

2002

Nutrient reserves of lesser scaup during spring migration in the Mississippi Flyway: a test of the spring condition hypothesis

Michael J. Anteau

Louisiana State University and Agricultural and Mechanical College

Follow this and additional works at: https://digitalcommons.lsu.edu/gradschool_theses



Part of the [Environmental Sciences Commons](#)

Recommended Citation

Anteau, Michael J., "Nutrient reserves of lesser scaup during spring migration in the Mississippi Flyway: a test of the spring condition hypothesis" (2002). *LSU Master's Theses*. 3191.
https://digitalcommons.lsu.edu/gradschool_theses/3191

This Thesis is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Master's Theses by an authorized graduate school editor of LSU Digital Commons. For more information, please contact gradetd@lsu.edu.

**NUTRIENT RESERVES OF LESSER SCAUP DURING SPRING MIGRATION IN
THE MISSISSIPPI FLYWAY: A TEST OF THE SPRING CONDITION
HYPOTHESIS**

A Thesis
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the degree of
Master of Science

in

The School of Renewable Natural Resources

by
Michael J. Anteau
B.S., Wildlife Biology, University of Alaska Fairbanks, 1997
B.S., Biological Sciences, University of Alaska Fairbanks, 1997
August 2002

DEDICATION

This thesis is dedicated to my wife, Andrea C. E. Anteau; for her moral, financial, and emotional support throughout my work. She has proven her dedication to me and my endeavors, with countless hours volunteering in the lab. Her willingness to help with carcass dissections when she was 8 months pregnant speaks for itself. Her dedication, along with her iron stomach, has been an inspiration to me.

ACKNOWLEDGMENTS

I thank J. H. Caswell, R. S. Durham, P. M. Dummer, A. P. Langlinais, B. C. Muller, K. D. Richkus, S. Talley, C. M. Tricou, and W. B. Wilson for assisting with collections or dissections. I am grateful for logistical support provided by R. V. Anderson, C. M. Custer, J. R. Fisher, R. N. Helm, S. P. Havera, T. J. Hess, J. D. Huener, T. C. Michot, P. B. Telander, and F. C. Rohwer. I thank the Muscle Foods Laboratory at Louisiana State University, Louisiana Universities Marine Consortium, Minnesota Department of Natural Resources, USGS-National Wetland Research Center, Rockefeller State Wildlife Refuge, USGS-Upper Midwest Environmental Sciences Center, Western Illinois University, Tri-Tronics Training Collars, and Federal, Winchester, Estate, and Kent Cartridge Companies for in-kind support. I acknowledge M. Anderson, M. G. Anderson, A. C. E. Anteau, F. Bolduc, E. F. Bowers, R. H. Hier, S. Kufrin, C. T. Pollet, and S. D. Wilds for their help or support of my project. I thank the following organizations for financial support: Delta Waterfowl Foundation, IWWR of Ducks Unlimited Canada, IWWR of Ducks Unlimited USA under the Edward D. and Sally Futch Fellowship program, U.S. Fish and Wildlife Service Regions 3 and 4, and USGS-Louisiana Cooperative Fish and Wildlife Research Unit, School of Renewable Natural Resources, and The Graduate School at Louisiana State University. I thank A. D. Afton, C. D. Ankney, R. R. Cox Jr., D. Esler, J. M. Fernandez, J. P. Geaghan, M. A. Hanson, and R. M. Kaminski for their helpful comments on the manuscript. Finally, I have

tremendous gratitude for my advisor Dr. Alan D. Afton for his expertise, guidance, patience, and his pursuit of excellence, regardless of how much red ink it takes.

TABLE OF CONTENTS

Dedication	ii
Acknowledgments	iii
Abstract	vi
Introduction	1
Methods	4
Study Areas	4
Collection of Specimens	6
Specimen Dissections and Body Composition Analyses	7
Statistical Analyses	9
Results	14
Louisiana	14
Keokuk Pool	14
Minnesota	15
Manitoba	15
Discussion	18
Louisiana	18
Keokuk Pool	18
Minnesota	20
Manitoba	21
The Importance of Northern Spring -Stopover Areas	22
The Spring Condition Hypothesis	24
Management Implications	32
Literature Cited	33
Vita	44

ABSTRACT

The continental scaup population (lesser [*Aythya affinis*] and greater scaup [*A. marila*] combined) has declined markedly during the past 20 years, and has remained below the population goal of the North American Waterfowl Management Plan since 1985. One hypothesis explaining the scaup population decline states that reproductive success has decreased because females presently are arriving on breeding areas in poorer condition than that historically (Spring Condition Hypothesis [SCH]). I tested the SCH by comparing fresh body masses (FBMs) and nutrient reserves (lipid, protein, and mineral) of lesser scaup at 4 locations (Louisiana, Illinois, Minnesota, and Manitoba) in the Mississippi Flyway between decades of the 1980s and 2000s. I found that mean FBMs of females were 58.5 g and 58.9 g lower in the 2000s than were those in the 1980s in northwestern Minnesota and near Erickson, Manitoba, respectively; mean FBMs of males similarly were 40.7 g lower in Minnesota. Mean lipid reserves of females in the 2000s were 28.8 g lower than those in the 1980s in northwestern Minnesota and 27.8 g lower near Erickson, Manitoba. Mean mineral reserves of females in the 2000s were 3.2 g lower than those in the 1980s near Erickson, Manitoba. Consequently, females arriving to breed near Erickson, Manitoba in the 2000s had accumulated lipid reserves for 4.1 fewer eggs and mineral reserves for 1 fewer egg than had those arriving to breed in the 1980s. Accordingly, my results clearly are consistent with predictions of the SCH and indicate that there has been a long-

term decline in female body condition, reflected by declines in FBMs, lipids and mineral reserves, which could significantly reduce reproductive success.

INTRODUCTION

The continental scaup population (lesser [*Aythya affinis*] and greater scaup [*A. marila*] combined) has declined markedly during the past 20 years (Austin et al. 1998, Afton and Anderson 2001). Annual population estimates of scaup have been below the population goal of the North American Waterfowl Management Plan since 1985 and recently approached an all-time low (Dubovsky et al. 2001). The scaup decline is a particular concern in the Mississippi Flyway because, on average, 40% of the continental scaup population winters there and 62% of the U.S. harvest of lesser scaup occurs in this flyway (Afton and Anderson 2001). Recruitment of lesser scaup in the Mississippi Flyway apparently has declined over the past 20 years, and female survival rates have declined relative to that of males (Afton and Anderson 2001).

Nutrient reserves acquired during winter and/or spring migration are important determinants of reproductive success in geese and some ducks (Ryder 1970, Ankney and MacInnes 1978, Afton et al. 1989, Afton and Ankney 1991, Alisauskas and Ankney 1992, Krapu and Reinecke 1992). Lesser scaup use endogenous and exogenous nutrients for clutch formation and incubation (Afton and Ankney 1991, Afton and Paulus 1992, Esler et al. 2001). In Manitoba, lipid reserves of female lesser scaup decline an average of 0.50 g for every gram of lipid deposited in eggs, and mineral reserves decrease 0.13 g for every gram of eggshell produced (Afton and Ankney 1991). In a recent combined analysis of breeding lesser scaup in Manitoba and Alaska, Esler et al. (2001) reported that

lipid and mineral reserves decline, on average, 0.68 g and 0.05 g, respectively, for every gram of that nutrient allocated to eggs. Protein reserves do not decrease during egg formation for lesser scaup nesting in Manitoba, presumably because of abundant, protein-rich invertebrate foods (Afton and Ankney 1991). However, for those nesting in Alaska, protein reserves declined 0.07 g for every gram of protein in eggs (Esler et al. 2001). Thus, lipids clearly are the most important nutrient reserves for female lesser scaup arriving on breeding areas.

Declines in body mass may result in decreased survival and/or reproductive success, especially in females (Afton and Ankney 1991, Pace and Afton 1999). Austin et al. (1999, 2000) and Afton and Anderson (2001) outlined several hypotheses explaining the scaup decline, 1 of which is the Spring Condition Hypothesis (SCH). The SCH states that reproductive success of lesser scaup has declined because females are arriving on breeding areas in poorer body condition than in the past, due to reduced food resources preventing females from acquiring sufficient nutrient reserves on wintering, spring migration, and/or breeding areas (Afton and Anderson 2001). If female lesser scaup are arriving on breeding areas in poor body condition, they might have to spend more time on breeding areas prior to laying eggs (*cf.* Afton and Anderson 2001) because of their reliance on nutrient reserves for egg production and incubation (Afton and Ankney 1991, Afton and Paulus 1992, Esler et al. 2001). Because nest success and/or duckling survival generally are negatively correlated with nest initiation date among waterfowl (Rohwer 1992, Flint and Grand 1996, Grand and Flint 1996, Dzús and

Clark 1998, Guyn and Clark 1999) and clutch size of lesser scaup declines seasonally (Afton 1984, Esler et al. 2001, Brook 2002), females arriving on breeding areas in poor condition probably nest later (Reynolds 1972, Esler et al. 2001) and concomitantly produce fewer young. Given that 1- and 2-year-old-female lesser scaup often do not breed when conditions are unfavorable (Afton 1984), it is likely that females in poor condition have a lower breeding propensity than do those in good condition.

