



LIPID RESERVES OF LESSER SCAUP (*AYTHYA AFFINIS*) MIGRATING ACROSS A LARGE LANDSCAPE ARE CONSISTENT WITH THE “SPRING CONDITION” HYPOTHESIS

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ABSTRACT.—The “spring condition” hypothesis (SCH) states that nutrition during spring migration affects survival, reproductive success, and, ultimately, population size of migratory birds. The North American population of Lesser Scaup (*Aythya affinis*) has experienced a marked decline, apparently because of poor recruitment. An important prediction of the SCH is that female Lesser Scaup have low lipid reserves during spring migration. We previously reported that lipid reserves and body mass of females collected on migratory stopover areas in northwestern Minnesota in springs 2000–2001 were lower than those on the same areas in the 1980s and markedly lower than those collected at Pool 19 of the Mississippi River in 2000–2001, an important preceding stopover area. However, it was unclear whether these findings represented a site-specific result or a landscape-scale phenomenon. Accordingly, we examined lipid and body mass of 641 female Lesser Scaup migrating across seven eco-physiographic regions of Iowa, Minnesota, and North Dakota during springs 2003–2005. We found that lipids and body mass of females throughout the Upper Midwest were similar to or less than the low values documented in northwestern Minnesota in springs 2000–2001 and markedly lower than those of females at Pool 19 in springs 2000–2001. Accordingly, our results are consistent with a prediction of the SCH, because lipid and body mass of females are low throughout this large landscape, lower than at an important preceding stopover area, and lower than all historical values. Finally, our results suggest the potential for cross-seasonal influences of nutrition on recruitment and that a stronger management focus on spring migration habitats may be necessary for conservation and recovery of declining migratory birds, especially Lesser Scaup. Received 30 September 2008; accepted 8 May 2009.

Key words: *Aythya affinis*, body condition, Lesser Scaup, lipids, migratory fattening, population regulation, stopover area, survival, waterfowl.

Las Reservas Lipídicas de *Aythya affinis* Observadas durante la Migración a través de un Paisaje Amplio Concuerdan con la Hipótesis de la Condición de Primavera

RESUMEN.—La hipótesis de la condición de primavera (HCP) postula que la nutrición durante la migración de primavera afecta la supervivencia, el éxito reproductivo y, de forma última, el tamaño poblacional de las aves migratorias. La población norteamericana de *Aythya affinis* ha sufrido una disminución marcada, aparentemente debida al bajo reclutamiento. Una predicción importante de la HCP es que las hembras de *A. affinis* cuentan con pocas reservas lipídicas durante la migración de primavera. Previamente, documentamos que las reservas lipídicas y la masa corporal de hembras coleccionadas en lugares de escala migratoria en el noroeste de Minnesota en las primaveras de 2000 y 2001 eran menores que las observadas en las mismas áreas en los años ochenta y marcadamente menores que las de las hembras coleccionadas en el estanque 19 del Río Mississippi, una importante área de escala precedente. Sin embargo, no fue claro si estos hallazgos representaban un resultado específico del sitio de estudio o de un fenómeno a nivel de paisaje. Por lo tanto, examinamos los lípidos y la masa corporal en 641 hembras de *A. affinis* que estaban migrando a través de siete regiones ecofisiográficas de Iowa, Minnesota y North Dakota durante las primaveras de 2003 a 2005. Encontramos que la masa de lípidos y la masa corporal de las hembras a lo largo de la parte alta del medio-oeste fueron similares a, o un poco menores que, los valores bajos documentados en el noroeste de Minnesota en 2000 y 2001, y marcadamente menores que los de las hembras del estanque 19 de 2000 y 2001. De este modo, nuestros resultados concuerdan con las predicciones de la HCP porque la masa lipídica y corporal de las hembras presentan valores bajos en todo este paisaje amplio, que son menores que los valores observados en un área de escala precedente de importancia y que todos los valores históricos. Finalmente, nuestros resultados potencialmente sugieren que existen influencias de la nutrición sobre el reclutamiento a través de distintas temporadas. Además, un enfoque más fuerte en el manejo de los ambientes de migración de primavera podría ser necesario para la conservación y recuperación de las aves migratorias que están disminuyendo, especialmente *A. affinis*.

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SPRING MIGRATION IS a period of high nutritional demand in the annual cycle of migratory birds, given high energetic costs of flight, extreme weather events, nutrient acquisition, contour-feather molt, and intense courtship activity in some species (Alisauskas and Ankney 1992, Arzel et al. 2006). Nutrient-reserve levels during spring migration or upon arrival on breeding areas can influence avian reproductive success directly (e.g., capital breeders) or indirectly, by allowing individuals with greater levels to arrive on breeding areas earlier and establish better-quality territories or nest earlier than those with lower reserves (e.g., Ankney and MacInnes 1978, Prop et al. 2003, Smith and Moore 2003, Drent et al. 2006). Moreover, spring nutrition also influences survival during migration (Newton 2006, 2007). Thus, food availability within spring migration corridors, especially on northern stopover areas, may have important effects on lipid reserves or arrival timing (or both), concomitant reproductive success, and, ultimately, population size.

Afton and Anderson (2001) proposed several hypotheses to explain the marked decline in the continental scaup population (Lesser Scaup [*Aythya affinis*] and Greater Scaup [*A. marila*] combined), one of which was later termed the “spring condition” hypothesis (SCH) by Anteau and Afton (2004). The SCH states that reproductive success of scaup has declined because females arrive on breeding areas in poorer body condition than they did in the past because reduced food resources prevent females from acquiring sufficient nutrient reserves on wintering, spring migration, or breeding areas. However, connections among nutrition during migration, survival, and subsequent reproductive success are not limited to issues unique to the scaup population decline (see Drent et al. 2006, Newton 2006). Accordingly, we extend and generalize the SCH to state that nutrition during spring migration or upon arrival at breeding areas influences survival, reproductive success, and, thus, population size of migratory avian species.

Afton and Anderson (2001) concluded that the decline in the continental scaup population likely is driven by declines in the Lesser Scaup (hereafter “scaup”) population and caused by reductions in recruitment. If scaup are experiencing a decline in recruitment because of processes described by the SCH, a large proportion of migrating females should have relatively low lipid reserves on stopover sites throughout a large landscape during spring.

