

Diet shifts of lesser scaup are consistent with the spring condition hypothesis

Michael J. Anteau and Alan D. Afton

Abstract: We compared diets of lesser scaup (*Aythya affinis* (Eyton, 1838)) in the springs of 2000 and 2001 to those reported in the 1970s and the 1980s to determine whether forage quality has declined as predicted by the spring condition hypothesis. In Minnesota, we found that the current aggregate percentage of Amphipoda (an important food item) in lesser scaup diets was 94% lower than that reported from the same locations in the 1980s. Current mean individual prey mass of Amphipoda and Bivalvia in Minnesota were 86.6% and 85.1% lower than historical levels, respectively. In Manitoba, current aggregate percentages of Trichoptera and Chaoboridae in lesser scaup diets (1% and 0%, respectively) were lower than those reported from the same location in the 1970s (14% and 2%, respectively), whereas the percentage of Chironomidae (40%) was higher than that of historical levels (19%). Current mean individual prey mass of all insects, seeds, Chironomidae, and Zygoptera in Manitoba were 63.5%, 65.4%, 44.1%, and 44.9% lower than those of historical levels, respectively. The observed dietary shift from Amphipoda to less nutritious prey in Minnesota, coupled with lower mean individual prey mass in both locations, likely constitutes lower forage quality in lesser scaup diets, which is consistent with the spring condition hypothesis.

Résumé : Nous comparons le régime alimentaire du petit fuligule (*Aythya affinis* (Eyton, 1838), désigné ci-dessous le fuligule) aux printemps de 2000 et de 2001 à ceux rapportés dans les années 1970 et 1980 pour déterminer si la qualité de l'alimentation s'est détériorée comme le prédit l'hypothèse des conditions printanières. Au Minnesota, le pourcentage combiné actuel d'Amphipoda (un aliment important) dans le régime des fuligules est de 94 % inférieur aux valeurs signalées dans les mêmes sites dans les années 1980. Les masses moyennes individuelles courantes des proies, Amphipoda et Bivalvia, au Minnesota sont respectivement 86,6 % et 85,1 % inférieures à celles du passé. Au Manitoba, les pourcentages totaux actuels de Trichoptera et de Chaoboridae dans les régimes des fuligules (respectivement 1 % et 0 %) sont plus bas que ceux rapportés au même site dans les années 1970 (respectivement 14 % et 2 %); en revanche, le pourcentage de Chironomidae (40 %) est plus élevé que les valeurs du passé (19 %). Les masses moyennes individuelles courantes des proies sont plus basses que par le passé au Manitoba, pour ce qui est des insectes totaux (de 63,5 %), des graines (de 65,4 %), des Chironomidae (44,1 %) et des Zygoptera (44,9 %). Le remplacement des Amphipoda dans l'alimentation par des proies moins nutritives, combiné à la masse moyenne individuelle réduite des proies, fournit vraisemblablement une qualité de nourriture moindre dans le régime des fuligules, ce qui est compatible avec l'hypothèse des conditions printanières.

[Traduit par la Rédaction]

Introduction

The North American scaup population (lesser scaup, *Aythya affinis* (Eyton, 1838), and greater scaup, *Aythya marila* (L., 1761), combined) has declined markedly during the past 25 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 were lowest on record in 2005 (Wilkins et al. 2005). Afton and Anderson (2001) reported that the decline in the continental scaup population likely is driven by a decline in the lesser scaup population. Recruitment of lesser scaup apparently has declined since 1978, and female survival rates have declined relative to

that of males (Afton and Anderson 2001). The segment of the continental scaup population that winters in states bordering the Gulf of Mexico and that migrates along the Mississippi River valley and through Minnesota comprises a major component (40%) of the continental population and is the segment that is experiencing the largest decline (Afton and Anderson 2001).

Nutrient reserves acquired during spring migration likely are important determinants of survival and reproductive success in lesser scaup (Afton 1984; Afton and Ankney 1991; Pace and Afton 1999; Anteau 2002; Anteau and Afton 2004). Austin et al. (1999; 2000) and Afton and Anderson (2001) outlined several hypotheses explaining the scaup population decline, one of which was the spring condition hypothesis.

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M.J. Anteau.^{1,2} School of Renewable Natural Resources, Louisiana State University, Baton Rouge, LA 70803, USA.

