

FACTORS AFFECTING LIPID RESERVES AND FORAGING ACTIVITY OF BUFFLEHEADS, COMMON GOLDENEYES, AND LONG-TAILED DUCKS DURING WINTER AT LAKE ONTARIO

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Abstract. To identify factors potentially limiting the abundance of ducks at the northern latitude of Lake Ontario, we investigated whether the lipid levels and foraging behavior of sea ducks wintering there were best explained by endogenous or exogenous mechanisms. We used an information-theoretic approach to evaluate if date (14 December–15 March; endogenous mechanism), percentage ice cover of Lake Ontario (long-term exogenous mechanism), short-term ambient temperature (exogenous mechanism), or some combination of these factors best explained variation in lipid reserves and foraging effort of the Bufflehead (*Bucephala albeola*), Common Goldeneye (*B. clangula*), and Long-tailed Duck (*Clangula hyemalis*). In the Long-tailed Duck, date explained lipid declines best, whereas in the Bufflehead and Common Goldeneye lipid reserves varied negatively with percentage ice cover. Conditions at our study site appeared to necessitate foraging because all species foraged, on average, $\geq 69\%$ of daylight hours, and they increased foraging through the winter and when temperatures decreased. We calculated the number of days until lipid reserves should reach zero (i.e., fasting potential). Fasting potential differed in December, when Buffleheads (11 fasting days) had proportionately more lipid than did Common Goldeneyes (8 days) and Long-tailed Ducks (5 days). By March, the fasting potentials of the three species were similar (4 days), suggesting their survival strategies during similar winter conditions differed. Spatial and temporal modeling of temperature and ice cover with sea duck abundance at Lake Ontario and other Great Lakes may clarify factors that limit sea duck use of the region during winter.

Key words: endogenous mechanism, exogenous, foraging behavior, Great Lakes, lipid reserve, sea duck, winter.

Factores que Afectan las Reservas de Lípidos y la Actividad de Forrajeo en *Bucephala albeola*, *B. clangula* y *Clangula hyemalis* durante el Invierno en el Lago Ontario

Resumen. Para identificar los factores que potencialmente limitan la abundancia de patos en la latitud norte del Lago Ontario, investigamos si los niveles de lípidos y el comportamiento de forrajeo de los patos marinos que invernán allí podían explicarse mejor por mecanismos endógenos o exógenos. Usamos un enfoque teórico de la información para evaluar si la fecha (14 diciembre–15 marzo; mecanismo endógeno), el porcentaje de hielo que cubre el lago (mecanismo exógeno de largo plazo), la temperatura ambiente de corto plazo (mecanismo exógeno) o alguna combinación de estos factores explicaba mejor la variación en las reservas de lípidos y en el esfuerzo de forrajeo de *Bucephala albeola*, *B. clangula* y *Clangula hyemalis*. En *C. hyemalis*, la fecha explicó mejor las disminuciones de los lípidos, mientras que en *B. albeola* y *B. clangula* las reservas de lípidos variaron negativamente con el porcentaje de cobertura de hielo. Las condiciones en nuestro sitio de estudio parecen exigir un alto esfuerzo de forrajeo porque todas las especies forrajearon, en promedio, $\geq 69\%$ de las horas de luz y aumentaron el esfuerzo de forrajeo a lo largo del invierno y cuando las temperaturas disminuyeron. Calculamos el número de días necesarios para que las reservas de lípidos llegaran a cero (i.e., potencial de ayuno). En diciembre, el potencial de ayuno fue distinto, cuando *B. albeola* (11 días de ayuno) presentó proporcionalmente más lípidos que *B. clangula* (8 días) y *C. hyemalis* (5 días). En marzo, los potenciales de ayuno de las especies fueron similares (4 días), sugiriendo que sus estrategias de supervivencia difirieron con condiciones invernales similares. El modelado espacial y temporal de la temperatura y la cobertura de hielo con la abundancia de los patos marinos en el Lago Ontario y otros Grandes lagos podría clarificar los factores que limitan el uso de la región en el invierno por parte de los patos marinos.