Up to 86% of the scaup population winters in states bordering the Gulf of Mexico and potentially migrates along the Mississippi River valley and through Iowa, Minnesota, and North Dakota (hereafter “Upper Midwest”; Bellrose 1980, Afton and Anderson 2001); this segment of the population likely is experiencing the largest decline (Afton and Anderson 2001). The availability of high-quality scaup foods currently is low during spring migration in the Upper Midwest and likely has declined there since the 1960s (Anteau and Afton 2006, 2008a, b). Female scaup on three migration stopover sites in northwestern Minnesota had lower lipid reserves in springs 2000–2001 than those that stopped there during 1986–1988 (Anteau and Afton 2004). Moreover, lipid-reserve levels of females in northwestern Minnesota were markedly lower than those at Pool 19 of the Mississippi River, an important middle-latitude stopover area. By contrast, scaup increased or at least maintained lipid reserves during spring migration historically (cf. Anteau and Afton 2004). Consequently, further research

was needed to determine whether the observed decrease in lipid reserves was localized or widespread throughout the Upper Midwest migration corridor.

In the present study, we tested one prediction of the SCH: that lipid-reserve levels of migrating female scaup are low across a large landscape during spring. Specifically, we tested whether female scaup migrating throughout the Upper Midwest had different levels of lipid reserves than those at Pool 19 of the Mississippi River and those in northwestern Minnesota in 2000–2001. If females in the Upper Midwest had lower levels of lipid reserves than those at Pool 19, this would be consistent with the prediction of the SCH, because females should be maintaining or increasing lipid reserves during migration (Anteau and Afton 2004). If females in the Upper Midwest had lower or similar lipid-reserve levels than those in northwestern Minnesota in 2000–2001, this also would be consistent with the prediction of the SCH, because lipid-reserve levels in northwestern Minnesota in 2000–2001 were lower than those observed there historically (Anteau and Afton 2004). Other studies have tried to test the SCH using body mass (DeVink et al. 2008); thus, we also examined variation in protein and mineral reserves and body mass of female scaup throughout the Upper Midwest during springs 2003–2005.

METHODS

Study Areas

Pool 19.—Pool 19 is an important middle-latitude stopover area on the Mississippi River (Fig. 1; between Hamilton and Niota, Illinois) where large numbers of scaup stop over before migration through the Upper Midwest (Havera 1999). In spring 2008, >350,000 scaup were observed at Pool 19 at or near peak migration (A. Yetter, Illinois Natural History Survey, unpubl. data). Pool 19 has been described in detail by Thompson (1973) and Havera (1999). We collected specimens at Pool 19 to examine female body condition and potential annual variation in body condition before migration into the Upper Midwest.

Upper Midwest.—Our primary study area included the Prairie Pothole Region of Iowa, Minnesota, and North Dakota (Fig. 1), which comprises critical spring migration stopover areas for scaup, according to anecdotal observations of local biologists, band-recovery data, sightings of color-marked scaup, aerial surveys in spring, and results from satellite telemetry (Low 1941, Afton et al. 1991, Pace and Afton 1999; cf. Anteau 2006, Afton 2008). We stratified the three-state area into seven eco-physiographic regions (hereafter “regions”) based on watershed and groundwater hydrology, geology, and plant communities (Fig. 1; Kantrud et al. 1989, Minnesota Department of Natural Resources unpubl. data). The Minnesota Glaciated Plains (MNGP) and the Minnesota Morainal (MOR) regions included areas outside the traditional Prairie Pothole Region (Fig. 1); however, we included them so that results would be relevant to state-specific management and conservation plans.

Sampling Design and Allocation

Pool 19.—In springs 2003–2005, we attempted to collect 25 female scaup annually at Pool 19 to examine annual variation there and reference body mass prior to their migration across the Upper