I tested the SCH by comparing fresh body masses (FBMs) and nutrient reserves of lesser scaup in the Mississippi Flyway between decades of the 1980s and 2000s. I analyzed FBMs to allow comparisons with other studies for which carcass composition data were not available. Finally, based on my findings, I discussed several hypotheses that may explain the observed decline in body condition of females on northern spring-stopover areas and upon arrival at breeding areas.

METHODS

Study Areas

I used band-recovery data and sightings of color-marked lesser scaup to select collection locations within the Mississippi Flyway (Afton and Hier 1987; Havera 1999; A. D. Afton, U.S. Geological Survey, unpublished data). I collected lesser scaup (hereafter scaup) during two decades (the 1980s and 2000s) at 4 locations in the Mississippi Flyway (Table 1): (1) southern Louisiana (hereafter Louisiana), (2) Pool 19 of the Mississippi River between Hamilton and Niota, Illinois (hereafter Keokuk Pool), (3) northwest Minnesota (hereafter Minnesota; including collection sites at Thief Lake Wildlife Management Area [WMA], Agassiz National Wildlife Refuge, and Roseau River WMA), and (4) on a Prairie-Parkland breeding area west of Erickson, Manitoba (hereafter Manitoba; between Sandy Lake and Elphinstone, Manitoba and the area 35 km south of these towns). Detailed descriptions of these locations are provided in Rogers (1959, 1964), Thompson (1973), Parker et al. (1980), and Afton et al. (1989).

Historical FBMs and nutrient reserve data from Louisiana (Afton et al. 1989) were collected at Rockefeller State Wildlife Refuge; however, few scaup used this area in 2000. Thus, I conducted the 2000 Louisiana collections near Lake Pelto, south of Cocodrie, Louisiana, where large numbers of scaup were using saline coastal fringe marsh composed mostly of smooth cord grass (*Spartina alterniflora*). In 2001, I did not repeat collections at either Louisiana site because preliminary analyses indicated that nutrient-reserve levels of scaup on wintering areas had

Table 1. Locations, dates, and numbers of lesser scaup collected during winter and spring migration by decade in the Mississippi Flyway.

Decade	Location	Year	Dates	Males	Females	
1980's	Southern Louisiana ^a	1986	14 - 24 Jan.	42	33	
		Keokuk Pool	1986	16 - 30 Mar.	22	22
	Northwestern Minnesota	1986	17 Apr. - 1 May	31	26	
			1987	17 - 30 Apr.	9	9
	Erickson, Manitoba ^b		1988	14 - 24 Apr.	27	34
		1977	13 May - 1 Jun.	3	4	
		1978	13 - 25 May	3	3	
2000's	Southern Louisiana		1979	7 May	0	1
			1980	7 May - 23 Jun.	9	7
	Keokuk Pool	2000	12 Feb. - 4 Mar.	34	45	
		2000	13 - 15 Mar.	40	40	
	Northwestern Minnesota	2001	14 - 17 Mar.	30	29	
2000		10-25 April	40	40		
Erickson, Manitoba		2001	27 Apr. - 3 May	30	30	
	2000	30 Apr. - 15 May	40	39		
	2001	6 - 15 May	30	34		
Total				390	396	

^a Data from Afton et al. 1989.

^b Data from Afton and Ankney 1991 (Pre-RFG samples only).

little influence on those of scaup on northern spring-stopover areas or upon arrival at breeding areas.

Collection of Specimens

I collected scaup with a shotgun (Louisiana State University, Institutional Animal Care and Use Committee Protocol #: 00-011 [for collections in 2000 and 2001]) by sneaking, pass shooting, or spotlighting at night to avoid potential condition biases associated with using decoys or baiting (Pace and Afton 1999). I determined pair status of individuals prior to collection using criteria outlined in Afton (1985). In Louisiana, I collected scaup just prior to spring migration. I timed collections to coincide with peak numbers of scaup using spring-stopover areas at Keokuk Pool and in Minnesota. I timed collections in Manitoba to begin when resident scaup first arrived and immediately began using small ponds (see below) and concluded before the start of Rapid Follicle Growth (RFG) in females.

I collected scaup from actively foraging or roosting flocks consisting of 5 or more scaup, except as described below. I limited collections in Minnesota and Manitoba to paired individuals, except for 26 unpaired males that were collected in Minnesota in 1986 and 1987. I included these 26 males in my analyses because FBMs and lipid, protein and mineral reserves did not differ between paired and unpaired males in 1986 (analyses of variance/covariance, $P = 0.104$, $P = 0.373$, $P = 0.479$, and $P = 0.351$, respectively; in 1987 too few specimens were collected to test for pairing effect [Table 1]). I further limited collections in Manitoba to isolated

pairs on smaller ponds which, based on observations of marked individuals, insured a sample of resident breeders (A. D. Afton, U.S. Geological Survey, unpublished data; R. G. Clark, Canadian Wildlife Service, personal communication).

Specimen Dissections and Body Composition Analyses

I recorded FBMs of scaup immediately upon collection (± 1 g), and generally preserved esophageal and proventricular contents by injecting a 10% buffered formaldehyde solution down the esophagus with a syringe. However, if the bird was observed feeding (in 1988 or earlier), esophageal and proventricular contents were removed, weighed, and preserved (Afton and Hier 1991, Afton et al. 1991). Specimens then were labeled, placed in double plastic bags, frozen, and transported to the laboratory for dissections.

In the laboratory, I thawed specimens and took the following morphometric measurements: (1) total length (± 1 mm), from tip of longest rectrix to tip of bill with bird stretched on its back (Afton and Ankney 1991), (2) wing length (± 1 mm; Carney 1992), and (3) rectrix length (± 1 mm), from body to tip of longest rectrix. I did not assess age of scaup because accuracy of aging techniques, such as presence or absence of bursa (Hochbaum 1942), eye color (Trauger 1974), notched rectrices (Kortright 1967), and wing plumage characteristics (Carney 1992) have not been verified during late-winter or spring.

I conducted dissections exactly as described in Afton et al. (1989) and Afton and Ankney (1991). Specimens collected in the 1980s were prepared for body composition analysis as described in Afton et al. (1989) and Afton and Ankney (1991). The 2000 and 2001 specimens were ground in a bowl chopper and grinder (Hobart, model 84145, Troy, Ohio). Samples were chopped in the bowl chopper for approximately 8 minutes then passed twice through the grinder attachment using 10- and 5-mm plates, respectively. Samples were thoroughly mixed, and a sub-sample of approximately 150 g was weighed and dried to a constant mass at 80° C and reweighed. The dry sub-sample then was reground in a coffee mill (Moulinex, Luxe 140 W, Concord, Ontario, Canada) until the sub-sample could pass through a 2-mm sieve. All body composition analyses were contracted out to the University of Western Ontario and were conducted as described in Afton and Ankney (1991).

I calculated nutrient-reserve levels using the following equations. To represent the sample upon which body composition analyses were conducted, I calculated carcass dry mass (CDM) by,

$$\text{CDM}_{1980\text{s}} = (\text{DM} / \text{WM}) \text{ IFFBM} - \text{AFM}$$

$$\text{CDM}_{2000\text{s}} = (\text{SDM} / \text{SWM}) \text{ IFFBM} - \text{AFM}$$

where DM is dry mass (sum of all dried components of the carcass), WM is wet mass (sum of all wet components of the carcass), SDM is sub-sample dry mass, SWM is sub-sample wet mass, IFFBM is ingesta free fresh body mass, and AFM is abdominal fat mass removed, weighed, and discarded during dissections. I used a

sampling method of calculating CDM rather than summing dried components of the carcass for comparability between historical (1980s) and current data sets (2000s) and to account for small amounts of carcass lost in the dissection and grinding processes. My estimates of lipid, protein, and mineral reserves were calculated by,

$$PLipid = (SDM_L - SLDM_L) / SDM_L$$

$$Lipid = PLipid (CDM) + AFM$$

$$CLDM = CDM - PLipid (CDM)$$

$$Protein = [(SLDM_c - ASH) / SLDM_c] CLDM$$

$$Mineral = CLDM - Protein$$

where PLipid is the proportion of lipids, SDM_L is sample dry mass before lipid extraction, $SLDM_L$ is sample lean dry mass after lipid extraction, CLDM is carcass lean dry mass, $SLDM_c$ is the sample lean dry mass remaining after transferred into the crucible for ashing in a muffle furnace, and ASH is the remains after ashing.