A.D. Afton. US Geological Survey (USGS), Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge, LA 70803, USA.

¹Present address: USGS Northern Prairie Wildlife Research Center, 8711 37th Street SE, Jamestown, ND 58401, USA.

²Corresponding author (e-mail: MAnteau@usgs.gov).

The spring condition hypothesis states that reproductive success of lesser scaup (hereafter scaup) has declined because females are arriving at breeding areas with fewer lipid reserves than in the past, owing to a decline in availability and (or) quality of food resources (Afton and Anderson 2001). Female scaup migrating through northwestern Minnesota and arriving to breed in southwestern Manitoba had lower lipid reserves in 2000 and 2001 than did those in earlier decades (Anteau 2002; Anteau and Afton 2004). Two untested predictions of the spring condition hypothesis are that forage availability and (or) quality on northern stopover areas have declined. Investigations of scaup food resources on northern spring stopover areas are needed because forage quality (nutritional value of prey) or availability (abundance of prey) could have large effects on female lipid reserves and concomitant reproductive success (Afton and Ankney 1991; Anteau 2002; Austin et al. 2002; Anteau and Afton 2004).

Historically, scaup consumed macroinvertebrates almost exclusively in spring, and Amphipoda were their single most consumed food during spring and summer in a variety of studies conducted throughout the Prairie Pothole Region (Rogers and Korschgen 1966; Bartonek and Hickey 1969; Swanson and Nelson 1970; Swanson and Duebbert 1989; Afton and Hier 1991; Afton et al. 1991). Scaup use of individual wetlands is positively correlated with Amphipoda densities during spring migration in the upper Midwest and breeding in prairie Canada (Lindeman and Clark 1999; Strand 2005; Anteau 2006). Accordingly, we assume that Amphipoda are an important food for scaup during spring migration in the upper Midwest and any decrease of Amphipoda in scaup diets would indicate a decrease in forage quality.

We tested a prediction of the spring condition hypothesis by comparing current and historical diets. Specifically, we compared (*i*) diets (mean aggregate percent dry mass of taxon) and mean individual prey mass (mean mass of individual taxon) of scaup at two important spring stopover sites in northwestern Minnesota in 2000 and 2001 to data from the same sites in 1986–1988 (Afton et al. 1991; hereafter 1980s), and (*ii*) diets and mean individual prey mass of scaup upon arrival at a southwestern Manitoba breeding area in 2000 and 2001 to data from the same site in 1977–1980 (Afton and Hier 1991; hereafter 1970s).

Materials and methods

Study areas

In springs of 2000 and 2001, we collected diet data in (*i*) northwestern Minnesota at Thief Lake and Roseau River Wildlife Management Areas and (*ii*) southwestern Manitoba, on a Prairie Parkland breeding area west of Erickson, 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), Parker et al. (1980), and Hohman (1985).

Collection of specimens

We collected scaup randomly with a shotgun, without decoys to avoid associated biases (Pace and Afton 1999); furthermore, collections were conducted using the same pro-

cedures as in Afton et al. (1991). We generally collected scaup that were actively feeding; however, this was not always possible and a few scaup were collected without being observed prior to collection (Afton et al. 1991). Afton and Hier (1991) only collected actively feeding scaup, whereas collections by Afton et al. (1991) were similar to ours. In northwestern Minnesota, we timed collections to coincide with the middle of migration, when relatively large numbers of migrating scaup were present. In southwestern Manitoba, we timed collections to begin when resident scaup (scaup attempting to breed locally) first arrived and began using small ponds and concluded before the start of rapid follicle growth in females. We further limited collections to isolated pairs on smaller ponds, which ensured a sample of resident breeding scaup (Anteau and Afton 2004).

Specimen preparation

Immediately after collection, we preserved esophageal and proventricular contents by slowly injecting a 10% buffered formaldehyde solution down the esophagus with a syringe. Specimens then were labeled, placed in double plastic bags, frozen, and transported to the laboratory for dissections. Our procedures varied slightly from historical studies, in which esophageal and proventricular samples were removed and preserved prior to carcasses being frozen (Afton and Hier 1991; Afton et al. 1991).