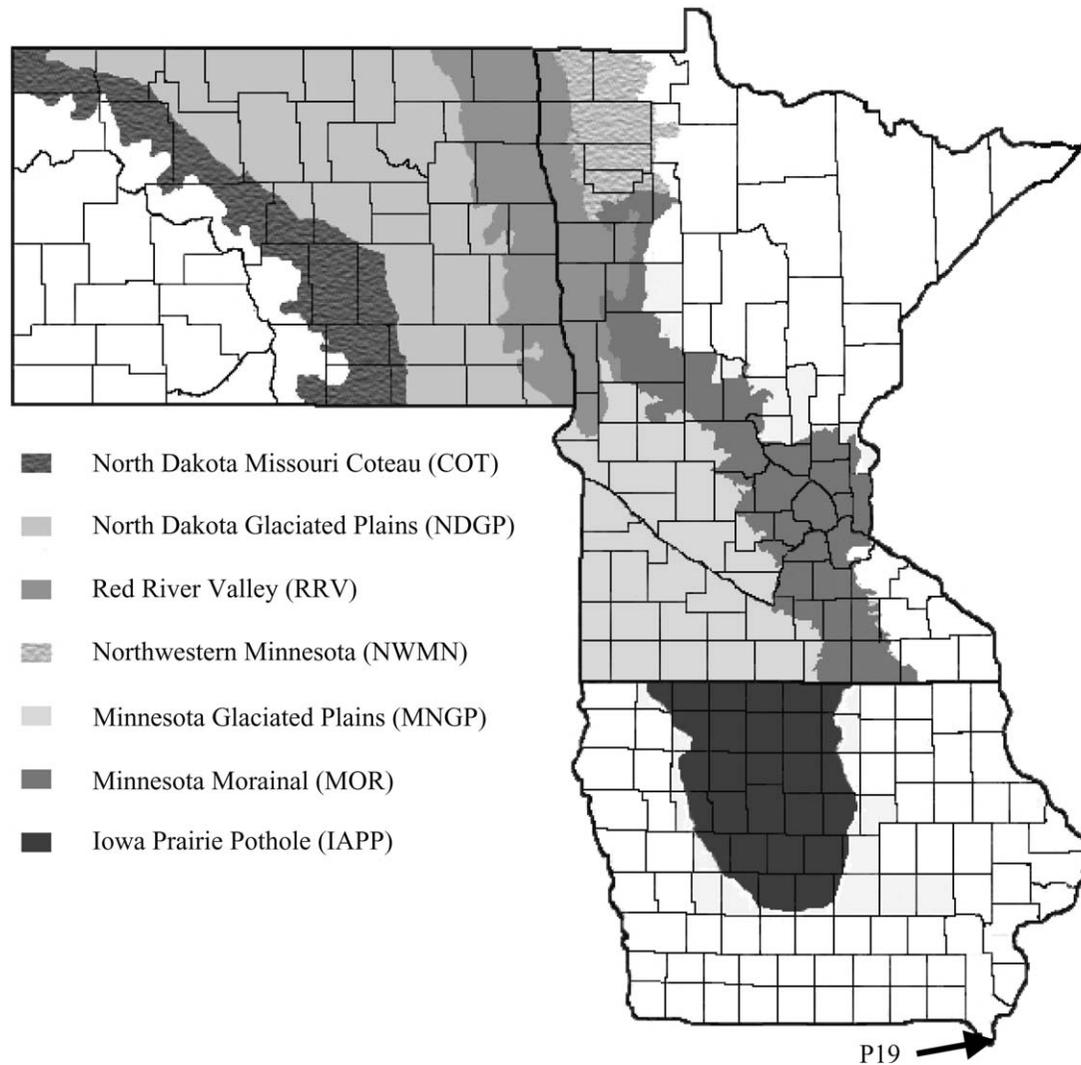


FIG. 1. Map of study area, depicting seven eco-physiographic regions and Pool 19 of the Mississippi River (P19) for Lesser Scaup collections during spring migration in the Upper Midwest, 2003–2005. Areas in white were not sampled.

Midwest. We also used data collected from Pool 19 in 2000 and 2001 to make *a-priori* contrasts, examining whether females, on average, were increasing or maintaining lipid reserves during spring migration throughout the Upper Midwest.

Northwestern Minnesota.—We used data collected from Northwestern Minnesota in 2000 and 2001 (hereafter “NW00”; we capitalize “Northwestern” when referring to the region mapped in Fig. 1) as a reference to make *a-priori* comparisons among other regions of the Upper Midwest, given the lack of historical data for other regions. In springs 2003–2005, we also attempted to collect 15 females annually at each of the historical sites in Northwestern Minnesota (hereafter “NWMN”; Agassiz National Wildlife Refuge and Thief Lake and Roseau River Wildlife Management Areas; Table 1).

Random site selection.—We used constrained-random sampling techniques to select collection sites in all other regions of the Upper Midwest. We first estimated numbers of townships

(6×6 mile block; 93.2 km^2) within each region that had ≥ 200 ha of semipermanent wetlands (candidate townships for random selection; Table 1), based on converged basin (Johnson and Higgins 1997) or comparable National Wetland Inventory data (cf. Anteau 2006). Because of lower wetland densities in Iowa, we broadened the constraint there to include townships with 200 ha of semi-permanent or permanent wetlands. We then allocated numbers of collection sites among the six regions (three to six sites per region; Table 1) on the basis of region size and number of candidate townships available (Table 1 and Fig. 1). Each region was divided into subregions based on latitude, such that there was one collection site per subregion annually (except in North Dakota Glaciated Plains [NDGP]). In NDGP, we assigned two collection sites for each subregion because of the larger width of this region (east to west) compared with other regions (Fig. 1).

Random collection sites.—Each collection site (27,972 ha) comprised three townships (9,324 ha) to ensure adequate

TABLE 1. Regions, years, dates, and numbers of female Lesser Scaup (*n*) collected during spring migration in the Upper Midwest, including numbers of collection sites (*S*) and numbers of candidate townships (*T*) for random selection of collection sites.

Region	Year	Dates	<i>n</i>	<i>S</i>	<i>T</i>
Iowa Prairie	2004	6–9 April	27	3	43 ^a
Pothole	2005	30 March–4 April	27	3	
Minnesota	2003	20 April–9 May	19	4	348 ^b
Morainal	2004	10–15 April	12	4	
	2005	8–16 April	30	4	
Minnesota Glaciated	2003	9–29 April	33	4	285 ^b
Plains	2004	8–19 April	30	4	
	2005	10–15 April	34	4	
Northwestern	2003	1–13 May	26	3	
Minnesota ^c	2004	4–13 May	44	3	
	2005	23–28 April	35	3	
Red River	2003	17 April–10 May	26	3	66 ^b
Valley	2004	24 April–2 May	17	3	
	2005	17–21 April	26	3	
North Dakota	2003	15 April–2 May	60	6	364 ^b
Glaciated Plains	2004	20 April–11 May	46	6	
	2005	9 April–2 May	59	6	
North Dakota	2003	14–23 April	30	3	208 ^b
Missouri Coteau	2004	15–22 April	30	3	
	2005	7 April–1 May	30	3	

^aTownships containing ≥ 200 ha of semipermanent and permanent wetlands.

^bTownships containing ≥ 200 ha of semipermanent wetlands.

^cFixed collection sites (same each year; see text); $>92\%$ of scaup were collected between 23 April and 7 May.

collection opportunities; however, we replaced some (17% of townships where collections occurred) with alternative, randomly selected townships when initial townships no longer had suitable scaup habitat (semipermanent or permanent wetlands) or few scaup used these sites. We attempted to collect 10 females from each collection site; we also attempted to collect our sample from multiple wetlands within each site. We randomly selected new townships annually without replacement within each subregion, from the list of candidate townships, to maximize representation of spatial variability in nutrient reserves of scaup. In 2004 and 2005, we further constrained township selection so that centroids of the second and third townships selected were within 50 km of the centroid of the first randomly selected township, to minimize travel by field crews.

Collection of Specimens

We collected female scaup randomly with a shotgun, without the use of decoys to avoid associated biases (Pace and Afton 1999); collections were conducted exactly as described by Afton et al. (1991) and Anteau and Afton (2004, 2006). We generally timed collections to occur during the middle of the spring migration period, coinciding with the presence of relatively large numbers of migrating scaup within each subregion. We timed collections to occur during similar migration phenology across our study area; thus, it was unnecessary to control for collection date in subsequent models. We collected 22, 20, and 25 female scaup from Pool 19 during 23–24 March 2003, 24–27 March 2004, and 21–23 March 2005, respectively. We collected 641 female

scaup from the Upper Midwest study area in springs 2003–2005 (Table 1). In the Iowa Prairie Pothole (IAPP) region, we collected scaup only in springs 2004–2005. Scaup were collected from 98 townships (9 in Iowa, 46 in Minnesota, and 43 in North Dakota) and from three fixed locations (in NWMN) in 2003–2005, representing 7.5% of the candidate collection townships in the Upper Midwest.