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INTRODUCTION

Lipid reserves in waterfowl often increase through the autumn before the onset of winter and then decline through early spring (Ryan 1972, Peterson and Ellerson 1979, Dugan et al. 1981, Baldassarre et al. 1986, McNamara and Houston 1990, Kestenholz 1994). Lipids supply energy for homeostasis and periods of fasting (i.e., migration, nighttime roosting, and periods of food shortage; Stokkan et al. 1985, Newton 2008). In some species of birds, declines in lipid reserves through the winter may be caused by an endogenous mechanism that presumably evolved in response to reduced probability of energy deficits as spring approaches (Dugan et al. 1981, Baldassarre et al. 1986, Witter and Cuthill 1993). However, the magnitude of changes in lipid reserves in birds during winter can be modified by relatively unpredictable exogenous factors such as prolonged periods of cold, snow and ice cover, or food shortages that influence energy expenditure and acquisition (King and Farner 1966, Dugan et al. 1981, Baldassarre et al. 1986, Rave and Baldassarre 1991, Cuthill et al. 2000). Energy expenditure by diving homeotherms increases with dive duration and with ambient temperatures decreasing below a critical threshold (Kendeigh et al. 1977, Lovvorn et al. 1991). Thus, in diving ducks, long- and short-term fluctuations in ambient temperature and ice coverage, as well as the geographic extent of such environmental conditions, could influence the energy expenditure and acquisition of these ducks, thereby influencing their ability to maintain lipid reserves adequate for survival (Albright et al. 1983, Alerstam 1990).

The lower Great Lakes, which includes lakes Erie, Ontario and St. Clair, provide staging and winter habitat for millions of ducks, geese, and swans in eastern North America (Dennis et al. 1984, Prince et al. 1992). In this region, most inland lakes, marshes, and other sheltered bodies of shallow water often freeze by early winter, but the wind-exposed shorelines and relatively deep waters of the lower Great Lakes often do not entirely freeze (Assel 2003) and thus provide foraging habitat for diving ducks (Prince et al. 1992, Petrie and Schummer 2002). The 10-fold increase in the abundance of diving ducks wintering in the lower Great Lakes from the late 1980s to the 1990s corresponded with the introduction and proliferation of dreissenid mussels (the zebra mussel, *Dreissena polymorpha*, and quagga mussel, *D. bugensis*; Wormington and Leach 1992, Hamilton and Ankney 1994, Petrie and Knapton 1999). After the introduction of dreissenid mussels, studies focused on determining if diving duck abundance was related to changes in food availability and diet (Hamilton and Ankney 1994, Petrie et al. 2007, Schummer et al. 2008a,b, Ware 2008, Brady 2009, Schummer et al. 2010). Although lipid levels during winter can influence survival, local abundance, and distributions of birds (Albright et al. 1983, Alerstam 1990, Newton 2008), no studies have evaluated how exogenous factors may influence lipid reserves in diving ducks wintering in the lower Great Lakes.

In winter, foraging and resting entail trade-offs (Lima 1986, Bednekoff and Houston 1994). Eating to increase lipid reserves can increase survival (Haramis et al. 1986, Bednekoff et al. 1994, Lilliendahl et al. 1996), but this activity carries risks of predation and environmental exposure that may affect energy expenditure and survival (Lima 1986, Bednekoff and Houston 1994). Thus birds must adjust time spent foraging (foraging effort) to a level necessary to meet current and predictable future nutritional needs (Lima 1986, Rogers 1987, Baldassarre and Bolen 2006). When it is anticipated that future energetic demands will exceed daily caloric intake, foraging effort is increased to store lipids (Lima 1986, Rogers 1987). Therefore, simultaneous monitoring of foraging effort and lipid reserves may provide insight into mechanisms influencing energy budgets in birds (sensu Raveling 1968, Whyte and Bolen 1984, Baldassarre et al. 1986).