In the laboratory, we thawed specimens and removed all food from the upper digestive tract (esophagus and proventriculus) and sorted it exactly as described in Afton and Hier (1991) and Afton et al. (1991). We weighed (± 0.0001 g) sorted diet samples after being dried to a constant mass. For subsequent analyses, we grouped prey items into taxonomic groups (response variables) as in Afton and Hier (1991) and Afton et al. (1991); data were summarized by percent occurrence and aggregate percent dry mass (Swanson et al. 1974; Afton and Hier 1991; Afton et al. 1991). We calculated mean individual prey mass for each food taxon within each scaup by dividing the total mass of each taxon by the count of individual prey items in that taxon.

Statistical analyses

We pooled samples collected in 2000 and 2001 into the 2000s decade and samples collected in 1977–1980 (Afton and Hier 1991) and 1986–1988 (Afton et al. 1991) into the 1970s and 1980s decades, respectively; samples sizes were inadequate to test for annual variation in diets. We also pooled samples collected at Thief Lake and Roseau River Wildlife Management Areas as in Afton et al. (1991); similar proportions of specimens were collected from each of these sites in both decades. Finally, we pooled all samples over sex because current and historical diets were similar between sexes in northwestern Minnesota and southwestern Manitoba (Afton et al. 1991; Afton and Hier 1991; multivariate analyses of variances (MANOVAs) of 2000s data: $F_{[7,14]} = 0.58$, $P = 0.764$; $F_{[7,53]} = 0.87$, $P = 0.535$, respectively).

Aggregate percent dry mass

We compared aggregate percent dry mass of prey items between decades separately for Minnesota (1980s vs. 2000s) and Manitoba (1970s vs. 2000s) using MANOVA (PROC

Table 1. Aggregate percent dry mass and percent occurrence (in parentheses) of taxa consumed by lesser scaup (*Aythya affinis*) during spring migration in northwestern Minnesota in decades of the 1980s ($n = 57$) and 2000s ($n = 22$).

Taxa	1980s*	2000s†
Amphipoda (species of <i>Gammarus</i> Fabricius, 1775 and <i>Hyaella</i> Smith, 1874; scuds)‡	33.2 (51)	2.1 (32)
Bivalvia (clams and mussels)‡	6.0 (19)	26.3 (55)
<i>Musculium</i> spp. (fingernail clams)	6.0 (19)	21.4 (55)
Sphaeriidae (non <i>Musculium</i> spp.; freshwater clams)	0 (0)	4.9 (23)
Insecta‡	16.0 (63)	24.1 (91)
Chaoboridae (phantom midges)	0 (0)	2.8 (5)
Chironomidae (midges)	2.3 (23)	12.5 (59)
Coleoptera (water beetles)	1.9 (11)	0.1 (5)
Corixidae (water boatmen)	1.5 (14)	TR§ (9)
Odonata	1.5 (7)	2.4 (5)
Anisoptera (dragonflies)	0.3 (4)	2.4 (5)
Zygoptera (damselflies)	1.2 (4)	0 (0)
Trichoptera (caddisflies)	8.8 (35)	6.2 (41)
Gastropoda‡	32.0 (53)	23.1 (59)
Hydrobiidae (spire snails)	4.0 (7)	8.1 (50)
Lymnaeidae (pond snails)	2.7 (14)	0 (0)
Physidae (pouch snails)	0.4 (4)	0.5 (9)
Planorbidae (orb snails)	11.1 (26)	10.6 (36)
Valvatidae (round-mouthed snails)	11.0 (21)	3.9 (45)
Viviparidae (snails)	1.0 (4)	0 (0)
Hirudinea (leeches)‡	1.3 (11)	6.2 (45)
Fish and fish parts (<i>Culaea inconstans</i> (Kirtland, 1840))	3.5 (12)	0 (0)
Seeds‡	6.0 (40)	6.8 (73)
Vegetation‡	2.2 (26)	1.3 (23)
Invertebrate egg masses	0 (0)	6.8 (14)
Unidentified fragments	1.8 (5)	3.0 (9)

*Collections conducted from 1986 to 1988 (Afton et al. 1991).

†Collections conducted in 2000 and 2001.

‡Response variable for overall MANOVA when testing for decadal effects.

§Trace amounts (<0.1 g).

