	678.4 ± 14.6
Fat	Erie	78.0 ± 5.4 a	100.9 ± 4.2 a	90.2 ± 8.1	95.9 ± 5.2
	Ontario	89.4 ± 5.7 b	112.3 ± 5.2 b	78.6 ± 6.9	110.4 ± 5.7
	St. Clair	92.2 ± 5.3 b	115.1 ± 5.4 b	99.5 ± 9.4	116.1 ± 9.4
Protein	Erie	109.1 ± 1.8 a	116.1 ± 1.2 a	112.4 ± 1.9	114.2 ± 1.2
	Ontario	119.0 ± 1.9 b	118.2 ± 1.5 a	117.4 ± 1.2	117.4 ± 1.2
	St. Clair	113.4 ± 1.6 c	122.2 ± 1.7 b	115.2 ± 1.5	120.5 ± 1.9
Mineral	Erie	24.8 ± 0.6 a	26.0 ± 0.3 a	25.6 ± 0.3	25.6 ± 0.3
	Ontario	26.3 ± 0.6 b	26.3 ± 0.5 a	26.3 ± 0.4	26.3 ± 0.4
	St. Clair	24.3 ± 0.5 a	26.9 ± 0.5 a	24.6 ± 0.5	26.6 ± 0.5

[a] Least squares means generated from models derived from data combined across stopover sites used to evaluate among-lake differences; different letters within sexes denote values that differed ($P \leq 0.10$).

[b] Estimates generated from site-specific models; used in comparisons with other nutrient-reserve studies.

Figure 5. Male lesser scaup spend time and energy courting females in order to develop and maintain pair-bonds while at spring stopover sites on the lower Great Lakes. (Photo by S. Badzinski)

Figure 6. Each spring, tens of thousands of lesser scaup congregate at stopover sites on the lower Great Lakes to increase their nutrient reserves for impending migration and for use after arrival at breeding sites dispersed throughout the prairie-parkland and boreal forest regions of North America. (Photo by S. Badzinski)

larger reserves than females intending to breed in Manitoba during the early 2000s; both of those areas are where female body condition is now suspected to be less than optimal (Anteau and Afton 2004). It also was notable that fat reserves of females at lakes Erie and St. Clair were within the range of values attained by prebreeding and breeding females in the late 1970s and early 1980s (Afton and Ankney 1991, Anteau and Afton 2004), when scaup populations were much higher than they are currently (Austin et al. 2000). Further, females at these 2 major LGL stopover sites during spring 2000 had fat reserves that were generally comparable to "historic" values reported for females at wintering (1986) and spring staging (1986–1988) areas (Anteau and Afton 2004); it should be noted, however, that Anteau and Afton's (2004) data were collected several years after the scaup population had already started to decline.

Based on comparisons presented above for upper midwestern United States staging and Manitoba breeding grounds, females did not appear to be in extremely poor condition, at least during spring 2000, while at 2 major LGL stopover sites. Females at Lake Ontario, however, appeared to have lower fat reserves than did staging, prebreeding, and breeding females during contemporary and historic times in the Mississippi Flyway (Afton and Ankney 1991, Anteau and Afton 2004). Another comparison suggests that LGL females during spring 2000 may not have been in the best condition possible. Females staging on the LGL, for example, overall had much lower (41–53%) midseason fat reserves than did females staging on Pool 19 of the Mississippi River in Illinois during the early 2000s (Anteau and Afton 2004). It is suspected that birds staging on the LGL largely originate from Atlantic Flyway wintering areas along the east coast of the United States (Bellrose 1980). Given this, it was notable that females collected during winter from the east coast of Florida (2002 and 2003) also had much lower fat reserves than females wintering in the Mississippi Flyway in Louisiana, USA, during the early 2000s (Anteau and Afton 2004). These differences could be related to spatial or temporal differences in food quality or availability or to study methodologies, but also further highlight the temporal and spatial variability in fat reserves of lesser scaup (Herring 2003, Anteau and Afton 2004, this study). It is also possible that these differences may indicate that factors specific to the Atlantic Flyway wintering and staging areas could be limiting nutrient acquisition in lesser scaup.