This study was part of a larger project to determine factors that could limit the number of sea ducks wintering at the lower Great Lakes (Schummer 2005, Schummer et al. 2008a, b, 2010, 2011). Lakes Erie and St. Clair are normally $\geq 80\%$ covered with ice by early January, whereas Lake Ontario has substantially less ice cover (35–50% maximum ice cover between February and the first week of March) through much of the winter (Assel and Rodionov 1998, Assel 2003, Assel 2005a). Our goal was to evaluate endogenous and exogenous models potentially influencing lipid levels and foraging effort by sea ducks wintering at Lake Ontario to determine if exogenous factors contributed to changes in sea duck abundance at this wintering location. We evaluated a set of candidate models to determine whether study date (endogenous mechanism), percentage ice cover of Lake Ontario (long-term exogenous mechanism), short-term ambient temperature (exogenous mechanism), or some combination of these factors best explained variation in lipid reserves and foraging effort in the Bufflehead (*Bucephala albeola*), Common Goldeneye (*B. clangula*), and Long-tailed Duck (*Clangula hyemalis*) during winter at Lake Ontario.

METHODS

STUDY AREA

Our study took place at Lake Ontario, along the southeast shoreline of Prince Edward County, Ontario (44° 00' N, 77° 55' W), during two winters, December–March 2002–2003 and 2003–2004. Within this area, the substrate and vegetation vary from mud and abundant aquatic macrophytes in the west to limestone rock with little or no vegetation at the east end of Prince Edward Bay (Barton 1986, see Schummer 2005 for more detailed descriptions). Therefore, during winter when shallow water at the west end of the bay was covered with ice, food was generally limited to benthic macroinvertebrates (Schummer 2008a,b). Dreissenid mussels, Amphipoda, Chironomidae, and other macroinvertebrates occur throughout the study area and provide an abundant and readily available food supply throughout the winter (Schummer 2008a).

BIRD COLLECTIONS AND FIELD MEASUREMENTS

Under Canadian Wildlife Service scientific-capture permit CA 0166, we collected 269 Buffleheads, 224 Common Goldeneyes, and 256 Long-tailed Ducks over the course of the study. We collected the birds by shooting over decoys ($n = 558$), jump shooting from shore ($n = 90$), pass shooting ($n = 5$), and shooting from a canoe after floating into flocks ($n = 96$). We attempted to collect 50 birds per species per month distributed evenly through each month, by rotating through 26 locations along 60 km of shoreline. On collection days, we selected one of the 26 potential shooting locations on the basis of ice cover, wind conditions, days since last collection at a location (≥ 2 days), and species collection needs. To minimize including spring migrants in the analysis, we ceased collecting when we observed large changes in waterfowl abundance during late-season weekly surveys (Schummer 2005). To index structural size of the birds, we took the following measurements: (1) Body length (BODY) from the tip of the bill to the base of the middle retriix (± 1 mm), (2) length of the flattened wing (WING; ± 1 mm), and (3) total tarsus (TARSUS; ± 0.1 mm; Dzubin and Cooch 1992). Ducks were tagged, double bagged, frozen, and transported to a lab at the University of Western Ontario, London, Ontario.

LAB MEASUREMENTS AND PROXIMATE ANALYSIS

In the lab, ducks were thawed at 3–5 °C and plucked by hand, skinned, and dissected. We took wet weights (± 0.01 g) of (1) the plucked skin weight (SKIN, including subcutaneous fat but excluding skin from the distal end of the humerus to the tip of the wing and the area surrounding the uropygial gland), (2) abdominal fat (ABDOMINAL), which lies in the abdominal cavity under the subcutaneous fat and partially surrounded by the pubic bone, and (3) fat from the large intestine, caecum, and small intestine (VISCERAL; Chappell and Titman 1983). We sexed each bird by examining its reproductive organs and aged it by the presence or absence of the bursa of Fabricius. We used a species-specific, subsampling approach to determine whether SKIN, ABDOMINAL, VISCERAL, or a combination of these weights best approximated the actual lipid content of each bird. For proximate analyses, we used ten birds of each age (juvenile and adult) and sex class of each species (40 birds per species). We removed the feet, bill, tongue, ingesta, and feathers, then combined the remainder of the carcass (including previously measured tissues), refroze it, and sent it to the Avian Energetics Lab (AEL) at Bird Studies Canada, Port Rowan, Ontario for proximate analyses. At the AEL, carcasses were thawed, homogenized in a Hobart meat grinder, and dried to a constant weight at 80 °C (Kerr et al. 1982). Proximate analyses of carcass homogenate, following Afton and Ankney (1991), included (1) extracting lipids from a 10-g subsample of ground homogenate with petroleum ether as a solvent (Dobush et al. 1985) in a modified Soxhlet apparatus and (2) multiplying the dry weight of the carcass by the proportion of lipid that the 10-g subsample contained to determine the dry weight of the carcass's fat (LAB