GLM; SAS Institute Inc. 2002). The response (dependent) variables were Amphipoda, Bivalvia, Insecta, Gastropoda, Hirudinea, seeds, and vegetation (Tables 1, 2). We also compared aggregate percent dry mass of Insecta subtaxa (with >1% aggregate percent dry mass in either decade) in scaup diets between decades (1970s vs. 2000s) in Manitoba using MANOVA because these subtaxa were a diverse and large part of scaup diets in Manitoba (Table 2). The response variables were Chaoboridae, Chironomidae, Corixidae, Anisoptera, Zygoptera, and Trichoptera. For significant MANOVAs, we conducted an a priori test for a decadal effect on Amphipoda (except insect model); we then conducted a posteriori tests of other response variables using the pdiff option of the least-squares means statement on the decade effect (PROC GLM; SAS Institute Inc. 2002).

Mean individual prey mass

We compared mean individual prey mass between decades separately for Minnesota (1980s vs. 2000s) and Manitoba (1970s vs. 2000s) using separate analyses of variances (ANOVAs; PROC GLM; SAS Institute Inc. 2002) for each response variable (Tables 1, 2). We could not use a MANOVA because not all response variables were represented in each individual diet sample. Vegetation was excluded from these analyses because we assumed that sizes of vegetation fragments varied randomly. We conducted decadal

tests of mean individual prey mass on Chironomidae and Zygoptera in Manitoba, but small sample sizes ($n \leq 15$ for both decades) precluded us from conducting decadal tests for other Insecta subtaxa.

Results

Northwestern Minnesota

Overall, mean aggregate percentages of taxa in scaup diets differed between decades ($F_{[7,71]} = 4.0$, $P < 0.001$). Mean aggregate percentage of Amphipoda in the 2000s (2%; hereafter current) was 94% lower than that in the 1980s (33%; hereafter historical); conversely, current mean aggregate percentage of Bivalvia (26%) was 77% higher than that of historical levels (6%; Fig. 1). Percent occurrence of Amphipoda in current diets was 19% lower than that in historical diets (51%); however, 32% of current scaup diets contained Amphipoda despite their low aggregate percentage (Table 1). Aggregate percentage of Chironomidae in current diets (12.5%, SE = 3.7%) was 82% higher ($R^2 = 0.07$, $F_{[1,77]} = 5.48$, $P = 0.022$) than that in historical diets (2.3%, SE = 2.3%).

The current mean individual prey mass of Amphipoda (1.22 mg, SE = 1.64 mg) was 87% ($R^2 = 0.35$, $F_{[1,34]} = 18.59$, $P < 0.001$) lower than the historical mean prey mass (9.10 mg, SE = 0.81 mg). The current mean indivi-

Table 2. Aggregate percent dry mass and percent occurrence (in parentheses) of taxa consumed by lesser scaup soon after arrival at a breeding area in southeastern Manitoba in decades of the 1970s ($n = 21$) and 2000s ($n = 61$).

Taxa	1970s*	2000s†
Amphipoda (<i>Gammarus</i> spp. and <i>Hyalella</i> spp.; scuds)‡	29.0 (48)	34.8 (51)
Bivalvia (<i>Musculium</i> spp.; fingernail clams)‡	0 (0)	0.9 (5)
Insecta‡	50.3 (81)	44.5 (75)
Chaoboridae (phantom midges)§	1.7 (10)	TR (2)
Chironomidae (midges)§	18.8 (38)	40.3 (66)
Coleoptera (water beetles)	0.6 (29)	0.2 (10)
Corixidae (water boatmen)§	4.9 (19)	0.2 (8)
Ephemeroptera (mayflies)	0.5 (10)	TR (2)
Odonata	9.6 (29)	3.0 (23)
Anisoptera (dragonflies)§	3.9 (5)	0 (0)
Zygoptera (damselflies)§	5.7 (29)	3.0 (23)
Tabanidae (horse flies)	0.1 (5)	0 (0)
Trichoptera (caddisflies)§	14.1 (43)	0.8 (10)
Gastropoda‡	0.3 (5)	4.7 (20)
Hirudinea (leeches)‡	17.4 (43)	8.6 (31)
Seeds‡	2.8 (33)	4.5 (46)
Vegetation‡	0.3 (5)	1.2 (23)
Unidentified fragments	0 (0)	0.9 (7)

*Collections conducted from 1977 to 1980 (Afton and Hier 1991; pre-rapid follicle growth).