Lesser scaup staging on the LGL combine with birds from major Mississippi Flyway stopover sites (e.g., Pool 19—Mississippi River, Illinois, USA) in the Upper Midwestern United States Minnesota and Manitoba later in spring (S. Badzinski and S. Petrie, Bird Studies Canada, Port Rowan, Ont., Canada, unpublished data). Given that LGL females also had substantially lower fat reserves than females staging in Illinois, it is plausible that LGL birds may have contributed to the poor condition of females at northern staging and breeding areas in the Mississippi Flyway during the early 2000s. This could result if LGL females flew directly to northern staging or breeding areas or failed to acquire sufficient reserves at intermediate stopover sites. Anteau and Afton (2004) also proposed this concept as a potential explanation for the lower condition of females at northern staging areas in the 2000s. However, the most likely and parsimonious explanation for the decrease in fat reserves between major stopover sites is reduced food availability or forage quality encountered upon arrival at staging areas in the upper Midwest (Anteau and Afton 2004).

Although upper midwestern United States staging areas appear to be important for nutrient limitation, the apparent differences in female condition between Atlantic and Mississippi Flyway wintering areas and midlatitude staging areas warrant further attention because 1) currently there are limited long-term, broad-scale data for lesser scaup nutrient-reserve dynamics, 2) LGL lesser scaup have much higher selenium burdens than Mississippi Flyway birds (Custer and Custer 2000, Custer et al. 2003, S. Petrie, S. Badzinski, and K. Drouillard, unpublished data) and it is unknown how this affects nutrient acquisition, survival, and reproduction. Thus, we suggest that factors or events originating on Atlantic Flyway wintering or LGL staging areas should not yet be discounted as potential factors contributing to nutrient-reserve limitation or to declining numbers of scaup in North America.

Management Implications

Lesser scaup traditionally concentrate at several major stopover sites on lakes Erie, Ontario, and St. Clair (Dennis et al. 1984), which this study has shown are important for nutrient-reserve acquisition. Because ability of scaup to acquire nutrient reserves outside of the breeding season likely affects their reproduction or survival (Afton and Ankney 1991, Pace and Afton 1999), it is imperative to ensure that the coastal wetland habitats upon which they rely along the LGL are protected (Crowder and Bristow 1988, Herdendorf 1990). Reducing disturbance at these major stopover sites also would better allow these birds to meet their demanding nutritional and energetic requirements during spring (Knapton et al. 2000). Elevated selenium burdens have been documented recently in female lesser scaup from the LGL (Custer and Custer 2000, S. Petrie, S. Badzinski, and K. Drouillard, unpublished data), but it is unknown how this affects their behavior, nutrient acquisition, survival, and reproduction. More research is clearly needed regarding interactions among foraging ecology, nutrient-reserve dynamics, and contaminant burdens during spring, and how these factors ultimately influence reproduction and survival of lesser scaup throughout their annual cycle.

Acknowledgments

Financial support was provided by the Long Point Waterfowl and Wetlands Research Fund, through funding provided by the Bluff's Hunting Club, as well as The Waterfowl Research Foundation, Ducks Unlimited Canada, Ontario Federation of Anglers and Hunters, Sydenham Conservation Foundation, Long Point and Area Fish and Game Club, Long Point Waterfowlers' Association, Aylmer Order of Good Cheer, S. C. Johnson & Son, Inc., MeesPierson Ltd, M. Betz, B. Howard, and D. Shade. We also thank Bird Studies Canada, Ducks Unlimited Canada, and the Canadian Wildlife Service for logistical support, numerous hunters and wildlife professionals for assistance with carcass collections and laboratory assistance (especially M. Brock, P. Gagnon, D. Bernard, J. Haggeman, and B. Mason), R. Cox, D. Lepage, and J. Yee for useful advice regarding statistical analyses, and M. Anteau and A. Afton for kindly providing data to facilitate comparisons between our studies. We thank D. Ankey, M. Anteau, J. Eadie, M. Gendron, and 2 anonymous reviewers for providing helpful and critical comments that improved the manuscript.

Literature Cited

Afton, A. D., and M. G. Anderson. 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management 65:781–796.

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., R. H. Hier, and S. L. Paulus. 1989. Nutrient reserves of lesser scaup in mid-winter in southwestern Louisiana. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 43:404–411.

Afton, A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62–108 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota, Minneapolis, USA.

Alisauskas, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Thesis, University of Western Ontario, London, Canada.

Alisauskas, R. T., and C. D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30–61 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota, Minneapolis, USA.