Statistical Analyses

I conducted separate, but identical analyses for each sex because predictions of the SCH concern only females; thus, sex-specific estimates of least-squares means for FBMs and nutrient reserves were required. For each sex, I conducted a principal components analysis of the correlation matrix for all morphometric measurements (PROC PRINCOMP; SAS Institute 1993). I then

used the first principal component scores (PC1) to index body size (Ankney and Afton 1988, Afton and Ankney 1991, Alisauskas and Ankney 1994).

I created a variable named collection day (CD) to adjust for varying lengths of collection periods (Table 1) because observed FBMs and nutrient reserves could change with time at a given location within years. I calculated CD for Louisiana, Keokuk Pool, and Minnesota data sets by subtracting the Julian date of the first day of collections per location and year from the Julian date when the individual was collected and then added 1. For Manitoba data, I subtracted the Julian date of the first day that isolated pairs were observed on small wetlands from the Julian date when the individual was collected and then added 1.

To test the SCH, I compared FBMs and nutrient reserves between 2 decades (historic [1980s] vs. current [2000s]; Table 1). For simplicity, samples collected in 1977-1980 (Afton and Ankney 1991) were included in the 1980s decade. For each sex and for 4 response variables (FBMs, lipid, mineral, and protein), I conducted an analysis of covariance (ANCOVA; PROC Mixed; SAS Institute 1993), with decade and location as class variables and PC1 and CD as covariates. To control for annual variation, while testing for a difference between decades, I specified collection year within decade as a random error term for all ANCOVAs (PROC Mixed; SAS Institute 1993). I used backwards elimination (P -values ≤ 0.05) with all possible interactions, excluding any interaction with PC1, to select the final models (Zar 1996a). I did not allow PC1 to interact with any other variable because these interactions were not considered to be biologically

significant. I conducted *a priori* statistical tests between decades; however, because the decade-by-location interaction was significant in all models except the female protein model (Tables 2 and 3), I conducted a separate test for each location in all models except the female protein model. I specified these *a priori* tests in the least-squares means statement of the decade-by-location interaction by the pdiff option (PROC Mixed; SAS Institute 1993). I set the critical value for all *a priori* tests as $P \leq 0.05$ except for the Manitoba data set, where $P \leq 0.10$ was used because of small sample sizes in the 1980s (Table 1; Zar 1996b, Anonymous 1995).

Table 2. Numerator df (N), denominator df (D), and *P*-values (*P*) of final analyses of covariance models of each response variable (fresh body mass, lipid, protein, and mineral) for female lesser scaup collected during winter and spring migration in the Mississippi Flyway.

Effect ^a	Fresh Body Mass			Lipid			Protein			Mineral		
	N	D	<i>P</i>	N	D	<i>P</i>	N	D	<i>P</i>	N	D	<i>P</i>
LOC ^{b, c}	3	377	0.0065	3	377	<0.0001	3	383	<0.0001	3	381	<0.0001
DEC ^{d, e}	1	6	0.3045	1	6	0.1524	1	7	0.1385	1	6	0.7403
PC1 ^{c, f}	1	377	<0.0001	1	377	<0.0001	1	383	<0.0001	1	381	<0.0001
CD ^{c, g}	1	377	0.5658	1	377	0.3580			^h			^h
DEC*LOC ^c	3	377	<0.0001	3	377	<0.0001			^h	3	381	<0.0001
CD*LOC ^c	3	377	0.0461	3	377	0.0165			^h			^h

^a Type III test of effects (Proc Mixed; SAS Inst., Inc. 1993).

^b Location (Louisiana, Keokuk Pool, Minnesota, and Manitoba).

^c Effect tested with model residual error term.

^d Decade (the 1980s and 2000s).

^e Effect tested with year within decade error term.

^f First principal component of morphometric measurements.

^g Collection day adjusted for year and location (see Methods).

^h Effect was not included in final model (see Methods).

Table 3. Numerator df (N), denominator df (D), and *P*-values (*P*) of final analyses of covariance models of each response variable (fresh body mass, lipid, protein, and mineral) for male lesser scaup collected during winter and spring migration in the Mississippi Flyway.

Effect ^a	Fresh Body Mass			Lipid			Protein			Mineral		
	N	D	<i>P</i>	N	D	<i>P</i>	N	D	<i>P</i>	N	D	<i>P</i>
LOC ^{b, c}	3	372	0.0002	3	372	<0.0001	3	375	<0.0001	3	375	0.0097
DEC ^{d, e}	1	5	0.0365	1	5	0.0056	1	5	0.8203	1	5	0.0275
PC1 ^{c, f}	1	372	<0.0001	1	372	0.0437	1	375	<0.0001	1	375	0.0018
CD ^{c, g}	1	372	0.2934	1	372	0.2034	1	375	0.0323	1	375	0.0132
DEC*LOC ^c	3	372	<0.0001	3	372	<0.0001	3	375	0.0164	3	375	0.0022
CD*LOC ^c	3	372	0.0110	3	372	0.0144			^h			^h

^a Type III test of effects (Proc Mixed; SAS Inst., Inc. 1993).

^b Location (Louisiana, Keokuk Pool, Minnesota, and Manitoba).

^c Effect tested with model residual error term.

^d Decade (the 1980s and 2000s).

^e Effect tested with year within decade error term.

^f First principal component of morphometric measurements.

^g Collection day adjusted for year and location (see Methods).

^h Effect was not included in final model (see Methods).

RESULTS

My final models for FBMs and nutrient reserves of females and males are summarized in Tables 2 and 3, respectively. I detected significant decade-by-location ($P < 0.0001$) and CD-by-location ($P < 0.05$) interactions for FBMs and lipid reserves of females and males (Tables 2 and 3). I also detected a significant ($P < 0.0001$) decade-by-location interaction in mineral reserves of females (Table 2). The decade-by-location interaction was not significant for protein reserves of females, nor did protein reserves of females differ by decade (Table 2). However, for males, the decade-by-location interaction was significant in the protein reserves model, but protein did not differ between decades except in Manitoba (see below).

Louisiana

Mean FBMs and lipid and mineral reserves of females were 80.0 g, 52.5 g, and 3.0 g greater, respectively, and those of males were 108.8 g, 72.5 g, and 2.4 g greater, respectively, in the 2000s than in the 1980s (Fig. 1).

Keokuk Pool

Mean FBMs and lipid reserves of females were 88.6 g and 56.5 g greater, respectively, and those of males were 80.6 g and 76.0 g greater, respectively, in the 2000s than in the 1980s (Fig. 1). Mean mineral reserves of males were 2.7 g greater in the 2000s than those in the 1980s, whereas mean mineral reserves did not differ between decades for females (Fig. 1).