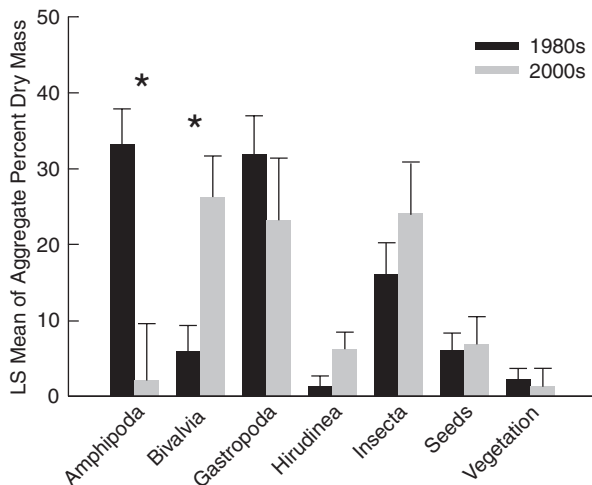
†Collections conducted in 2000 and 2001.

‡Response variable for overall MANOVA testing for decadal effects.

§Response variable for insect MANOVA testing for decadal effects.

^{||}Trace amounts (<0.1 g).

Fig. 1. Least-square means (\pm SE) from MANOVA testing for decadal effects (1986–1988 versus 2000 and 2001) on foods (aggregate percent dry mass) consumed by lesser scaup in northwestern Minnesota during spring migration. Asterisks above bar groups indicate significant differences ($\alpha = 0.05$) between decades.

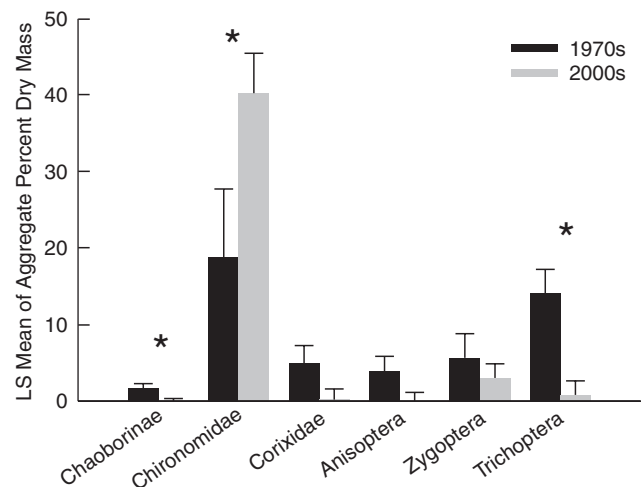


dual prey mass of *Bivalvia* (3.31 mg, SE = 8.73 mg) appeared 85% (nearly one order of magnitude; $R^2 = 0.10$, $F_{[1,21]} = 2.24$, $P = 0.149$) lower than that of historical prey mass (22.21 mg, SE = 9.12 mg), although this difference was not statistically significant ($\alpha = 0.05$).

Southwestern Manitoba

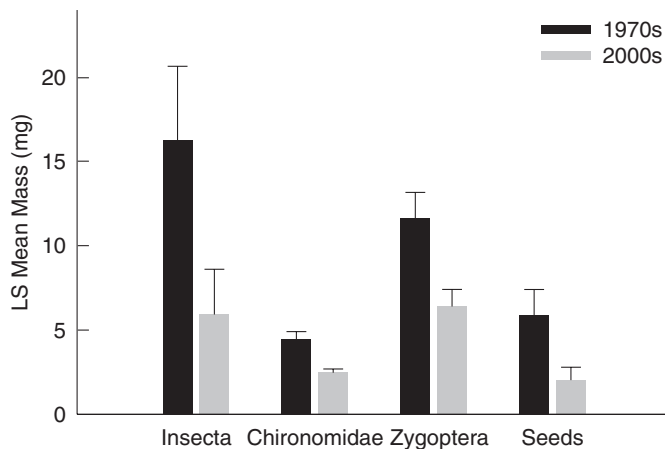
Mean aggregate percentages of all main taxa (Table 2) in scaup diets were similar between decades ($F_{[7,74]} = 0.99$, $P =$

Fig. 2. Least-square means (\pm SE) from MANOVA testing for decadal effects (1977–1980 versus 2000 and 2001) on *Insecta* (aggregate percent dry mass) consumed by lesser scaup soon after their arrival at a breeding area in southwestern Manitoba. Asterisks above bar groups indicate significant differences ($\alpha = 0.05$) between decades.