Anteau, M. J. 2002. Nutrient reserves of lesser scaup during spring migration in the Mississippi Flyway: a test of the spring condition hypothesis. Thesis, Louisiana State University, Baton Rouge, USA.

Anteau, M. J., and A. D. Afton. 2004. Nutrient reserves of lesser scaup (*Aythya affinis*) during spring migration in the Mississippi Flyway: a test of the spring condition hypothesis. Auk 121:917–929.

Austin, J. E., A. D. Afton, M. G. Anderson, R. G. Clark, C. M. Custer, J. S. Lawrence, J. B. Pollard, and J. K. Ringelman. 2000. Declining scaup populations: issues, hypotheses, and research needs. Wildlife Society Bulletin 28:254–263.

Austin, J. E., A. D. Afton, and C. M. Custer. 1998. Lesser scaup (*Aythya affinis*). Account no. 338 *in* A. Poole, and F. Gill, editors. The birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, and American Ornithologists' Union, Washington, D.C., USA.

Austin, J. E., and L. H. Fredrickson. 1987. Body and organ mass and body composition of postbreeding female lesser scaup. Auk 104:694–699.

Badzinski, S. S., and S. A. Petrie. 2006. Diets of lesser and greater scaup during autumn and spring on the lower Great Lakes. Wildlife Society Bulletin 70:in press.

Bain, G. A. C. 1980. The relationship between preferred habitat, physical condition, and hunting mortality of canvasbacks (*Aythya valisineria*) and redheads (*Aythya americana*) at Long Point, Ontario. Thesis, University of Western Ontario, London, Canada.

Baldassarre, G. A., R. J. Whyte, and E. G. Bolen. 1986. Body weight and carcass composition of nonbreeding green-winged teal on the Southern High Plains of Texas. Journal of Wildlife Management 50:420–426.

Ball, H., J. Jalava, T. King, L. Maynard, B. Potter, and T. Pulfer. 2003. The Ontario Great Lakes coastal wetland atlas: a summary of information (1983–1997). Unpublished report, Environment Canada – Canadian Wildlife Service and Ontario Ministry of Natural Resources, Toronto, Canada.

Bellrose, F. C. 1980. Ducks, geese, and swans of North America. Stackpole, Harrisburg, Pennsylvania, USA.

Chappell, W. A. 1982. Aspects of the energetics of greater scaup (*Aythya marila*) and lesser scaup (*A. affinis*) during migration. Thesis, McGill University, Montreal, Quebec, Canada.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C., USA.

Crowder, A. A., and J. M. Bristow. 1988. The future of waterfowl habitats in the Canadian lower Great Lakes wetlands. Journal of Great Lakes Research 14: 115–127.

Custer, C. M., and T. W. Custer. 2000. Organochlorine and trace element contamination in wintering and migrating diving ducks in the southern Great Lakes, USA, since zebra mussel invasion. Environmental Toxicology and Chemistry 19:2821–2829.

Custer, C. M., T. W. Custer, M. J. Anteau, A. D. Afton, and D. E. Wooten. 2003. Trace elements in lesser scaup (*Aythya affinis*) from the Mississippi Flyway. Ecotoxicology 12:47–54.

Davies, J. C., and F. Cooke. 1983. Annual nesting productivity in snow geese: prairie droughts and arctic springs. Journal of Wildlife Management 47:291–296.