Minnesota

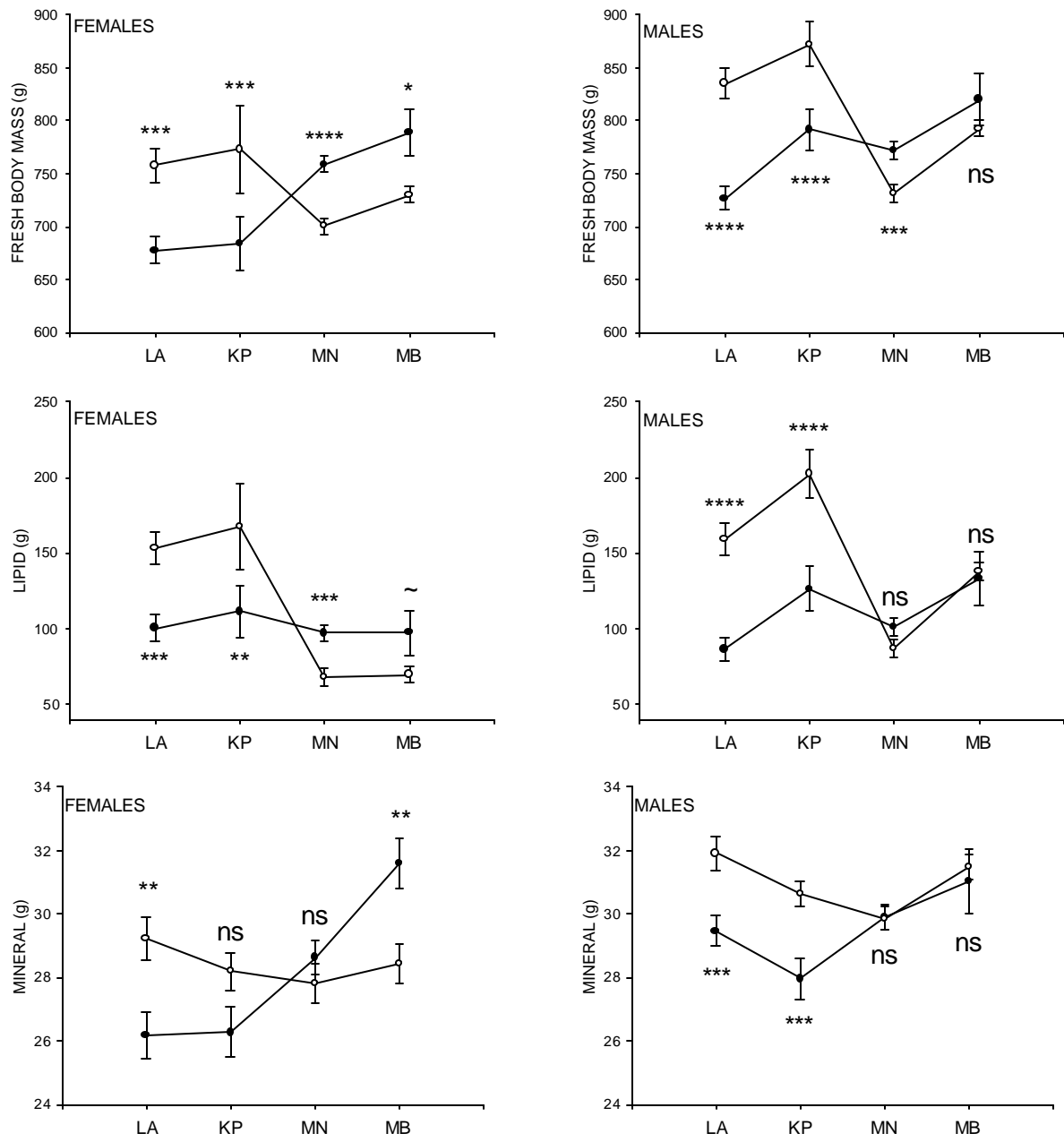
Mean FBMs were 58.5 g and 40.7 g lower in the 2000s than those in the 1980s for females and males, respectively (Fig. 1). Mean lipid reserves of females also were 28.8 g lower in the 2000s than in the 1980s (Fig. 1). Mean mineral reserves did not differ between decades for either sex (Fig. 1).

Manitoba

Mean FBMs of females were 58.9 g lower in the 2000s than those in the 1980s (Fig. 1). Mean lipid reserves of females also were 27.8 g lower in the 2000s than in the 1980s (Fig. 1). Mineral reserves of females were, on average, 3.2 g lower in the 2000s than in the 1980s (Fig. 1). Mean protein reserves of males were 14.3 g lower in the 2000s than those in the 1980s ($P = 0.016$; Table 3).

Fig. 1. Least-square means ($g \pm SE$) of fresh body mass and lipid and mineral reserves for female and male lesser scaup collected at four locations (southern Louisiana [LA], Keokuk Pool, Illinois [KP], northwestern Minnesota [MN], and near Erickson, Manitoba [MB]) in the Mississippi Flyway during spring migration in decades of the 1980s (closed circles) and 2000s (open circles). Significant differences between decades at a given locations are indicated as **** = $P \leq 0.0001$, *** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$, ~ = $P \leq 0.1$ (MB only; see Methods), and ns = $P > 0.05$ (except MB, where ns = $P > 0.1$).

Fig. 1.



DISCUSSION

Louisiana

My results suggest that FBMs and lipids and mineral reserves were greater in the 2000s than those in the 1980s for both sexes; however, these results must be viewed with caution. The 1980s and 2000s collections in Louisiana were not made in the same sites or exact times of year, and such differences could affect FBMs and nutrient reserves of scaup. I detected a significant CD-by-location interaction in final models of FBMs and lipid reserves for both sexes (Tables 2 and 3), but interestingly CD was not related to FBMs or lipid-reserve levels in Louisiana. My findings, that CD was not a significant variable for Louisiana collections, suggest that FBMs and nutrient reserves of scaup do not change greatly during winter. Thus, my comparisons of FBMs and nutrient reserves by decade are confounded by potential differences in collection sites, but probably are not biased by differences in collection dates between decades.

Keokuk Pool

Keokuk Pool is one of the most important migration stopover areas for scaup in the lower-Midwest (Thompson 1973, Korschgen 1989, Havera 1999). However, in recent years scaup use at this location apparently has declined (Austin et al. 1998, Havera 1999). I suspect that this decline in use is an artifact of the continental population decline because, based on present condition of these birds, forage conditions at this location appear to be good.

The significant CD-by-location interactions in my final models, concerning FBMs and lipid reserves, fit the data very poorly at Keokuk Pool for both sexes. This poor fit inflated the standard errors around means of FBMs and lipid reserves at Keokuk Pool (Fig. 1) and thus decreased the precision of my tests. I believe this occurred because collection periods were too short in duration in the 2000s (Table 1) for CD to affect FBMs or lipid reserves at this location. However, this poor fit for the Keokuk Pool data makes my tests between decades very conservative at this location.

Despite decreased precision of these tests, I documented marked increases in FBMs and lipid reserves in the 2000s over the 1980s for both sexes. I suspect that these current increases in FBMs and lipid reserves are due to increases in availability and/or quality of forage at Keokuk Pool and perhaps at preceding stopover areas to the south. In Keokuk Pool, abundance of fingernail clams (*Musculium transversum*), a preferred scaup food (Thompson 1973, Afton et al. 1991), generally is positively correlated with the previous mean spring hydraulic discharge (Wilson et al. 1995). Accordingly, fingernail clam abundance probably was high in 2000 and 2001, given that mean spring hydraulic discharge has been relatively high since 1991 (LaTour et al. 2001). Additionally, zebra mussels (*Dreissena polymorpha*), another preferred scaup food (Wormington and Leach 1992, Mitchell and Carlson 1993, Hamilton et al. 1994, Custer and Custer 1996, Mazak et al. 1997), were first discovered in the upper Mississippi River in 1991

(Cope et al. 1997) and their abundance has increased markedly since 1995 (Sauer 2001).

Minnesota

I selected collection sites in Minnesota because of their historical importance as northern stopover areas for migrating scaup in spring and fall (Korschgen 1989, Afton et al. 1991, Austin et al. 1998, Pace and Afton 1999). Scaup color marked on my collection sites in fall returned the following spring, and were later seen in southwestern Manitoba (A. D. Afton, U.S. Geological Survey, unpublished data). Minnesota is not an important breeding area for scaup (Austin et al. 1998); however, wetlands in Minnesota are important spring-stopover areas for scaup based on aerial surveys of waterfowl breeding populations conducted annually during mid-May in Minnesota. Historically in delayed springs (e.g. 1979; Afton 1984), mid-May counts indicate that migrating scaup far outnumber other locally breeding waterfowl species in Minnesota (Maxson and Pace 1989).

Numbers of scaup using Thief Lake and Roseau River WMAs appeared lower in the 2000s than that in the 1980s (A. D. Afton, U.S. Geological Survey, personal observations). The observed decline in scaup use of these spring-stopover areas could reflect declines in the continental population or selection of habitats elsewhere where better forage conditions exist (Afton et al. 1991, Afton et al. 1991, Hanson and Butler 1994a, Lindeman and Clark 1999).

I observed the greatest declines in FBMs and lipid reserves of females between decades in Minnesota. Moreover, in the 2000s FBMs and lipid reserves

of females were lower in Minnesota than at other locations. If my collection sites and other areas through which scaup migrated had greatly different food resource levels, I would expect to find large variation in the FBMs and lipid-reserve levels of scaup collected in Minnesota because my collections probably represented scaup that had arrived recently as well as those that had been on the site for several days. However, I generally observed low levels and little variation in FBMs and lipid reserves of both sexes in Minnesota (Fig. 1), suggesting poor forage resources in northwestern Minnesota and at other preceding stopover areas.

Manitoba

My Manitoba collection location has received extensive study with regard to breeding ecology of scaup (Rogers 1959, 1964; Hammell 1973; Austin 1983; Afton 1984, 1985; Koons 2001). However, historical data concerning FBMs or nutrient-reserve levels upon arrival in spring are limited to 1 data set with small sample sizes (Table 1; Afton and Ankney 1991). Accordingly, I selected an *alpha* level of 0.10 to decrease the probability of a type II error because of low statistical power at this location (Zar 1996b, Anonymous 1995).