FAT). We restricted our analysis to factors influencing lipid reserves in wintering sea ducks. In winter, fluctuations in the body mass of waterfowl are attributable to changes in lipid reserves; protein, water, and ash do not change appreciably and are not substantial sources of energy for homeostasis (Baldassarre et al. 1986, Baldassarre and Bolen 2006).

FORAGING EFFORT OF DIVING DUCKS

We observed behavior of diving ducks during daylight from 14 December 2002 to 15 March 2003 and 22 December 2003 to 10 March 2004 with 10 × 40 binoculars and a 10–60× spotting scope. We attempted to record 10 hr of observation per month per species and to distribute observations evenly among morning (sunrise to 10:00), mid-day (10:00 to 14:00), and evening (14:00 to sunset) periods. We spread observations throughout the study area by rotating through 31 locations along 60 km of shoreline. Observations were randomized by assignment of a species, start location, and a list of alternative locations. If the assigned species was not present at the first location or the location could not be reached because of snow or ice, the observer traveled to the next location, until the assigned species was encountered. The distances between observation locations were generally > 1 km. We defined five divisions of the study area on the basis of aspect, bathymetry, and primary substrate (see Schummer et al. 2008a). If more than one flock was present, we arbitrarily selected a flock by swinging the scope across the range of visible flocks and selecting the one closest to the center of field of view when the scope came to rest (Quinlan and Baldassarre 1984, Lovvorn 1989, Poulton et al. 2002). On arriving at a site we waited 5 min to determine the number of individuals in a flock for calculating percent foraging during the observation (Erskine 1971) and to minimize the influence of observers on behavior. Observations typically were made at distances ≥ 50 m and from blinds to limit such effects. We recorded behavior every 60 sec for 30 min, categorizing it as foraging (diving and pausing between dives), loafing (resting, preening, sleeping), locomotion (swimming and flying), courtship, or agonistic (Goudie and Ankney 1986). We recorded number of birds in each activity (later converted to percent of flock within each behavior category) every 60 sec. Data recorded by minute were averaged for the entire 30-min period. To account for changing day length we standardized data by multiplying day length by percent time foraging to determine minutes foraging per day (FORAGING EFFORT). We included only diurnal activity budgets because we observed ducks leave nearshore areas at dusk and fly toward the middle of Lake Ontario ($n > 10$). Furthermore, during four nocturnal observations (21:00) with $\geq 3/4$ moon no birds were visible or audible (e.g., Long-tailed Duck vocalizations) from shore. Thus we assumed that at night ducks roosted over deep water on Lake Ontario.

ENVIRONMENTAL CONDITIONS

We determined the percentage of ice covering the study area once each week from December to March, 2002–2003

and 2003–2004. During weekly surveys and from elevated vantage points (i.e., lake bluffs and rocks), we drew the extent of ice onto a map with a grid of 500 × 500 m cells. We determined the percentage ice cover by dividing the number of cells at least 50% covered with ice by the total number of cells within our study area. We obtained percentage daily ice-cover data for Lake Ontario from Assel (2005b), and used these values as an independent variable for ice coverage in statistical analyses because there was a high, positive correlation with ice-cover estimates for our study area (2002–2003, $r = 0.89$, $P < 0.001$, $n = 16$; 2003–2004, $r = 0.97$, $P < 0.001$, $n = 14$) and those data were available for each day of the study. We obtained daily mean temperatures from the weather station at Point Petre, at the southwestern edge of the study area (43° 83' N, 77° 15' W) (Environment Canada, Canadian Daily Climate Data; ftp://arcdm20.tor.ec.gc.ca/pub/dist/CDCD).