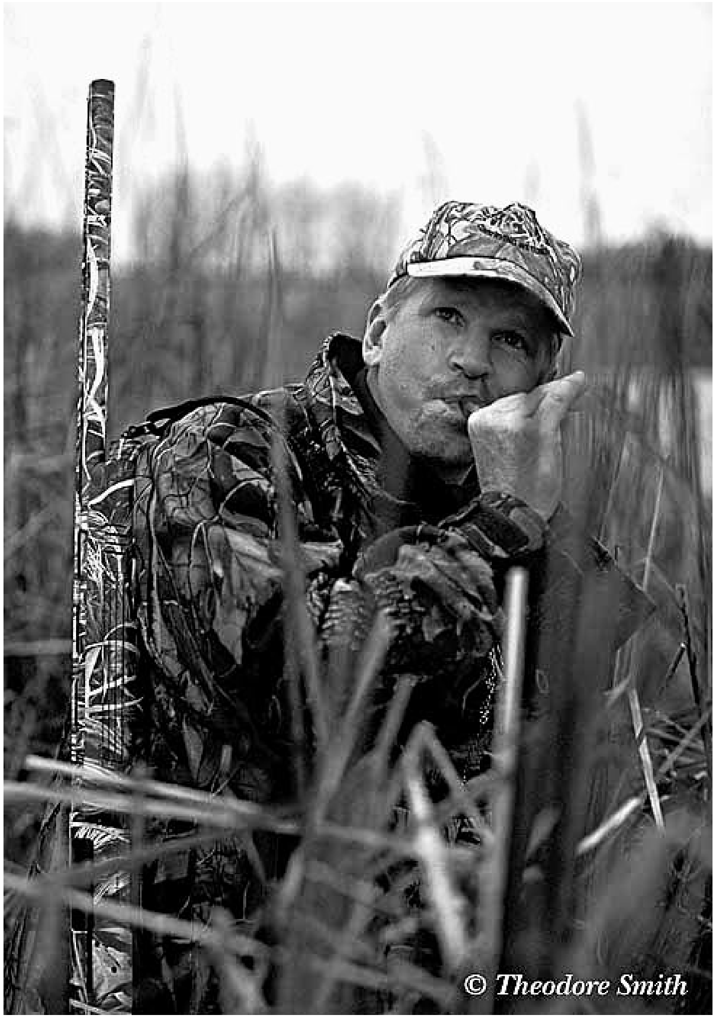
Dennis, D. G., G. B. McCullough, N. R. North, and R. K. Ross. 1984. An updated assessment of migrant waterfowl use of Ontario shorelines of the southern Great Lakes. Pages 37–42 *in* S. G. Curtis, D. G. Dennis, and H. Boyd, editors. Waterfowl studies in Ontario. Canadian Wildlife Service Occasional Paper 54, Canadian Wildlife Service, Ottawa, Ontario, Canada.

Dufour, K. W., C. D. Ankney, and P. J. Weatherhead. 1993. Condition and vulnerability to hunting among mallards staging at Lake St. Clair, Ontario. Journal of Wildlife Management 57:209–215.

Dzubin, A., and E. G. Cooch. 1992. Measurements of geese: general field methods. California Waterfowlers Association, Sacramento, USA.