Koons (2001) reported that the local scaup population breeding near Erickson, Manitoba has declined for the period 1981-2000. Similarly, his estimated local population growth, using recent vital rates, also indicates a declining local population (Koons 2001). Because female scaup are highly philopatric to breeding areas (Anderson et al. 1992), the decline in this local population probably is not a

change in numbers of females using this area, but rather a local population decline driven by declines in recruitment (Afton and Anderson 2001, Koons 2001).

Average scaup eggs contain 6.8 g lipids and 4.1 g minerals (Afton and Ankney 1991). Based on these averages, my results indicate that female scaup presently arriving to breed in southwestern Manitoba had accumulated lipid reserves for 4.1 fewer eggs and mineral reserves for 1 fewer egg than had those arriving in the 1980s. These documented declines in lipid and mineral reserves of females probably are caused by factors operating on preceding spring migration stopover areas because I collected specimens soon after arrival in Manitoba.

The Importance of Northern Spring-Stopover Areas

Nutrient-reserve dynamics of waterfowl, especially diving ducks, during spring migration are poorly understood. A better understanding of areas in which scaup and other species accumulate nutrient reserves during spring migration, which are used later for breeding, is an important step toward understanding their breeding ecology as well as to focus habitat management on crucial spring-stopover areas.

Heitmeyer (1988) suggested that wintering and southern stopover areas were important for the accumulation of lipid reserves in mallards (*Anas platyrhynchos*). However, mallards on his collection sites likely were optimizing their lipid storage by consuming large quantities of acorns and crustaceans, which are a good source of high energy, compact storage fatty acids (Heitmeyer and

Fredrickson 1990). In contrast, Alisauskas (1988) demonstrated that lesser snow geese (*Chen caerulescens caerulescens*) accumulated most of their lipid reserves for breeding at northern spring-stopover areas. Similarly, Gauthier et al. (1992) reported that pre-breeding lipid accumulation in greater snow geese (*Chen caerulescens atlantica*) began after they departed from wintering areas.

Scaup migrating through Klamath Basin, California in spring had FBMs near mid-winter levels but still below those of scaup arriving on breeding areas (Gammonley and Heitmeyer 1990), suggesting the importance of more northern stopover areas for nutrient-reserve accumulation in this species. My results suggest that scaup do not accumulate significant amounts of reserves for breeding on wintering areas in Louisiana. Moreover, Chappell (1982) reported that scaup increased FBMs and lipid reserves at a northern stopover area in Quebec between early and late spring. Given high wing-loading effects due to relatively small body size of scaup in relation to other waterfowl and various adaptations in body shape and physiology for diving (Hedenstrom and Alerstam 1992, Lovvorn and Jones 1994), female scaup probably accumulate lipid reserves for breeding late in migration to minimize energetic costs of migration and body maintenance. However, I did not find that lipid reserves in the historical data increased greatly as they migrate north. Although, lipid-reserve levels in northern locations were greater in the 1980s than in the 2000s, I suspect in the 1980s they were not as great as true pre-decline values. Accordingly, I believe that northern spring-stopover areas, such as those in northwestern Minnesota, are crucial to migrating

scaup for accumulation of lipid reserves used for breeding. Moreover, scaup on northern spring-stopover areas, at least historically, consumed primarily amphipods (Afton et al. 1991), which are good sources of fatty acids that can be stored more compactly than are other fatty acids (Heitmeyer and Fredrickson 1990).

The Spring Condition Hypothesis

My results clearly are consistent with predictions of the SCH (Afton and Anderson 2001), given the documented declines in FBMs, lipids, and mineral reserves of females in Minnesota and Manitoba. Moreover, my results suggest that there has been a long-term decline in female body condition on northern spring-stopover areas, which affects female condition upon arrival on breeding areas in southwestern Manitoba.

Examination of FBMs and nutrient reserves of males between decades, although unimportant for the SCH, shows FBMs of males closely track those of females. Accordingly, the current decline in FBMs of males at Minnesota and Manitoba further supports the SCH, that present forage conditions are poorer than were those historically. However, unlike females, current lipid and mineral reserves of males did not decline from historic levels at Minnesota and Manitoba, suggesting that behavioral or physiological differences exist between sexes, with regard to lipid and mineral accumulation at these locations. A better understanding of mechanisms that affect the differential accumulation of lipids

between sexes is important for understanding nutrient-reserve dynamics of scaup during spring migration, and in turn, may provide a better understanding of the mechanisms of the decline in body condition.

Esler et al. (2001) reported that female scaup with non-developed ovaries had smaller lipid and protein reserves than did those that had initiated RFG, which is consistent with the hypothesis of a nutrient-reserve threshold that females must exceed before the initiation of RFG (Reynolds 1972). Accordingly, I predict that females arriving on breeding areas with smaller lipid and mineral reserves are unable to quickly exceed their nutrient-reserve threshold and thus may not breed at all, or have to spend more time on breeding areas feeding prior to laying eggs (*cf.* Afton and Anderson 2001). In corroboration, scaup breeding near Erickson, Manitoba initiated laying markedly later in 1999 and 2000 (Koons 2001) as compared to historical records (Afton 1984). Similarly, mean nest initiation date of scaup nesting near Yellow Knife, Northwest Territories was 19 and 21 June in 1999 and 2000, respectively, whereas peak initiation dates (back-calculated from brood observations) at that same location ranged from 7–13 June during 1967–1970 (Brook 2002). Because nest success and/or duckling survival generally are negatively correlated with nest initiation date among northern nesting waterfowl (Rohwer 1992, Flint and Grand 1996, Grand and Flint 1996, Dzus and Clark 1998, Guyn and Clark 1999) and clutch size of scaup declines seasonally (Afton 1984, Esler et al. 2001, Brook 2002), those females arriving on breeding areas in poor condition that do breed, probably nest later (Reynolds 1972, Esler et al. 2001) and

concomitantly produce fewer young. Moreover, some females arriving in poor condition may not be able to accumulate adequate reserves on breeding areas to attempt breeding.

As discussed earlier, FBMs and lipid reserves of migrating scaup likely are linked from one spring stopover area to the next. Considering the present poor body condition of scaup in northwestern Minnesota and southwestern Manitoba, any future decline in forage conditions at Keokuk Pool, as occurred from 1985 to 1991 (Wilson et al. 1995, Havera 1999), likely would have a catastrophic affect on body condition of scaup in Minnesota and in turn in Manitoba. Moreover, the decline in FBMs and lipid reserves in Minnesota is of special concern given the present good condition of scaup at Keokuk Pool.

My findings suggest that the most likely and parsimonious explanation for the observed decline in female body condition is reduced availability and/or quality of forage on northern spring-stopover areas beyond Keokuk Pool to northwestern Minnesota and perhaps extending further north into Manitoba. Possible factors affecting availability and/or quality of forage in semipermanent and permanent wetlands in the prairies and upper-Midwest include (1) loss of semipermanent and permanent wetlands, (2) a landscape-scale increase in numbers or foraging effectiveness of fish or other macroinvertebrate predators (e.g., salamanders), (3) an increase in anthropogenic sedimentation, (4) an increase in agricultural chemicals leached into wetlands (Neely and Baker 1989, Tome et al. 1995), (5) changes in water chemistry induced by acid rain (Baker and Christensen 1991,

Cook and Jager 1991), and (6) global climate change effects (e.g., winter kill frequency, snowfall patterns, and water depths; Poiani and Johnson 1991, Sweeney et al. 1992).

Migrating scaup rely on semipermanent and permanent wetlands during spring in the upper-Midwest (Korschgen 1989). Many of these wetlands have been lost through draining or accelerated sedimentation (Austin et al. 1998; Gleason and Euliss 1998a,b). In the prairie pothole region, anthropogenic influences (e.g., agriculture) accelerate wind and water facilitated erosion, and subsequently sedimentation into prairie wetlands (Martin and Hartman 1987; Dieter 1991; Gleason and Euliss 1998a,b). Such sedimentation can fill wetlands completely in one catastrophic event or gradually over time (Martin and Hartman 1987; Dieter 1991; Luo et al. 1997; Gleason and Euliss 1998a,b). Loss of wetland depth often leads to monotypic stands of cattail (*Typha spp.*; Gleason and Euliss 1998a,b), which provide little benefit to scaup (Murkin et al. 1997). Loss of wetland depth also may convert wetlands that were historically good scaup habitat to wetlands that favor species that prefer shallower water. Scaup typically forage in deeper open-water wetlands than do most other duck species (Murkin et al. 1997), which suggests that scaup would be one of the first waterfowl species noticeably affected by habitat degradation of this kind in the upper-Midwest.