Specimen Preparation

Immediately after collection, we extracted 1–1.5 mL of blood from specimens by cardiac puncture. We prepared and stored blood samples exactly as described by Anteau and Afton (2008c). We recorded body mass immediately upon collection (± 1 g), and then specimens were labeled, placed in double plastic bags, frozen, and transported to the laboratory for dissections. In the laboratory, carcasses were thawed, reweighed (± 1 g), and the following morphometrics were recorded: (1) total length (± 1 mm), from tip of longest rectrix to tip of bill with bird stretched on its back, (2) keel length (± 0.1 mm; externally measured), (3) wing chord (± 1 mm; Carney 1992), (4) rectrix length (± 1 mm), from body to tip of longest rectrix, and (5) tarsus bone (± 0.1 mm; Dzubin and Cooch 1992). We then removed and weighed upper- and lower-gut contents (Anteau 2002). Carcass preparation and body-composition analyses were conducted by the Avian Energetics Laboratory (AEL) of Long Point Waterfowl and Wetlands Research Fund, Port Rowan, Ontario. At AEL, carcasses were weighed (± 0.01 g), dried to a constant mass, reweighed, and homogenized so that the carcass could pass through a 2-mm sieve (see Anteau and Afton 2004). Nutritional analyses of prepared carcasses were conducted exactly as described by Afton and Ankney (1991). Following these analyses, estimates of lipid reserves were estimated exactly as described by Anteau and Afton (2004).

Statistical Analyses

Annual variation.—We conducted two principal component analyses (PCA) of the correlation matrix for morphometrics: body length (total length – rectrix length), wing chord, tarsus bone, and keel length (PROC PRINCOMP; SAS Institute 2002) separately for females collected in 2000–2005 from Pool 19 (first PCA) and Northwestern Minnesota (second PCA). We then used the first principal component scores (PC1; for each location) to index body size (Afton and Ankney 1991). For both locations separately, we tested for annual differences in body mass of females collected in 2000–2005 with an analysis of covariance (ANCOVA; PROC MIXED; SAS Institute 2002), with year as a class (categorical) variable and PC1 as a covariate. We used the PDMIX800 macro (Saxton 1998) in each model to calculate Tukey-Kramer adjusted mean letter groupings for years.

We conducted a third PCA of the correlation matrix on the same morphometrics (PROC PRINCOMP) for all females collected from across the Upper Midwest in 2003–2005. We conducted preliminary analyses to evaluate annual variation in body mass and nutrient reserves (lipid, protein, and mineral) of females collected in 2003–2005 with separate ANCOVAs (PROC MIXED), in which year, region, and subregion within region were class variables and PC1 was a covariate. These analyses indicated that body mass ($F = 0.11$, $df = 2$ and 615 , $P = 0.895$) and lipid reserves ($F = 0.67$, $df = 2$ and 615 , $P = 0.513$) did not vary among years 2003–2005;

thus, we pooled data over years 2003–2005 for subsequent models of lipid reserves and body mass.

Lipid reserves and body mass in the Upper Midwest.—We conducted a fourth PCA of the correlation matrix on the same morphometrics (PROC PRINCOMP), including an additional 69 and 70 females collected in 2000–2001 from Pool 19 and NW00, respectively (Anteau and Afton 2004; PROC PRINCOMP).

We tested for regional differences in lipid reserves and body mass of females with separate ANCOVAs (PROC MIXED) in which region was a class variable and PC1 was a covariate. We also included subregion within region as a fixed blocking variable to account for spatial variability within regions. We specified Pool 19 and NW00 as separate regions and conducted *a-priori* tests by contrasting body mass or lipid reserves of females collected at Pool 19 and NW00 to those of all other regions using the Dunnett-adjusted pdiff-control option of the least-squares means statement for region (PROC MIXED).

Protein and mineral reserves in the Upper Midwest.—We examined regional variation in protein and mineral reserves of females collected from the Upper Midwest in 2003–2005 for potential deficiencies and to improve interpretations of body-mass data. We used separate ANCOVAs (PROC MIXED) for each nutrient, in which year and region were class variables and PC1 was a covariate. We also included subregion within region as a fixed blocking variable to account for spatial variability within regions. We used the PC1 scores from the third PCA to index body size in these analyses (Afton and Ankney 1991). We used the PDMIX800 macro (Saxton 1998) in each model to get Tukey-Kramer adjusted mean letter groupings for each region and year ($\alpha = 0.05$).

RESULTS

Annual variation in body mass.—In the first PCA, for females collected at Pool 19 from 2000–2005, eigenvectors for PC1 ranged from 0.461 to 0.537; PC1 accounted for 41% of the variation in morphometrics. Body mass was positively correlated with PC1 ($X = 21.12 \pm 4.06$ [SE], $F = 27.06$, $df = 1$ and 130 , $P < 0.001$) at Pool 19. Body mass differed ($F = 2.63$, $df = 4$ and 130 , $P = 0.037$) among years at Pool 19, after adjusting for variation in body size. Multiple comparison tests indicated that body mass varied little among years, except females in 2004 were heavier than those in 2001 (Fig. 2).

In the second PCA, for females collected in Northwestern Minnesota in 2000–2005, eigenvectors for PC1 ranged from 0.448 to 0.534; PC1 accounted for 53% of the variation in morphometrics. Body mass of females in Northwestern Minnesota was positively correlated with PC1 ($X = 23.59 \pm 9.81$ [SE], $F = 57.62$, $df = 1$ and 169 , $P < 0.001$) and differed among years ($F = 2.45$, $df = 4$ and 169 , $P = 0.048$). Multiple-comparison tests indicated that body mass varied little among years, except females in 2005 were heavier than those in 2001 (Fig. 2).