Ebbinge, B., A. St Joseph, P. Prokosch, and B. Spaans. 1982. The

importance of spring staging areas for arctic-breeding geese, wintering in western Europe. Aquila 89:249–258.
Esler, D., J. B. Grand, and A. D. Afton. 2001. Intraspecific variation in nutrient reserve use during clutch formation by lesser scaup. Condor 103:810–820.
Gammonley, J. H., and M. E. Heitmeyer. 1990. Behavior, body condition, and foods of buffleheads and lesser scaup during spring migration through the Klamath Basin, California. Wilson Bulletin 102:672–683.
Gauthier, G., J. Bédard, J. Huot, and Y. Bédard. 1984. Spring accumulation of fat by greater snow geese in two staging habitats. Condor 86:192–199.
Herdendorf, C. E. 1990. Great Lakes estuaries. Estuaries 13:493–503.
Herdendorf, C. E., C. N. Raphael, and E. Jaworski. 1986. The ecology of Lake St. Clair wetlands: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.7), Washington, D.C., USA.
Herring, G. 2003. Assessing nutrient reserves and local population dynamics of wintering lesser scaup in east-central Florida. Thesis, North Carolina State University, Raleigh, USA.
Hipes, D. L., and G. R. Hepp. 1995. Nutrient-reserve dynamics of breeding male wood ducks. Condor 97:451–460.
Hohman, W. L. 1986. Changes in body weight and body composition of breeding ring-necked ducks (*Aythya collaris*). Auk 103:181–188.
Hohman, W. L., T. Scott, and M. W. Weller. 1988. Annual body weight change in ring-necked ducks (*Aythya collaris*). Pages 257–269 *in* M. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, USA.
Knapton, R. W., S. A. Petrie, and G. Herring. 2000. Human disturbance of diving ducks on Long Point Bay, Lake Erie. Wildlife Society Bulletin 28:923–930.
LaGrange, T. G., and J. J. Dinsmore. 1988. Nutrient reserve dynamics of female mallards during spring migration through central Iowa. Pages 287–297 *in* M. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, USA.
Lovvorn, J. R., and D. R. Jones. 1994. Biomechanical conflicts between adaptations for diving and flying in estuarine birds. Estuaries 17:62–75.
Miller, M. R. 1986. Northern pintail body condition during wet and dry winters in the Sacramento Valley, California. Journal of Wildlife Management 50: 189–198.
Pace, R. M., III, and A. D. Afton. 1999. Direct recovery rates of lesser scaup banded in northwest Minnesota: sources of heterogeneity. Journal of Wildlife Management 63:389–395.
Peterson, S. R., and R. S. Ellarson. 1979. Changes in oldsquaw carcass weight. Wilson Bulletin 91:288–300.
Petrie, S. A., and R. W. Knapton. 1999. Rapid increase and subsequent decline of zebra and quagga mussels in Long Point Bay, Lake Erie: possible influence of waterfowl predation. Journal of Great Lakes Research 25:772–782.
Prince, H. H. 1979. Bioenergetics of postbreeding dabbling ducks. Pages 103–117 *in* T. A. Bookhout, editor. Waterfowl and wetlands—an integrated review. Proceedings of the 39th Midwest Fish and Wildlife Conference — 1977. North Central Section of The Wildlife Society, 5 Dec 1977, Madison, Wisconsin, USA.
Prince, H. H., P. I. Padding, and R. W. Knapton. 1992. Waterfowl use of the Laurentian Great Lakes. Journal of Great Lakes Research 18:673–699.
Ross, R. K., S. A. Petrie, S. S. Badzinski, and A. Mullie. 2005. Autumn diet of greater scaup, lesser scaup, and long-tailed ducks on eastern Lake Ontario prior to zebra mussel invasion. Wildlife Society Bulletin 33:81–91.
SAS Institute. 1990. SAS/STAT user's guide. Version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.
Serie, J. R., and D. E. Sharp. 1989. Body weight and composition dynamics of fall migrating canvasbacks. Journal of Wildlife Management 53:431–441.
Stephenson, R. 1994. Diving energetics in lesser scaup (*Aythya affinis* Eyton). Journal of Experimental Biology 190:155–178.
Teunissen, W., B. Spaans, and R. Drent. 1985. Breeding success in brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. Ardea 73:109–119.
Tietje, W. D., and J. G. Teer. 1988. Winter body condition of northern shovelers on freshwater and saline habitats. Pages 353–376 *in* M. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, USA.
Vangilder, L. D., L. M. Smith, and R. K. Lawrence. 1986. Nutrient reserves of premigratory brant during spring. Auk 103:237–241.
Vest, J. L. 2002. Body mass and gastrointestinal parasites in lesser scaup (*Aythya affinis*) in the Mississippi Flyway. Thesis, Mississippi State University, Mississippi State, USA.
Whyte, R. J., and E. G. Bolen. 1984. Impact of winter stress on mallard body composition. Condor 86:477–482.
Wormington, A., and J. H. Leach. 1992. Concentrations of diving ducks at Point Pelee National Park, Ontario, in response to zebra mussels, *Dreissena polymorpha*. Canadian Field-Naturalist 106:376–380.
Wypkema, R. C. P., and C. D. Ankney. 1979. Nutrient reserve dynamics of lesser snow geese staging at James Bay, Ontario. Canadian Journal of Zoology 57:213–219.
Zar, J. H. 1996. Biostatistical analysis. Third edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.



Shannon Badzinski (above) earned his B.S. in wildlife ecology from the University of Wisconsin – Stevens Point (1995) and his M.Sc. (1998) and Ph.D. in zoology (2003) from the University of Western Ontario. Shannon is the Research Scientist of the Long Point Waterfowl and Wetlands Research Fund. His research interests include all aspects of waterfowl–wetland ecology and management. Shannon currently is studying the migration chronology and strategies of lesser and greater scaup staging and wintering on the lower Great Lakes. ***Scott Petrie*** (left) received a B.Sc. from the University of Guelph in 1990 and a Ph.D. from the University of the Witwatersrand, South Africa, in 1998. His work has focused primarily on the ecology of waterfowl in semiarid environments and the staging ecology of north-temperate–occurring waterfowl. Scott is the Research Director of the Long Point Waterfowl and Wetlands Research Fund and is an Adjunct Professor at the University of Western Ontario, where he teaches wildlife ecology and management. Scott and his students are presently studying numerous aspects of the staging ecology of mute swans, tundra swans, and lesser and greater scaup on the lower Great Lakes.

Associate Editor: Eadie.