Scaup consume macroinvertebrates almost exclusively in spring, and amphipods are their single most important food during spring and summer throughout the upper-Midwest (Rogers and Korschgen 1966, Swanson and Nelson

1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991).

Because amphipods and perhaps other scaup food densities affect scaup use of particular wetlands in spring (Afton and Hier 1991, Afton et al. 1991, Hanson and Butler 1994a, Lindeman and Clark 1999), I believe that a landscape-scale decline in amphipods and/or other scaup foods is required to cause declines in scaup body condition at one location during spring migration.

Recent natural invasions or introductions of minnows (including fathead minnows [*Pimephales promelas*]) and/or other aquaculture practices (i.e., rearing and stocking of walleyes and other game fish) in semipermanent and permanent wetlands of the upper-Midwest adversely affects the abundance of amphipods (Austin 1983; Hanson and Butler 1994a; Zimmer et al. 2000, 2001a) and other important scaup foods in this region (Hanson and Riggs 1995; Bouffard and Hanson 1997; Zimmer et al. 2000, 2001a). Fish directly affect the abundance and size of macroinvertebrate communities (including amphipods and other scaup foods) through predation (Held and Peterka 1974, Price et al. 1991, Bouffard and Hanson 1997, Duffy 1998, Wooster 1998, MacNeil et al. 1999). Indirectly, fish also cause dramatic changes in aquatic communities upon which macroinvertebrates depend (Hanson and Butler 1994b; Bouffard and Hanson 1997; Zimmer et al. 2001a,b). Recently, roadside ditches, culverts, and wetland drainage canals have increased connectivity of semipermanent and permanent wetlands, allowing fish to colonize traditionally fish-free wetlands, and thus potentially altering ecological

characteristics of prairie wetlands at a landscape scale (Zimmer et al. 2000, 2001a).

In addition to filling wetlands, anthropogenic sedimentation can affect both primary production and invertebrate communities in wetlands (Gleason and Euliss 1998a,b). Suspended sediment reduces the depth of the photic zone, which provides less light to macrophytes on or near the bottom of the wetland (Dieter 1991, Gleason and Euliss 1998b). Sediments can bury macrophytic photosynthetic substrates (Gleason and Euliss 1998b), and reduces stem densities (van der Valk et al. 1983). Excessive sediments prevent seed banks from germinating (Hartleb et al. 1993, Jurik et al. 1994, Wang et al. 1994) and prevent tubers from surviving to mature plants (Rybicki and Carter 1986). Sediments bury eggs and clog the filtering apparatuses of some aquatic invertebrates, and high levels of silt or clay are toxic to certain invertebrate taxa (reviewed by Gleason and Euliss 1998b). Sediments also cover decomposing organic matter and epibenthic algae (Gleason and Euliss 1998b) on which many scaup foods (e.g., amphipods, chironomids, and gastropods) forage (Swanson and Duebbert 1989, Brown 1991, Covich and Thorp 1991, Murkin and Ross 2000). Reductions in primary productivity cause declines in invertebrate productivity (Krull 1970, Euliss and Grodhaus 1987, Neill and Cornwell 1992, Schriver et al. 1995, Gleason and Euliss 1998b). Moreover, loss of vegetative structure in wetlands due to decreases in primary production also may make macroinvertebrates more susceptible to predation by fishes.

Other possible explanations and/or interacting factors affecting the observed decline in female body condition include (1) increases in human disturbances which may reduce foraging time or increase flight energy expenditures (Korschgen et al. 1985, Kahl 1991, and Knapton et al. 2000), (2) increased occurrences of disease, (3) increases in environmental contaminants, and (4) increased parasitism. Austin et al. (1998, 1999, 2000) and Afton and Anderson (2001) previously outlined concerns that excessive parasites and/or high contaminant levels may be affecting scaup populations. Increases in parasites, contaminant loads, or disease may affect the ability of females to accumulate nutrient reserves during spring migration. Consequently, these possibilities deserve future research efforts to determine the rate at which they occur and to test their affect on body condition of scaup.

In conclusion, I speculate that a landscape-scale decline in availability and/or quality of forage has caused the decline in body condition of scaup that migrate through the upper-Midwest in spring. Moreover, scaup arriving on other breeding areas also may be in poor condition if they are leaving northern spring-stopover areas in poor condition, as are those presently in Minnesota. If females nesting in the Boreal Forest are arriving in poor condition, delays in nest initiation should have a greater effect on recruitment there than for those arriving in the Prairie Parklands because in the Boreal Forest less time is available between arrival and egg laying to acquire nutrients for breeding (Austin et al. 1998, Afton

and Anderson 2001). Notably, Afton and Anderson (2001) reported that the steepest scaup population declines have occurred in the Boreal Forest Biome.

MANAGEMENT IMPLICATIONS

Consistent with the SCH, female scaup migrating through Minnesota and arriving to breed in Manitoba presently exhibit lower FBMs and have fewer lipid reserves than did females collected in the same locations historically. These results indicate that there has been a long-term decline in female body condition, which could significantly reduce reproductive success. These findings also suggest that there has been a landscape-scale decline in availability and/or quality of forage on northern spring-stopover areas in the upper-Midwest.

Despite the fact that specific factors affecting female body condition are not precisely known, I believe that providing important scaup foods (e.g., amphipods), especially at known spring-stopover areas, in the prairies and upper-Midwest should be a management priority. Moreover, I encourage further research to clarify the factors affecting and interacting with availability and quality of scaup foods in the upper-Midwest. I encourage future research to determine how widespread recent losses of semipermanent and permanent wetland habitats are through sedimentation in the prairies and upper-Midwest, and to develop management techniques to prevent this type of wetland degradation. Finally, I encourage further research to determine (1) the condition of female scaup migrating through other northern spring-stopover areas (e.g. North and South Dakota and other parts of Minnesota) and (2) whether scaup arriving on other breeding areas are as in poor condition as those presently in Manitoba.

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. 1985. Forced copulation as a reproductive strategy of male lesser scaup: a field test of some predictions. *Behaviour* 92:146-167.
- 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 Wildlife Agencies* 43:404-411.
- Afton, A. D., and R. H. Hier. 1987. Recovery rates and distribution of color-marked lesser scaup using stopover areas in northwest Minnesota. Minnesota Department of Natural Resources Wildlife Research Unit 1986-1987 Report:80-94.
- 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 Press, Minneapolis, Minnesota, USA.
- 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.
- Alisauskas, R. T. 1988. Nutrient reserves of lesser snow geese during winter and spring migration. Dissertation, University Western Ontario, London, Ontario, 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 Press, Minneapolis, Minnesota, USA.
- Alisauskas, R. T., and C. D. Ankney. 1994. Nutrition of breeding female ruddy ducks: the role of nutrient reserves. *Condor* 96:878-897.
- Anderson, M. G., J. M. Rhymer, and F. C. Rohwer. 1992. Philopatry, dispersal and genetic structure of waterfowl populations. Pages 365-395 *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 Press, Minneapolis, Minnesota, USA.
- Ankney, C. D., and A. D. Afton. 1988. Bioenergetics of breeding northern shovelers: diet, nutrient reserves, clutch size, and incubation. *Condor* 90:459-472.
- Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser Snow Geese. *Auk* 95:459-471.
- Anonymous. 1995. Journal News. *Journal of Wildlife Management* 59:196-198.
- Austin, J. E. 1983. Postbreeding ecology of female lesser scaup. Thesis, University of Missouri-Columbia, Columbia, Missouri, USA.
- 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. 1999. Declines of greater and lesser scaup populations: issues, hypotheses, and research directions. Summary Report for the Scaup Workshop. U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. Web-based report available online at <http://www.npwrc.usgs.gov/resource/2000/dscaup/dscaup.htm>
- 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., C. M. Custer, and A. D. Afton. 1998. Lesser scaup (*Aythya affinis*). The birds of North America, number 338. The American Ornithologists' Union, Washington, D. C., USA, and the Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