STATISTICAL ANALYSES

Lipid-reserve index. We used an information-theoretic approach for model selection and to calculate Akaike's information criterion (AIC) for each model (Burnham and Anderson 2002). For each species, we used Δ AIC and AIC weights (w_i) to assess relative support for linear relationships between LAB FAT and ABDOMINAL, SKIN, VISCERAL, or the sum of these three measures (PROC Mixed, SAS Institute 2009). For each species, we identified the sum of ABDOMINAL, SKIN and VISCERAL (FAT) as the best model that explained considerable variation in LAB FAT for each species (Table 1). Thus FAT was a good proxy for total lipid reserves and was used as the response variable in subsequent analyses.

Model development. We developed a candidate set of five models based on effects that represented endogenous and exogenous mechanisms that may affect lipid reserve (FAT)

dynamics and foraging behavior (FORAGING EFFORT) of wintering diving ducks:

(1) Study date (DATE [continuous]; endogenous mechanism). In birds, lipid dynamics are often explained by a seasonal, endogenous rhythm irrespective of weather severity, food availability, or availability of foraging time (Gwinner 1977, Reinecke et al. 1982, Baldassarre et al. 1986, Loesch et al. 1992).

(2) Percentage daily cover of ice on Lake Ontario (ICE [continuous]; exogenous mechanism). Ice can reduce the area available for foraging by diving ducks, and on Lake Ontario percent ice cover is positively related to the number of days with temperatures ≤ 0 °C (Assel 1980, 2003, 2005c). Thus percent ice cover may influence energy acquisition (i.e., food accessibility) and long-term energy expenditure (i.e., ambient temperature), thereby affecting lipid reserves and behavior in diving ducks.

(3) Daily mean temperature (TEMP [continuous]; exogenous mechanism). Ambient temperature influences energy budgets of homeotherms and affects their ability to store and catabolize lipids (Blem 2000). On the basis of our observations, we assumed that the sea ducks we studied roosted at night primarily over deepwater areas of Lake Ontario without feeding. Nocturnal roosting increases the likelihood that ambient temperature influences short-term, overnight changes in lipids (Biebach 1996) and foraging effort the following day. In statistical models, we used the mean temperature for the day prior to collection of specimens to determine if recent and overnight temperatures explained variation in lipid reserves. (4) DATE + TEMP and (5) ICE + TEMP. We included ICE with TEMP and DATE with TEMP because the daily mean temperature may influence the short-term amplitude of trends in lipids and foraging effort in addition to effects associated with DATE or ICE.

TABLE 1. General linear models of total lipids (g) in Buffleheads ($n = 40$), Common Goldeneyes ($n = 40$), and Long-tailed Ducks ($n = 40$) on northeastern Lake Ontario, December–March, 2002–2003 and 2003–2004.

Species _{df}	Lipid index (g) ^a	Intercept	β	Δ AIC ^b	w_i	R^2
Bufflehead _{1,38}	Skin + abdominal + visceral	-11.99	0.98	0.00	0.97	0.95
	Skin			7.3	0.03	
	Abdominal			51.2	—	
	Visceral			55.2	—	
Common Goldeneye _{1,38}	Skin + abdominal + visceral	-27.22	1.02	0.00	0.95	0.92
	Skin			6.1	0.05	
	Abdominal			47.0	—	
	Visceral			58.0	—	
Long-tailed Duck _{1,38}	Skin + abdominal + visceral	-28.76	0.97	0.00	0.95	0.92
	Skin			7.1	0.03	
	Abdominal			7.9	0.02	
	Visceral			29.3	—	

^aSkin = plucked skin wet weight; abdominal = abdominal lipid wet weight; visceral = visceral lipid wet weight.