Lipid reserves and body mass in the Upper Midwest.—In the fourth PCA, which included Pool 19 and NW00 data, eigenvectors for PC1 ranged from 0.485 to 0.517; PC1 accounted for 50% of the variation in morphometrics. Lipid reserves were positively correlated with PC1 ($X = 3.08 \pm 1.01$ [SE], $F = 9.39$, $df = 1$ and 752 , $P = 0.002$) and varied among regions ($F = 26.15$, $df = 8$ and 752 , $P < 0.001$) and subregions within regions ($F = 2.26$, $df = 18$ and 752 , $P = 0.002$). Our first *a-priori* test indicated

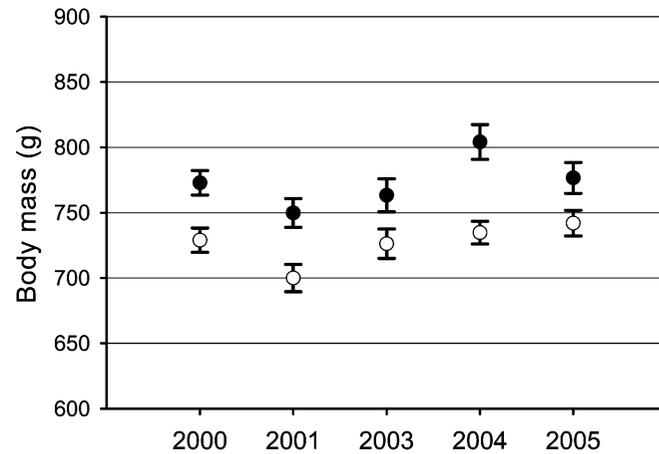


FIG. 2. Annual variation of least-square mean body mass (\pm SE), adjusted for body size, of female Lesser Scaup collected during spring migration at Pool 19 (Mississippi River; shaded circles) and in Northwestern Minnesota (unshaded circles) during spring migration, 2000–2005.

that regional mean lipid reserves of females were markedly lower (58–77 g) throughout the Upper Midwest than those of females at Pool 19 (Fig. 3A). Although lipid reserves varied somewhat among regions of the Upper Midwest, our first *a-priori* tests indicated that all Upper Midwest regions were similar to NW00 (Fig. 3A).

Body mass was positively correlated with PC1 ($X = 19.18 \pm 1.57$ [SE], $F = 149.93$, $df = 1$ and 752 , $P < 0.001$) and varied among regions ($F = 23.09$, $df = 8$ and 752 , $P < 0.001$) and subregions within regions ($F = 3.61$, $df = 18$ and 752 , $P < 0.001$). Body mass of females was lower in IAPP and MOR than in NW00 but was similar between NW00 and other regions, except Pool 19 (Fig. 3B). Body mass of females at Pool 19 was higher than that of females in all other regions in the Upper Midwest, except NDGP (Fig. 3B). In IAPP, 20% and 48% of females weighed ≤ 600 g and ≤ 650 g, respectively. Overall, 5% and 15% of females collected throughout the Upper Midwest weighed ≤ 600 g and ≤ 650 g, respectively.

Protein and mineral reserves in the Upper Midwest.—In the third PCA, eigenvectors for PC1 ranged from 0.476 to 0.523; PC1 accounted for 50% of the variation in morphometrics. Protein reserves were positively correlated with PC1 ($X = 3.88 \pm 0.30$, $F = 167.44$, $df = 1$ and 617 , $P < 0.001$) and varied among regions ($F = 14.71$, $df = 6$ and 617 , $P < 0.001$) and subregions within regions ($F = 3.09$, $df = 16$ and 617 , $P < 0.001$) but did not vary annually ($P = 0.612$). Mean protein reserves of females in North Dakota Missouri Co-teau (COT), NDGP, the Red River Valley (RRV), and NWMN were greater than those in MOR and IAPP (Fig. 4A).

Mineral reserves were positively correlated to PC1 ($X = 0.96 \pm 0.08$, $F = 138.33$, $df = 1$ and 631 , $P < 0.001$) and varied among regions ($F = 2.43$, $df = 6$ and 631 , $P = 0.025$) and years ($F = 18.25$, $df = 2$ and 631 , $P < 0.001$) but not among subregions within regions ($P = 0.134$). Mean (\pm SE) mineral reserves in 2004 and 2005 (28.7 ± 0.2 and 29.4 ± 0.2 , respectively) were greater than those in 2003 (27.7 ± 0.2). Mineral reserves of females in RRV and NDGP were greater than those of females in IAPP (Fig. 4B).

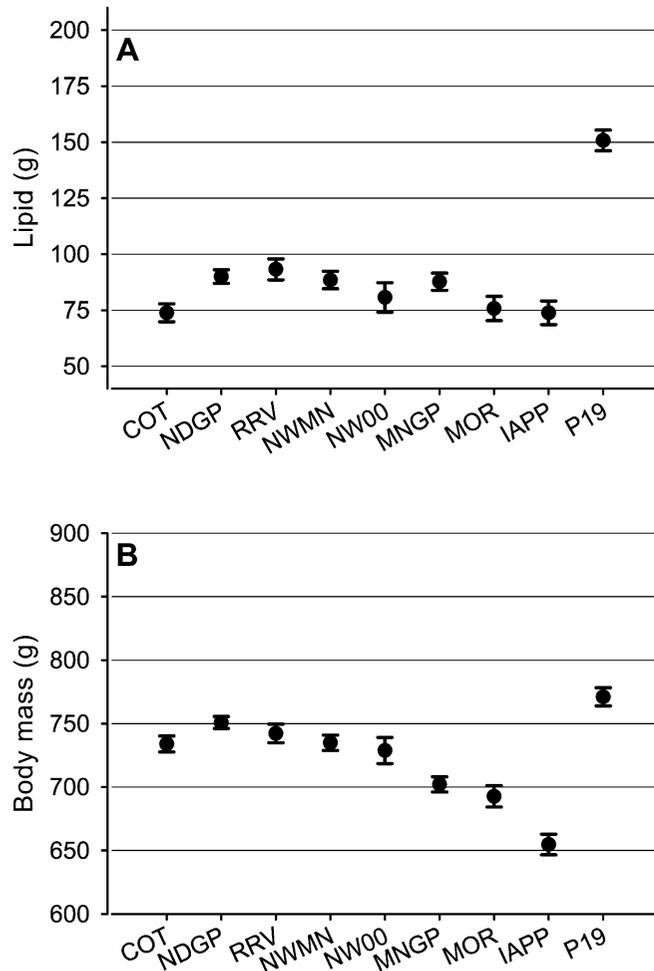


FIG. 3. Least-square mean (\pm SE) (A) lipid reserves and (B) body mass of female Lesser Scaup collected during spring migration (years 2003–2005 pooled) by regions. COT = North Dakota Missouri Coteau, NDGP = North Dakota Glaciated Plains, RRV = Red River Valley of Minnesota and North Dakota, NWMN = Northwestern Minnesota, NW00 = NWMN in 2000–2001 (Anteau and Afton 2004), MNGP = Minnesota Glaciated Plains, MOR = Minnesota Morainial, IA = Iowa Prairie Pothole, and P19 = Pool 19.