0.443), but insect composition of diets has shifted between decades ($F_{[7,74]} = 5.24$, $P < 0.001$; Fig. 2). Specifically, current aggregate percentages of *Trichoptera* (1%) and *Chaoboridae* (trace amounts) in diets were lower than that in historical diets (14% and 2%, respectively; 1970s); however, aggregate percentage of *Chironomidae* in current diets (40%) was 53% higher than that of historical diets (19%; Fig. 2).

Fig. 3. Least-square means (\pm SE) from significant ANOVAs ($\alpha = 0.05$) testing for decadal effects (1977–1980 versus 2000 and 2001) on mean individual prey mass of foods consumed by lesser scaup soon after their arrival at a breeding area in southwestern Manitoba.



Current mean individual prey mass of all Insecta (5.92 mg) was 64% lower ($R^2 = 0.06$, $F_{[1, 61]} = 3.99$, $P = 0.050$) than that in historical diets (16.24 mg; Fig. 3); current mean individual prey mass of Chironomidae (2.47 mg) and Zygoptera (6.40 mg) were 44% ($R^2 = 0.23$, $F_{[1, 46]} = 13.37$, $P < 0.001$) and 45% ($R^2 = 0.31$, $F_{[1, 18]} = 7.92$, $P = 0.012$) lower than those in historical diets (4.42 and 11.62 mg), respectively (Fig. 3). Similarly, current mean individual prey mass of seeds (2.03 mg) was 65% lower ($R^2 = 0.13$, $F_{[1, 33]} = 5.06$, $P = 0.031$) than that in historical diets (5.88 mg; Fig. 3).

Discussion

Northwestern Minnesota

In the 1960s, aggregate percentages of Amphipoda in scaup diets during spring and early summer throughout the Prairie Pothole Region were mainly from 46% to 67% (Rogers and Korschgen 1966; Bartonek and Hickey 1969; Swanson and Nelson 1970; Swanson and Duebbert 1989). In the 1970s and 1980s, aggregate percentages of Amphipoda were from 29% to 33% (Afton and Hier 1991; Afton et al. 1991). Thus, historical data dating back to the 1960s in relation to our current data suggest a declining pattern in the amount of Amphipoda consumed. Furthermore, our historical reference data may not represent optimal conditions for consumption of adequate amounts of Amphipoda.

Amphipoda overwinter as adults in semipermanent and permanent wetlands, and their lipid reserves are highest in late fall and early spring (Mathias et al. 1982; Arts et al. 1995; Meier et al. 2000), whereas lipid reserves in Bivalvia and Insecta generally peak in mid- to late summer (Davis and Wilson 1983; Meier et al. 2000). Amphipoda generally have over 4 times higher gross energy, over 3 times higher protein, and over 4 times higher lipids than do Bivalvia or Gastropoda (Sugden 1978; Jorde and Owen 1988; Ballard et al. 2004). The relatively large lipid reserves of Amphipoda in spring probably facilitate accumulation of lipid reserves by scaup, given that scaup diets primarily are protein based (Afton and Hier 1991; Afton et al. 1991). In the absence of

dietary lipids, scaup must synthesize endogenous lipid reserves from dietary protein or carbohydrate, which is less efficient than simply assimilating fatty acids from their diet to endogenous lipid reserves (Alisauskas and Ankney 1992).

Amphipoda seemingly are the single most preferred food of scaup during spring migration and early summer in the Prairie Pothole Region because (i) Amphipoda historically constituted large proportions of scaup diets (1960s–1980s; Rogers and Korschgen 1966; Bartonek and Hickey 1969; Swanson and Nelson 1970; Swanson and Duebbert 1989; Afton and Hier 1991; Afton et al. 1991), (ii) Amphipoda densities are a good predictor of wetland use by scaup, but Chironomidae densities are not (Lindeman and Clark 1999; Strand 2005; Anteau 2006), (iii) Amphipoda have relatively high nutritional values during spring, and (iv) percent occurrence of Amphipoda observed in current scaup diets remained high relative to the 94% decrease in aggregate percentage of Amphipoda consumed. Accordingly, we conclude that the observed decadal shift from Amphipoda to Bivalvia in scaup diets in Minnesota has resulted in a decrease in forage quality that is consistent with the spring condition hypothesis.