^bThe AIC values for the top models were 291.2, 331.3, and 301.7 for the Bufflehead, Common Goldeneye, and Long-tailed Duck, respectively.

We evaluated Pearson correlation coefficients (PROC CORR, SAS Institute 2009) derived from all pairwise combinations of explanatory variables and determined that TEMP was confounded with neither DATE ($-0.20 \leq r \leq 0.43$) nor ICE ($-0.41 \leq r \leq 0.10$) for any species but that DATE and ICE were positively correlated ($0.64 \leq r \leq 0.78$). Because of the latter results, we did not include DATE and ICE together in models.

Lipid-reserve dynamics. For each species, we used Δ AIC and AIC weights (w_i) to assess the relative support for linear or quadratic effects of DATE, TEMP, and ICE to explain variation in FAT (PROC Mixed, SAS Institute 2009). We included the quadratic term to account for potential nonlinear responses lipid reserves to nonlinear increases in photoperiod and ice cover (Assel 2003). We considered models ≤ 2.0 Δ AIC units from top models and used model averaging to estimate parameters, 95% CI, and model-adjusted FAT (Burnham and Anderson 2002) when effect terms of competing models were similar (i.e., linear or quadratic). We report model-averaged parameter estimates and 95% CI from the relationship (i.e., linear or quadratic) with the lowest AIC value when both linear and quadratic models were ≤ 2.0 Δ AIC units from top models. Because DATE and ICE were correlated we also report the Δ AIC for models with the lowest AIC value that include DATE or ICE. For each set of species-specific analyses, we included PERIOD (2002–2003 or 2003–2004) in all models as a random categorical effect and we used variance components from a suite of tested covariance structures (Littell et al. 2007). Because birds collected by means of decoys may represent a biased sample (Bain 1980, Greenwood et al. 1986, Dufour et al. 1993, Pace and Afton 1999), we accounted for potential bias by including collection method as a random categorical effect. In species-specific principal components analyses (PCA) on the correlation matrices of BODY, WING, and TARSUS we found that PC1 explained substantial variation in the structural size of Buffleheads (95.2%), Common Goldeneyes (96.2%), and Long-tailed Ducks (83.9%). Therefore, we included PC1 scores as a covariate in all models to control for individual differences in structural size and enable better interpretation of results by age and sex class. We included main effects of age and sex (categorical) as well as their interactions as fixed effects in each candidate model to determine if amount and rates of change in FAT varied by age and sex classes. Studentized residual plots from all models approximated a normal distribution (Littell et al. 2007).

Foraging effort of diving ducks. For each species, we used Δ AIC and w_i to assess relative support for DATE, TEMP, or ICE (linear and quadratic relationships) in explaining variation in FORAGING EFFORT. We considered models ≤ 2.0 Δ AIC units from top models and used model averaging to estimate parameters, 95% CI, and model-adjusted FAT (Burnham and Anderson 2002) when effect terms of competing models were similar (i.e., linear or quadratic). We report model-averaged parameter estimates and 95% CI from the relationship (i.e., linear or quadratic) with the lowest AIC value when both linear and quadratic models were ≤ 2.0 Δ AIC units from top models. Because DATE and ICE

were correlated, we also report the Δ AIC for models with the lowest AIC value that include DATE or ICE. We classified PERIOD and observation location ($n = 5$) as random variables. We created two additional candidate models (TEMP [continuous] + DATE; TEMP + ICE) because proximate cues may influence the short-term amplitude of long-term trends in behavior influenced by DATE and ICE. We inspected studentized residuals (STDRES) of models for normality and identified and inspected outliers ($-3.5 \leq \text{STDRES} \leq 3.5$). We compared outcomes of statistical analyses both with the full dataset and with outliers removed.