- Baker, J. P., and S. W. Christensen. 1991. Effects of acidification on biological communities in aquatic ecosystems. Pages 83-106 in D. F. Charles editor. Acidic deposition and aquatic ecosystems: regional case studies, Springer-Verlag, New York, New York, USA.
- Bouffard, S. H., and M. A. Hanson. 1997. Fish in waterfowl marshes: waterfowl manager's perspective. Wildlife Society Bulletin 25:146-157.
- Brook, R. W. 2002. Breeding ecology and local population dynamics of lesser scaup (*Aythya affinis*) in Boreal Forest of western Canada. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.
- Brown, K. M. 1991. Mollusca: gastropoda. Pages 285-314 in J. H. Thorp and A. P. Covich editors. Ecology and classifications of North American freshwater invertebrates. Academic Press, San Diego, California, USA.
- Carney, S. M. 1992. Species, age and sex identification of ducks using wing plumage. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C, 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.
- Cook, R. B., and H. I. Jager. 1991. Upper Midwest. Pages 421-466 in D. F. Charles editor. Acidic deposition and aquatic ecosystems: regional case studies, Springer-Verlag, New York, New York, USA.
- Cope, W. G., M. R. Bartsch, and R. R. Hayden. 1997. Longitudinal patterns in abundance of the zebra mussel (*Dreissena polymorpha*) in the Upper Mississippi River. Journal of Freshwater Ecology 12:235-238.
- Covich, A. P., and J. H. Thorp. 1991. Crustacea: introduction and peracarida. Pages 665-689 in J. H. Thorp and A. P. Covich editors. Ecology and classifications of North American freshwater invertebrates. Academic Press, San Diego, California, USA.
- Custer, C. M., and T. W. Custer. 1996. Food habits of diving ducks in the Great Lakes after the zebra mussel invasion. Journal of Field Ornithology 67:86-99.
- Dieter, C. D. 1991. Water turbidity in tilled and untilled prairie wetlands. Journal of Freshwater Ecology 6:185-189.

- Dubovsky, J. A., C. T. Moore, J. P. Bladen, G. W. Smith, and P. D. Keywood. 2001. Trends in duck breeding populations, 1959-2001. U.S. Department of the Interior, Fish and Wildlife Service, Administrative Report, Laurel, MD, USA.
- Duffy, W. G. 1998. Population dynamics, production, and prey consumption of fathead minnows (*Pimephales promelas*) in prairie wetlands: a bioenergetics approach. *Canadian Journal of Fisheries and Aquatic Sciences* 54:15-27.
- Dzus, E. H., and R. G. Clark. 1998. Brood survival and recruitment of mallards in relation to wetland density and hatching date. *Auk* 115:311-318.
- Esler, D., J. B. Grand, and A. D. Afton. 2001. Intraspecific variation in nutrient reserve use during clutch formation by lesser scaup. *Condor* 130:810-820.
- Euliss, N. H. Jr., and G. Grodhaus. 1987. Management of midges and other invertebrates for waterfowl wintering in California. *California Fish and Game* 73:238-243.
- Flint, P. L., and J. B. Grand. 1996. Nesting success of northern pintails on the coastal Yukon-Kuskokwim Delta, Alaska. *Condor* 98:54-60.
- Gammonley, J. H., and M. E. Heitmeyer. 1990. Behavior, body condition, and foods of buffleheads and lesser scaups during spring migration through the Klamath Basin, California. *Wilson Bulletin* 102:672-683.
- Gauthier, G., J.-F. Giroux, and J. Bedard. 1992. Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. *Canadian Journal of Zoology* 70:2077-2087.
- Gleason, R. A., and N. H. Euliss Jr. 1998a. Sedimentation of prairie pothole wetlands: the need for integrated research by agricultural and wildlife interests. J. Schaack, and S. S. Anderson editors. *Water for Agriculture and Wildlife and the Environment Win-Win Opportunities. Proceedings of the U.S. Committee of Irrigation and Drainage*, Bismarck, North Dakota, USA. Web-based report available online at <http://www.npwrc.usgs.gov/resource/1998/sediment/sediment.htm>
- Gleason, R. A., and N. H. Euliss Jr. 1998b. Sedimentation of prairie wetlands. *Great Plains Research* 8:97-112. Web-based report available online at <http://www.npwrc.usgs.gov/resource/1998/pprwtlnd/pprwtlnd.htm>

- Grand, J. B., and P. L. Flint. 1996. Survival of northern pintail ducklings on the Yukon-Kuskokwim Delta, Alaska. *Condor* 98:48-53.
- Guyn, K. L., and R. G. Clark. 1999. Factors affecting survival of northern pintail ducklings in Alberta. *Condor* 101:369-377.
- Hamilton, D. J., C. D. Ankney, and R. C. Bailey. Predation of zebra mussels by diving ducks: an exclosure study. *Ecology* 75:521-531.
- Hammell, G. S. 1973. The ecology of the lesser scaup (*Aythya affinis eyton*) in southwestern Manitoba. Thesis, University of Guelph, Guelph, Ontario, Canada.
- Hanson, M. A., and M. G. Butler. 1994a. Response of food web manipulation in a shallow waterfowl lake. *Hydrobiologia* 279/280:457-466.
- Hanson, M. A., and M. G. Butler. 1994b. Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1180-1188.
- Hanson, M. A., and M. R. Riggs. 1995. Potential effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. *Wetlands* 15:167-175.
- Hartleb, C. F., J. D. Madsen, and C. W. Boylen. 1993. Environmental factors affecting seed germination in *Myriophyllum spicatum* L. *Aquatic Botany* 45:15-25.
- Havera, S. P. 1999. Waterfowl of Illinois: status and management. Illinois Natural History Survey, Special Publication 21.
- Heitmeyer, M. E. 1988. Body composition of female mallards in winter in relation to annual cycle events. *Condor* 90:669-680.
- Heitmeyer, M. E., and L. H. Fredrickson. 1990. Fatty acid composition of wintering female mallards in relation to nutrient use. *Journal of Wildlife Management* 54:54-61.
- Held, J. W., and J. J. Peterka. 1974. Age, growth, and food habits of the fathead minnow, *Pimephales promelas*, in North Dakota saline lakes. *Transactions of the American Fisheries Society* 4:743-756.
- Hedenstrom, A., and T. Alerstam. 1992. Climbing performance of migrating birds

- as a basis for estimating limits for fuel-carrying capacity and muscle work. *Journal of Experimental Biology* 164:19-38.
- Hochbaum, H. A. 1942. Sex and age determination in waterfowl by cloacal examination. *Transactions of the North American Wildlife Conference* 7:299-307.
- Jurik, T. W., S. -C. Wang, and A. G. van der Valk. 1994. Effects of sediment on seedling emergence from wetland seed banks. *Wetlands* 14:159-165.
- Kahl, R. 1991. Boating disturbance of canvasbacks during migration at Lake Poygan, Wisconsin. *Wildlife Society Bulletin* 19:242-249.
- Koons, D. N. 2001. Lesser scaup breeding ecology in the Canadian parklands. Thesis, Montana State University, Bozeman, Montana, 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.
- Korschgen, C. E. 1989. Riverine and deepwater habitats for diving ducks. Pages 157-180 *in* L. M. Smith, R. L. Pederson, and R. M. Kaminski editors. *Habitat management for migrating and wintering waterfowl in North America*. Texas Tech University Press, Lubbock, Texas, USA.
- Korschgen, C. E., L. S. George, and W. L. Green. 1985. Disturbance of diving ducks by boaters on a migrational staging area. *Wildlife Society Bulletin* 13:290-296.
- Kortright, F. H. 1967. Ducks geese and swans of North America. Stackpole, Harrisburg, PA, and Wildlife Management Institute, Washington D. C.
- Krapu, G. L., and K. J. Reinecke. 1992. Foraging ecology and nutrition. Pages 1-29 *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 Press, Minneapolis, USA.
- Krull, J. H. 1970. Aquatic plant-macroinvertebrate associations and waterfowl. *Journal of Wildlife Management* 34:707-718.
- LaTour, J. K., J. M. Gioja, J. C. Maurer, and T. L. Wicker. 2001. Water resources data, Illinois, water year 2000. U.S. Geological Survey Water-Data Annual Report IL-00. Web-based report available online at

http://il.water.usgs.gov/annrep_2001/start.htm.