DISCUSSION

Pool 19 of the Mississippi River.—Pool 19 likely is a critical middle-latitude stopover area for female Lesser Scaup to accumulate lipid reserves because (1) large numbers of scaup use Pool 19 in spring (Havera 1999; A. Yetter, Illinois Natural History Survey, unpubl. data) and (2) female scaup have relatively high lipid reserves at Pool 19, but relatively low lipid reserves on stopover areas in the Upper Midwest. Annual variations in food resources at Pool 19 and other preceding migration stopover areas likely influence lipid reserves of female scaup on higher-latitude sites in the Upper Midwest. However, we did not detect annual variation in body mass of females at Pool 19 for years 2003–2005; thus, it was unnecessary

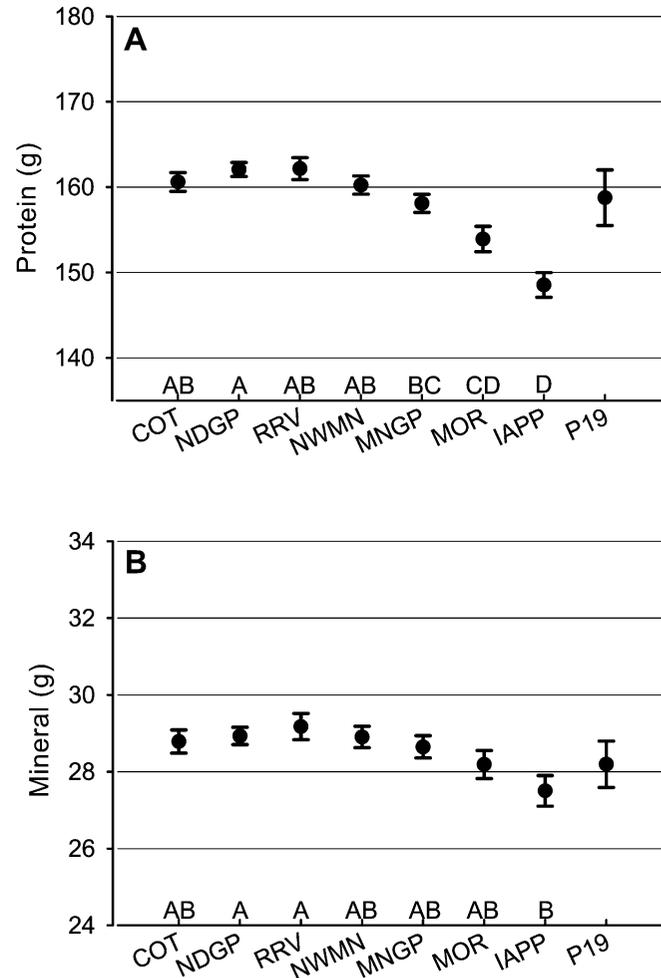


FIG. 4. Least-square mean (\pm SE) (A) protein and (B) mineral reserves of female Lesser Scaup collected during spring migration (years 2003–2005 pooled) by regions (abbreviations are the same as in Fig. 3). Capital letters are Tukey-Kramer adjusted mean grouping at $P < 0.05$. Pool 19 data are from Anteau (2002) and are included as a reference; no statistical comparisons were made to P19.

to consider potential annual variations at Pool 19 in our statistical models of lipid reserves and body mass in the Upper Midwest.

Lipid reserves and body mass in the Upper Midwest.—Anteau and Afton (2004) hypothesized that current low lipid-reserve levels of female scaup in northwestern Minnesota indicated a landscape-scale decline in lipid reserves occurring somewhere between Pool 19 and northwestern Minnesota. In the present study, we documented low levels of lipid reserves and body mass across Iowa, Minnesota, and North Dakota, which were similar to or less than values reported as low for northwestern Minnesota and markedly lower than values reported at Pool 19 (Anteau and Afton 2004). Moreover, similar to our data, lipid reserves of female scaup collected in eastern South Dakota in 2003 and 2004 also were low (83.3 ± 4.5 [SE] g; Strand 2005). Collectively, these results are of concern because females should be, on average, accumulating or at least maintaining lipid reserves during spring migration (Anteau and Afton 2004).

Lipid reserves of scaup during migration are influenced by habitat conditions at the collection site and previous stopover sites on their migration path (Anteau and Afton 2004). However, plasma-lipid-metabolite levels of scaup during migration are influenced only by habitat conditions at the collection site, because lipid metabolites have rapid turnover rates in scaup and other birds (Anteau and Afton 2008c). Based on plasma-lipid-metabolite data, female scaup increased lipid reserves at Pool 19, but catabolized lipid reserves while on stopover areas throughout the Upper Midwest in springs 2004–2005 (Anteau 2006). Generally, regions of the Upper Midwest where females had the highest rate of lipid catabolism were the same regions where we observed the lowest lipid reserves (Anteau 2006). Our results indicate that a large portion of females in the continental scaup population have low levels of lipid reserves and catabolize lipid reserves while migrating through the Upper Midwest, which is consistent with a major prediction of the SCH.

The observed low lipid reserves of female scaup probably are attributable to the reduced availability of macroinvertebrate prey—specifically their preferred food, amphipods—on spring stopover areas in the Upper Midwest (Strand 2005; Anteau and Afton 2006, 2008a, b, 2009; Anteau et al. 2007). Wetland quality and amphipod densities currently are low in the Upper Midwest and especially low in Iowa and southern Minnesota (Anteau and Afton 2008a, Strand et al. 2008). Aggregate percentages of amphipods in scaup diets were lower throughout Iowa and Minnesota than those reported historically, and scaup currently consume less food (49–52% dry mass), on average, than they did historically throughout the Upper Midwest (Anteau and Afton 2006, 2008b).

Macroinvertebrate densities vary annually within wetlands in response to varying water regimes and winter severity (Euliss et al. 1999) and could influence annual levels of nutrient reserves in scaup. However, we found that spring body mass and lipid and protein reserves of females did not vary annually in the Upper Midwest in 2003–2005. Scaup are highly mobile during spring migration and move relatively slowly across the Upper Midwest (Afton 2008); the observed middle of spring migration is ~45 days later 900 km farther north, in Northwestern Minnesota, than at Pool 19 (Anteau and Afton 2004). Therefore, small annual variations in food resources available to scaup may not greatly influence nutrient reserves in scaup, because mobile females select the best wetlands to forage on in any given year (Anteau and Afton 2009).