RESULTS

LIPID-RESERVE DYNAMICS

Bufflehead. The top model that best explained FAT included ICE as a quadratic function and a negative relationship with TEMP (Table 2, Fig. 1). Furthermore, model-averaged parameter estimates included age-specific differences in lipids (Table 3, Fig. 1). The next closest model that included DATE was 34.3 AIC units from the top ICE model. Values for FAT were greatest when ICE was near zero and declined by 60% in adults (69 g) and 59% in juveniles (67 g) to the lowest FAT values at 30% and 27% ICE, respectively. In adults, FAT increased by 14% (7 g) as ICE increased from 27% to 39%, whereas juveniles showed a 28% (13 g) increase in FAT under similar ice conditions. On average, over the range of ice conditions during our study (0–39%), a change in temperature of -10°C on the day prior to specimen collection (i.e., TEMP) was related to an increase in FAT by 7.4 g (12%).

Common Goldeneye. The top model explaining variation in FAT included ICE as a quadratic function and a negative relationship with TEMP (Table 2). Furthermore, the amount and rates of change in FAT varied by age and sex class (Table 3, Fig. 2). The next closest model that included DATE was 35.4 AIC units from the top ICE model. Values for FAT were greatest when ICE was near 0% and declined to their lowest level when ICE was between 27% and 29%, depending on age/sex class (Fig. 2). Declines in FAT were 65% (111 g) in adult females, 52% (106 g) in adult males, 67% (112 g) in juvenile females, and 69% (128 g) in juvenile males (Fig. 2). On average, over the potential range of ice conditions during our study (0–39%), a change in temperature of -10°C on the day prior to specimen collection (i.e., TEMP) was related to a 4% (3.4 g) increase in FAT.

Long-tailed Duck. The top model for FAT included DATE as a linear relationship, a negative relationship with TEMP, and sex as a covariate (Table 2). Models ≤ 2 Δ AIC units from the top model also included DATE as a quadratic function (Table 2), but unexplained variation remained substantial under either linear or quadratic relationships (Fig. 3). The next closest model that included ICE was 7.4 AIC units from the top DATE model. Values of FAT for females and males declined seasonally by 21% (22 g) and 18% (20 g), respectively. After correction for structural size, males still maintained greater FAT (adjusted

TABLE 2. Mixed-effects models of FAT^a of Buffleheads ($n = 259$), Common Goldeneyes ($n = 218$), and Long-tailed Ducks ($n = 244$) collected during winter at northeastern Lake Ontario, December–March 2002–2003 and 2003–2004.

Taxon	Models ^b	K	ΔAIC^c	w_i
Bufflehead	PC1, TEMP, ICE, ICE \times ICE	5	0.0	0.48
	PC1, TEMP, age, ICE, ICE \times ICE	7	1.4	0.24
	Null	1	319.9	0.00
Common Goldeneye	PC1, age, sex, age \times sex, ICE, ICE \times ICE	12	0.0	0.29
	PC1, TEMP, age, sex, age \times sex, ICE, ICE \times ICE	13	0.5	0.23
	PC1, TEMP, age, sex, ICE, ICE \times ICE \times age \times sex	12	0.6	0.22
	PC1, age, sex, ICE, ICE \times ICE \times age \times sex	11	1.6	0.13
	Null	1	252.7	0.00
Long-tailed Duck	PC1, TEMP, sex, DATE	6	0.0	0.20
	PC1, sex, DATE, DATE \times DATE	6	1.4	0.10
	PC1, TEMP, sex, DATE, DATE \times DATE	7	1.4	0.10
	PC1, sex, DATE	5	1.5	0.09
	Null	1	145.4	0.00

^aFAT = the sum of wet weights of plucked skin, abdominal fat and visceral fat (g).

^bModels incorporated parameters of structural size (PC1), age, sex, percent ice cover on Lake Ontario (ICE), daily mean temperature for the day prior to specimen collection (TEMP), and study date (DATE). Collection PERIOD (2002–2003 or 2003–2004) and collection method were included as random variables.

^cModels are sorted by AIC, and models with $\Delta AIC \leq 2.0$ and null models are shown. The AIC values for the top models were 2314.8, 2156.7, and 2300.8 for Bufflehead, Common Goldeneye, and Long-tailed Duck, respectively.