Declines in mean individual prey mass of Amphipoda and Bivalvia between decades also may be indicative of a decline in forage quality and perhaps profitability (net nutritional gain, including foraging costs). Small prey items often require longer foraging and handling times to procure similar amounts of nutrients (Matthews et al. 1992; Lovvorn and Gillingham 1996; Richman and Lovvorn 2004). In addition, larger prey items within a given taxa (e.g., Amphipoda and Bivalvia) might be more nutritious because they have lower ratios of chitin or shell to meat owing to the allometric relationship of surface area to volume (Ricklefs 1990). On Pool 19 of the Mississippi River, scaup use was higher in areas that had higher proportions of larger fingernail clams (*Musculium* spp.; >2 mm wide); scaup also consumed higher proportions of larger fingernail clams than were available in areas where scaup were present (Thompson 1973). The percentage of shell is higher in mussels 5–10 mm long than in those 10–15 mm long, but at longer lengths (>15 mm) the percentages of shell increase (Bustnes 1998); these results suggest that meat to shell ratios follow a quadratic relationship. Diving ducks selected against consuming Bivalvia of large size (~260–570 mg or ~15–24 mm; De Leeuw and Van Eerden 1992; Hamilton et al. 1999; Richman and Lovvorn 2004). However, mean individual mass of Bivalvia observed in scaup diets (3.31 mg currently and 22.21 mg historically) were much smaller than those selected against in previous studies; thus, we speculate that consuming larger Bivalvia prey is more nutritious, within the range of mass that we observed.

Amphipoda generally yield over 2 times higher true metabolizable energy (TME) than do Bivalvia and Gastropoda in black ducks (*Anas rubripes* Brewster, 1902; Jorde and Owen 1988), 3 times higher TME than do Bivalvia and Gastropoda in northern pintails (*Anas acuta* L., 1758); Ballard et al. 2004), and 3 times higher TME than Gastropoda in blue-winged teal (*Anas discors* L., 1766; Sugden 1978). Scaup are more efficient at assimilating energy from Amphipoda than are blue-winged teals (Sugden 1978). The observed

diet shift, from 33% Amphipoda and 6% Bivalvia historically to 2% Amphipoda and 26% Bivalvia currently, results in TME that is 65% and 94% lower based on TME estimates of Amphipoda and Bivalvia for black ducks and northern pintails, respectively (Jorde and Owen 1988; Ballard et al. 2004). However, we caution that these calculations are based on TME of similar prey taxa, but for different duck species and do not account for changes in prey size, seasonal variation in nutritional values of prey, and subtle changes in other taxa.

Diet data can be used to assess forage quality; however, such data alone cannot be used to directly assess availability of forage or profitability. The observed shift in diets from Amphipoda to Bivalvia could be the result of an increase in the abundance of Bivalvia, making consumption of Bivalvia more profitable despite their lower forage quality. If consuming Bivalvia has become more profitable than consuming Amphipoda, we predict that current lipid reserves of scaup would be similar or even higher than that historically, which clearly is not the case; Anteau (2002) and Anteau and Afton (2004) reported a 28.8 g (30%; equivalent to 4.2 eggs) decadal decrease in lipid reserves of scaup. Thus, our results that scaup shifted their diets from primarily Amphipoda (thought to be a highly preferred food) to Bivalvia (thought to be a lesser preferred food) suggest that abundance of Amphipoda has declined. Similarly, mean Amphipoda densities in the spring of 2004 and 2005 were low across the upper Midwest and appeared to have declined from historical levels (Anteau 2006).

The observed decreases in abundance and size of Amphipoda in scaup diets are consistent with increased fish predation on Amphipoda in wetlands (Matthews et al. 1992; Wellborn 1994; Wooster 1998; Hilton et al. 2002; Anteau 2006). However, global climate change, sedimentation, and agricultural runoff also could be contributing or interacting factors that affect the availability of Amphipoda and other food items for scaup (Anteau 2002; Anteau and Afton 2004; Anteau 2006).

Although consistent with the spring condition hypothesis, our results were from only 2 sites in northwestern Minnesota and sample sizes were relatively small in 2000 and 2001; however, observed effect sizes in diet differences were relatively large. Accordingly, we recommend landscape scale studies of numerous wetlands to determine the scope of this apparent decline in forage quality and profitability and to estimate forage availability for scaup during spring migration in the upper Midwest.