Females in IAPP, MOR, and MNGP generally had lower body mass than those in other regions; however, lipid reserves of females generally varied less among regions. Females in IAPP, MOR, and MNGP also generally had lower protein and mineral reserves than females in more northerly regions, and this likely explains some of the regional variation in body mass. As reported for Lesser Snow Geese (*Chen caerulescens caerulescens*; Alisauskas 1988), protein and mineral reserves of female scaup generally increase with latitude of collection sites during spring migration (see Anteau 2002). Accordingly, latitude must be considered as an interacting factor when researchers use body mass as an index for lipid reserves during spring migration or early summer.

The spring condition hypothesis.—Two key factors affecting continental waterfowl populations include female survival and recruitment (Newton 1998, Hoekman et al. 2002). With the

exception of exceedingly heavy individuals, migratory birds generally exhibit a positive relationship between body condition and survival (for scaup, see Pace and Afton 1999), which may be especially strong during spring migration, a nutritionally costly period with potential for extreme weather events (Newton 2006, 2007). Furthermore, foraging efficiency of scaup is low in the Upper Midwest and, especially, in Iowa, which causes females there to forage more intensively while obtaining less food (Anteau and Afton 2009). Increased foraging activity generally increases predation risk (Lima and Dill 1990, Drent et al. 2003, Prop et al. 2003). A relatively large proportion of females collected throughout the Upper Midwest appeared to be emaciated and weighed <650 g, especially in Iowa. Moreover, the observed low lipid reserves of migrating females suggests that female survival during migration through the Upper Midwest may be lower now than it was historically. For example, females that stop in Iowa or southern Minnesota with low lipid reserves may have a particularly reduced likelihood of surviving spring migration because food resources and foraging efficiency are low in these areas (Anteau and Afton 2008a, b, 2009).

Nutrition during migration also may influence the probability that a female will attempt to breed. The onset of rapid ovarian follicle development in scaup appears to be regulated by a nutrient-reserve threshold (Reynolds 1972, Esler et al. 2001, DeVink et al. 2008). Early ovarian follicle development begins ~60 days before initiation of rapid follicle development (Bluhm 1992). Given a six-day rapid follicle development (Afton and Ankney 1991, Alisauskas and Ankney 1992) and average nest-initiation dates (Afton 1984, Austin et al. 1998, Brook 2002, Koons and Rotella 2003), scaup would be initiating early ovarian follicle development in early to mid-April, while migrating through the Upper Midwest. If early stages of follicle development also are regulated by nutrition, then nutritional stress during migration may delay nest initiation or decrease nesting propensity, regardless of female body condition upon arrival on breeding areas. In a population of Eurasian Teal (*Anas crecca*), an income breeder, mean body mass during late winter and early spring accounted for >40% of the variation in the proportion of juveniles in the subsequent fall (Guillemain et al. 2008), which suggests that some mechanism regulating breeding productivity acts early in the annual cycle.

Scaup may adjust their migratory behavior to skip over the Upper Midwest because of decreases in high-quality food resources across this landscape (Anteau and Afton 2008a, b; Strand et al. 2008). Observed lipid reserves of females at Pool 19 (Anteau and Afton 2004) are large enough for scaup to fly 1030–1380 km to skip over the Upper Midwest, but such a flight would, on average, nearly deplete their lipid reserves, according to calculations by Badzinski and Petrie (2006). However, scaup may be able to accumulate needed reserves on stopover areas north of the Upper Midwest; wild scaup were capable of increasing body mass by ≤60 g per day under ideal foraging conditions at Pool 19, where abundant natural foods were supplemented by corn (Anteau 2006, Anteau and Afton 2008c). However, female scaup implanted with satellite transmitters at Pool 19 in springs 2007 and 2008 did not skip over the Upper Midwest (Afton 2008). Furthermore, decreases in availability and quality of scaup foods in the Upper Midwest have been linked to agricultural impacts on wetland quality and increased abundance of fish (Anteau 2006, Anteau and Afton 2008a). Current scaup food resources in prairie Canada are unknown, but

wetlands in this area also are located within a similarly agriculturally dominated landscape (Gleason et al. 2005, Euliss et al. 2006). Thus, scaup may not be able to quickly increase lipid reserves on stopover sites in prairie Canada and may arrive on breeding areas farther north with small lipid reserves.

Clutch size, nest success, duckling survival, and post-fledging survival generally are negatively correlated with nest initiation dates among northern nesting waterfowl (Afton 1984, Rohwer 1992, Esler et al. 2001, Blums et al. 2002, Brook 2002). Female Barnacle Geese (*Branta leucopsis*) that arrived late or in poor condition on breeding areas had greater lipid-deposition rates, but did not achieve the final lipid reserves of those that arrived earlier or in better condition (Prop et al. 2003). Accordingly, females that arrive on breeding areas late or with small lipid reserves and do breed probably nest later (Reynolds 1972, Esler et al. 2001) and, concomitantly, fledge fewer young.

Previous studies concluded that scaup are nesting later than they did historically (Brook 2002, Koons and Rotella 2003). However, DeVink et al. (2008) recently concluded that there was no directional pattern in nest initiation dates of scaup at Erickson, Manitoba (25 June [Hammell 1973], 15 June [Afton 1984], and 24 June [Koons and Rotella 2003]) and Yellowknife, Northwest Territories (7–13 June [Toft et al. 1984], 19 and 21 June [Brook 2002], and 12 June [DeVink et al. 2008]). However, DeVink et al. (2008) cited data from Hammell (1973) that were biased late because most of the study area was searched only once between June and August and portions of the study area were not searched until mid-July. Accordingly, early nests would be included in Hammell's (1973) analysis only if those nests survived until near hatching date. Moreover, Hammell (1973) likely included many re-nests, but re-nests were excluded by much more intensive efforts of Afton (1984) and Koons and Rotella (2003). Furthermore, DeVink et al. (2008) estimated nest initiation date from examination of ovarian follicle development of collected females. However, this estimate was biased early because (1) the timing of collections (May 24–June 21) was too early to include late-nesting females and (2) females that had not yet initiated rapid follicle development at the time of collection, but would have initiated later, were excluded from the analysis. Thus, excluding these biased data (Hammell 1973, DeVink et al. 2008), scaup currently are nesting later than they did historically on important breeding areas (Brook 2002, Koons and Rotella 2003). Thus, the fixed-cue threshold for timing reproduction, as proposed by DeVink et al. (2008) for scaup, is not supported, because recent nest-initiation dates are later than those reported historically.