- Lindeman, D. H., and R. G. Clark. 1999. Amphipods, land-use impacts, and lesser scaup (*Aythya affinis*) distribution in Saskatchewan wetlands. *Wetlands* 19:627-638.
- Lovvorn, J. R., and D. R. Jones. Biomechanical conflicts between adaptations for diving and aerial flight in estuarine birds. *Estuaries* 17:62-75.
- Luo, H. -R., L. M. Smith, B. L. Allen, and D. A. Haukos. 1997. Effects of sedimentation on playa wetland volume. *Ecological Applications* 7:247-252.
- MacNeil, C., J. T. A. Dick, and R. W. Elwood. 1999. The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). *Biological Reviews of the Cambridge Philosophical Society* 74:375-395.
- Martin, D. B., and W. A. Hartman. 1987. The effect of cultivation on sediment composition and deposition in prairie pothole wetlands. *Water, Air, and Soil Pollution* 34:45-53.
- Maxson, S. J., and R. M. Pace III. 1989. Summary and evaluation of Minnesota's waterfowl breeding population survey, 1972-1986. Minnesota Department of Natural Resources, Wildlife Report 7, St. Paul, Minnesota, USA.
- Mazak, E. J., H. J. MacIsaac, M. R. Servos, and R. Hesslein. 1997. Influence of feeding habits on organochlorine contaminant accumulation in waterfowl on the Great Lakes. *Ecological Applications* 7:1133-1143.
- Mitchell, C. A., and J. Carlson. 1993. Lesser scaup forage on zebra mussels at Cook Nuclear Plant, Michigan. *Journal of Field Ornithology* 64:219-222.
- Murkin, H. R., E. J. Murkin, and J. P. Ball. 1997. Avian habitat selection and prairie wetland dynamics: a 10-year experiment. *Ecological Applications* 7:1144-1159.
- Murkin, H. R., and L. C. M. Ross. 2000. Invertebrates in prairie wetlands. Pages 201-248 in H. R. Murkin, A. G. van der Valk, and W. R. Clark editors. *Prairie wetland ecology: the contribution of the Marsh Ecology Research Program*. Iowa State University Press, Ames, IA.
- Neely, R. K., and J. L. Baker. 1989. Nitrogen and phosphorus dynamics and the

fate of agricultural runoff. Pages 92-131 in A. G. van der Valk editor. Northern prairie wetlands. Iowa State University Press, Ames, Iowa, USA.

Neil, C., and J. C. Cornwell. 1992. Stable carbon, nitrogen, and sulfur isotopes in a prairie marsh food web. *Wetlands* 12:217-224.

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.

Parker, J. M., K. R. Hennings, and J. L. Hansen. 1980. Thief Lake Wildlife Management Area master plan, 1980-1989. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA.

Poiani, K. A., and W. C. Johnson. 1991. Global warming and prairie wetlands: potential consequences for waterfowl management. *BioScience* 41:611-618.

Price, C. J., W. M. Tonn, and C. A. Paszkowski. 1991. Intraspecific patterns of resource use by fathead minnows in a small boreal lake. *Canadian Journal of Zoology* 69:2109-2115.

Reynolds, C. M. 1972. Mute swan weights in relation to breeding. *Wildfowl* 23:111-118.

Rogers, J. P. 1959. Low water and lesser scaup reproduction near Erickson, Manitoba. *Transactions of the North American Wildlife Conference* 24:216-224.

Rogers, J. P. 1964. Effect of drought on reproduction of lesser scaup. *Journal of Wildlife Management* 28:213-222.

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.

Rohwer, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pages 486-539 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 Press, Minneapolis, Minnesota, USA.

Rybicki, N. B., and V. Carter. 1986. Effects of sediment depth and sediment type

on the survival of *Vallisneria americana* michx grown from tubers.
Aquatic Botany 24:233-240.

Ryder, J. P. 1970. A possible factor in the evolution of clutch size in Ross' goose.
Wilson Bulletin 82:5-13.

SAS Institute. 1993. SAS/STAT user's guide, version 6, fourth edition. SAS
Institute, Cary, NC, USA.

Sauer, J. 2001. Macroinvertebrate sampling in six reaches of the Upper
Mississippi River System, 2000. U.S. Geological Survey, Upper
Midwest Environmental Sciences Center, La Crosse, Wisconsin. Long
Term River Monitoring Plan. Web-based report available online at
http://www.umesc.usgs.gov/reports_publications/ltrmp/macro.html.

Schriver, P., J. Bogestrand, E. Jeppesen, and M. Sondergaard. 1995. Impact of
submerged macrophytes on fish-zooplankton-phytoplankton
interactions: large-scale enclosure experiments in a shallow eutrophic
lake. Freshwater Biology 33:255-270.

Swanson, G. A., and H. F. Duebbert. 1989. Wetland habitats of waterfowl in the
prairie pothole region. Pages 228-267 in A. G. van der Valk editor.
Northern prairie wetlands. Iowa State University Press, Ames, Iowa,
USA.

Swanson, G. A., and H. Nelson. 1970. Potential influence of fish rearing
programs on waterfowl breeding habitat. Pages 65-71 in E.
Schneberger editor. Symposium on the management of midwestern
winterkill lakes. North Central Division of the American Fisheries
Society, Winnipeg, Manitoba, Canada.

Sweeney, B. W., J. K. Jackson, J. D. Newbold, and D. H. Funk. 1992. Climate
change and the life histories and biogeography of aquatic insects in
eastern North America. Pages 143-176 in P. Firth and S. G. Fisher
editors. Global climate change and freshwater ecosystems, Springer-
Verlag, New York, New York, USA.

Thompson, D. 1973. Feeding ecology of diving ducks on Keokuk Pool,
Mississippi River. Journal of Wildlife Management 37:382-389.

Tome, M. W., C. E. Grue, and M. G. Henry. 1995. Case studies: effects of
agricultural pesticides on waterfowl and prairie pothole wetlands.
Pages 565-576 in D. J. Hoffman, B. A. Rattner, G. A. Burton Jr., and J.

Cairns Jr. editors. Handbook of ecotoxicology. Lewis Publishers, CRC Press, Boca Raton, Florida, USA.

- Trauger, D. L. 1974. Eye color of female lesser scaup in relation to age. *Auk* 91:243-254.
- van der Valk, A. G., S. T. Swanson, and R. F. Nuss. 1983. The response of plant species to burial in three types of Alaskan wetlands. *Canadian Journal of Botany* 61:1150-1164.
- Wang, S. -C., T. W. Jurik, and A. G. van der Valk. 1994. Effects of sediment load on various stages in the life and death of cattail (*Typha x glauca*). *Wetlands* 14:166-173.
- Wilson, D. M., T. J. Naimo, J. G. Wiener, R. V. Anderson, M. B. Sandheirich, and R. E. Sparks. 1995. Declining populations of fingernail clam *Musculium transversum* in the upper Mississippi River. *Hydrobiologia* 304:209-220.
- Wooster, D. E. 1998. Amphipod (*Gammarus minus*) responses to predators and predator impact on amphipod density. *Oecologia* 115:253-259.
- Wormington, A., and J. H. Leach. 1992. Concentrations of migrant diving ducks at Point Pelee National Park, Ontario, in response to invasions of zebra mussels, *Dreissena polymorpha*. *Canadian Field-Naturalist* 106:376-380.
- Zar, J. H. 1996a. Selection of independent variables. Pages 423-427 in S. L. Snaveley editor. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- Zar, J. H. 1996b. Introduction to statistical hypothesis testing. Pages 79-86 in S. L. Snaveley editor. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries and Aquatic Sciences* 57:76-85.

- Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2001a. Effects of fathead minnow colonization and removal on a prairie wetland ecosystem. *Ecosystems* 4:346-357.
- Zimmer, K. D., M. A. Hanson, M. G. Butler, and W. G. Duffy. 2001b. Influences of fathead minnows and aquatic macrophytes on nutrient partitioning and ecosystem structure in two prairie wetlands. *Archiv Fur Hydrobiologie* 150:411-433.

VITA

Michael J. Anteau was born in 1975 in Denver, Colorado; he moved to Anchorage, Alaska in 1976. Growing up in Alaska, with moose and ducks literally in his back yard, Michael learned to appreciate nature, the outdoors, and wildlife. Michael has had a long interest with waterfowl that dates back to his early childhood. His father Thomas J. Anteau, a Michigan native, helped instill a special fondness for lesser scaup in Michael at a young age.

Michael graduated from University of Alaska Fairbanks in 1997 with two Bachelor of Science degrees (Wildlife Biology and Biological Sciences). At the University of Alaska Fairbanks, Michael studied under Dr. James S. Sedinger as well as worked for him on the Yukon-Kuskakwim Delta studying the breeding ecology of black brant. After graduating from University of Alaska Fairbanks, Michael set off to see the rest of North America. He worked as an environmental consultant in New Mexico, studied songbird breeding distributions on the north rim of the Grand Canyon, worked on a mourning dove telemetry study in South Carolina, studied the wintering ecology of black brant in Baja California, Mexico, and worked on a mottled duck breeding study in Cameron Parish, Louisiana.

Michael's long-term interest in lesser scaup took him to Louisiana State University to study under Dr. Alan D. Afton, where he became a Master of Science student in August of 1999. Michael now intends to remain at Louisiana State University to continue his research in a doctoral program studying aspects of lesser scaup spring ecology that relate to their present population decline.