Female scaup arrived at the Manitoba breeding area in springs of 2000 and 2001 with 3.2 g fewer mineral reserves than did those in the 1970s (equivalent to 0.8 eggs of minerals), but had similar amounts of mineral reserves between decades in Minnesota (Anteau and Afton 2004). Scaup currently may be deriving a calcium benefit from consuming larger amounts of Bivalvia than that historically. However, accumulation of calcium reserves probably is not driving the selection of dietary prey because, unlike lipid reserves, calcium is largely acquired from exogenous sources in breeding areas (Afton and Ankney 1991; Esler et al. 2001); a pattern mirrored by the peak in consumption of Bivalvia during rapid follicle development and egg laying (Afton and Hier 1991).

Southwestern Manitoba

Female scaup arrived at the Manitoba breeding area in springs of 2000 and 2001 with 27.8 g fewer lipid reserves than did those in the 1970s (Anteau 2002; Anteau and Afton 2004). Anteau (2002) speculated that the current low levels of lipid reserves were due to factors on preceding migration stopover areas because scaup were collected in Manitoba soon after arrival. Thus, current diets of scaup in Manitoba probably had little influence on lipid-reserve levels observed by Anteau (2002) and Anteau and Afton (2004), but they may influence lipid-reserve levels later in the breeding season.

Compositions of scaup diets in Manitoba were similar between decades, indicating no change in forage quality, but sample sizes were small for the 1970s. However, we documented a decadal shift from Trichoptera to Chironomidae in scaup diets (Fig. 2), but it is unclear whether these observed differences in diet composition affected forage quality of scaup. In a review of available literature, we found no clear, marked, or consistent indications of differences in nutritional quality between Chironomidae and Trichoptera (Driver et al. 1974; Driver 1981; Sushchik et al. 2003). TME estimates of these prey for scaup would be informative in understanding how this diet shift affected forage quality for scaup. The observed lower mean individual prey mass of Insecta in current diets was partly due to a shift from large taxa (Anisoptera and Trichoptera) to smaller taxa (Chironomidae; Table 2). However, mean individual prey mass of Chironomidae and Zygoptera decreased by 44.1% and 44.9%, respectively, between the 1970s and 2000s (Fig. 3), which indicated that these prey currently may be under more predation pressure (Matthews et al. 1992; Wellborn 1994; Hilton et al. 2002). Declines in mean individual prey mass might result in a decrease in forage quality for scaup.

Mean individual prey mass of seeds in current diets also were lower than those historically, possibly because of a species shift in seeds consumed. However, we did not identify taxa of seeds because of their low fraction in scaup diets (Table 2). Afton and Hier (1991) found that seeds were a preferred food item of scaup during pre-rapid follicle growth and egg laying in Manitoba. A diet shift from larger to smaller seeds could influence the ability of scaup to accumulate lipid reserves because seeds are a good source of carbohydrates and lipids (Afton and Hier 1991; Ballard et al. 2004). However, the decadal differences in individual seed mass in scaup diets probably had a minimal effect on scaup lipid reserves, given the low percentage of seeds in scaup diets in both decades (Table 2).

Implications for conservation of lesser scaup

Availability of highly nutritious forage for scaup on northern spring stopover areas could be one of the factors influencing the scaup population decline and deserves further research (Afton and Anderson 2001; Anteau 2002; Anteau and Afton 2004). Restoring wetland quality to historical levels and increasing availability of nutritional foods, such as Amphipoda, at spring stopover areas in the upper Midwest should help to increase lipid reserves of female scaup and may help to reverse the population decline. Finally, the following research questions should be addressed to further test the spring condition hypothesis and to provide

for effective scaup conservation. (i) Are decreases in scaup lipid reserves and in forage quality and availability widespread on northern spring stopover areas in the upper Midwest? (ii) Are decreases in scaup lipid reserves causing reduced reproductive success or survival of females? (iii) Are factors other than forage quality and availability involved in declines in scaup lipid reserves? (iv) What factors influence the availability of quality scaup forage in the upper Midwest? Finally, (v) what management strategies and techniques are effective in preventing further losses in forage and wetland quality and for restoring critical spring stopover habitat for scaup and other species?

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