The steepest population declines of scaup likely are occurring in the Boreal Forest of western Canada (Afton and Anderson 2001). DeVink et al. (2008) reported that body mass of females collected in springs 2003–2004 at Slave Lake in Alberta and at Yellowknife and Inuvik in the Northwest Territories were, respectively, higher than, lower than, and similar to those of females collected at Yellowknife in 1968–1970. However, our results suggest that body mass is a poor indicator of lipid reserves in comparisons among sites of different latitudes. We suspect that many migrating female scaup arrive late on breeding areas, with low lipid reserves, or not at all, because they had low lipid-reserve levels and catabolized lipid reserves on stopover areas in the northern portions of the Upper Midwest (Anteau 2006). Indeed, DeVink et al. (2008)

reported lipid-reserve levels of 61.7 ± 2.8 (SE) g for female scaup during pre-rapid follicle development at these three discrete locations in the Canadian Boreal Forest. This level of lipid reserves is markedly lower than historical values in females in northwestern Minnesota and southwestern Manitoba (Anteau and Afton 2004) and is similar to or lower than those observed in the present study. Scaup initiate nesting at similar times in Boreal Forest and in the Prairie Parklands despite later arrival times in the Boreal Forest (Austin et al. 1998). Therefore, nutrients acquired during migration likely are more important for those nesting in the Boreal Forest because there is less time for females between arrival and egg laying to acquire nutrients in the Boreal Forest (Austin et al. 1998, Afton and Anderson 2001).

The relationship between body condition during spring migration and recruitment in various migratory bird species generally is positive and consistent with the SCH (Arzel et al. 2006, Drent et al. 2006, Newton 2006). In both capital and income breeders, body condition during winter and spring were positively related to proportions of juveniles later that fall (Alisauskas 2002, Guillemain et al. 2008). Ebbinge and Spaans (1995) reported that female Dark-bellied Brant (*B. bernicla bernicla*) with the most nutrient reserves in spring were more likely to return with young in the autumn than were lighter females. American Redstarts (*Setophaga ruticilla*) with greater lipid reserves arrived earlier on breeding areas, laid larger clutches, and had heavier nestling mass than did those that arrived on breeding areas with smaller lipid reserves (Smith and Moore 2003). However, proximate mechanisms causing relationships between nutrition during spring migration and subsequent recruitment likely differ between passerines and larger-bodied waterfowl. In passerines, lipid reserves allow males to arrive earlier and establish high-quality nesting territories or have more opportunities for mate acquisition (Smith and Moore 2003, Kokko et al. 2006); however, in waterfowl, lipid reserves of females apparently allow for earlier breeding and, thus, greater reproductive success (Prop et al. 2003). Regardless of the proximate mechanisms acting upon recruitment in migratory birds, body condition during migration or upon arrival on breeding areas can be an important factor influencing recruitment.

Implications for conservation.—The observed low levels of lipid reserves of female scaup within the Upper Midwest are consistent with a major prediction of the SCH. However, to more rigorously evaluate the importance of the SCH to the scaup decline and the potential for population recovery, further information is needed concerning (1) migration corridors, distances and rates of migratory flights, stopover times, and breeding affinities of female scaup during spring migration; (2) spring survival of females and how it is influenced by nutrition during migration; (3) nutrient-reserve levels, lipid metabolism, and food resources of female scaup migrating through the Prairie Pothole, Parkland, and Boreal Forest regions of Canada; (4) lipid-reserve levels and arrival times of females that do arrive on randomly selected breeding areas across the breeding range; and (5) at what point (if any) a nutrient reserve threshold initiates or regulates ovarian follicle development in female scaup, and how breeding propensity is influenced by nutrient reserves.

Growing evidence suggests that underlying mechanisms of the SCH play an important role in influencing avian populations (Arzel et al. 2006, Drent et al. 2006, Newton 2006), which

has important implications for avian conservation. When conservation programs and activities to increase recruitment are warranted, a management focus on spring-migration stopover habitats may be beneficial for effective conservation, protection, and management of migratory avian populations.

ACKNOWLEDGMENTS

We thank the following for assistance with collection of birds or laboratory analyses: L. Ball, R. Brady, W. Brininger, Jr., P. Bultsma, S. Caron, R. Durham, R. Faulkner, A. Greer, A. Hancock, D. Hoffman, J. Huener, R. Jensen, J. Kavanagh, A. Leach, J. Leslie, P. Mathews, S. McLoed, R. Meidinger, B. Meixell, D. Nelson, M. Olinde, R. Olsen, R. Renner, D. Soehren, S. Solieu, S. Stephens, M. Szymanski, A. Tobiason, T. Vidrine, J. Vorland, J. Walker, R. Warhurst, and G. Zenner. We acknowledge numerous landowners that allowed us to work on their property. We thank M. Anderson, A. Anteau, J. Austin, B. Batt, J. Berdeen, F. Bolduc, E. Bowers, T. Bishop, K. Brennan, R. Durham, J. Fernandez, M. Gulick, A. Hancock, R. Helm, D. Hertel, R. Hier, K. Howard, M. Johnson, R. Johnson, J. Lawrence, C. Loesch, J. Markl, R. Markl, T. Michot, E. Moser, W. Norling, J. Nyman, M. Ohide, B. Pardo, S. Piegras, D. Rave, R. Reynolds, J. Ringelman, F. Rohwer, T. Rondeau, B. Schultz, S. Stephens, M. Szymanski, P. Telander, B. Wehrle, and G. Zenner for their help or support of the project. We thank the following organizations for financial or in-kind support: Ducks Unlimited Inc. USA, Federal and Winchester Cartridge companies, Iowa Department of Natural Resources, Institute for Wetland and Waterfowl Research (IWWR) of Ducks Unlimited Canada, IWWR of Ducks Unlimited Canada through the Bonnycastle Fellowship, Louisiana Department of Wildlife and Fisheries, Louisiana State University through the Bosch Fellowship, Minnesota Department of Natural Resources, Minnesota Waterfowl Association, North Dakota Game and Fish Department, Prairie Pothole Joint Venture, Upper Mississippi River and Great Lakes Region Joint Venture, U.S. Fish and Wildlife Service Regions 3 and 6 Habitat and Population Evaluation Team offices, U.S. Geological Survey (USGS) Louisiana Cooperative Fish and Wildlife Research Unit, and USGS National Wetland Research Center. Lastly, we thank D. Ankney, Q. Guo, S. McWilliams, and anonymous reviewers for providing valuable comments to improve the manuscript.

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Associate Editor: S. R. McWilliams