$\bar{x} = 100.53 \pm 1.21$) than females (92.85 ± 0.84) through the winter (Table 3, Fig. 3). On average, over the range of dates of our study, late December through March, a change in temperature of -10 °C on the day prior to specimen collection (i.e., TEMP) was related to an increase in FAT by 4.3 g (4%).

FORAGING EFFORT

We recorded 124, 135, and 124 diurnal observations to determine the FORAGING EFFORT of Buffleheads, Common

Goldeneyes, and Long-tailed Ducks, respectively. The data on Bufflehead foraging contained three outliers ($STDRES > -3.5$)/leverage points, so residuals did not conform to a normal distribution; they approximated a normal distribution after removal of the outliers (Littell et al. 2007). Analyses produced similar results with and without outliers removed, so results that follow for all species are based on analyses of full datasets.

Bufflehead. Variation in FORAGING EFFORT was best explained by a quadratic function of DATE (Table 4, Fig. 4).

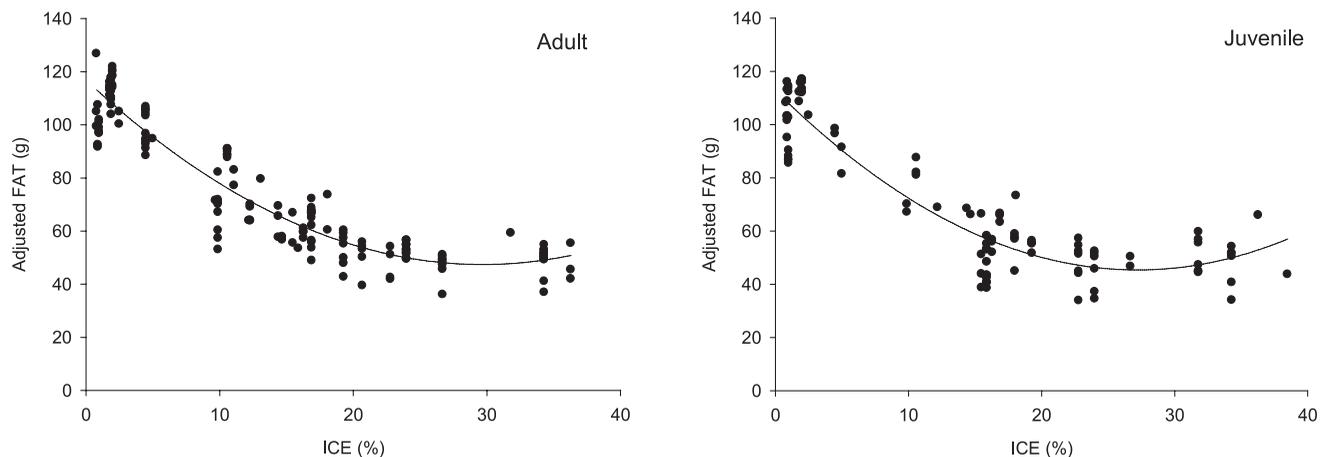


FIGURE 1. Lipid-reserve index (FAT) in relation to percentage ice cover of Lake Ontario (ICE) for Buffleheads collected on northeastern Lake Ontario, December–March 2002–2003 and 2003–2004, adjusted for variation explained by model parameters; thus plot residuals represent variation remaining unexplained after modeling.

TABLE 3. Parameter estimates (θ), standard errors, and 95% confidence intervals derived from candidate models ($\Delta AIC \leq 2$) for FAT^a in Buffleheads ($n = 259$), Common Goldeneyes ($n = 218$), and Long-tailed Ducks ($n = 244$) wintering on northeastern Lake Ontario, December–March, 2002–2003 and 2003–2004.

Taxon ^b	Parameter ^c	θ	SE	95% CI
Bufflehead	Intercept	114.246	6.757	92.937 to 135.552
	Structural size	3.783	0.771	2.265 to 5.301
	TEMP	-0.744	0.172	-1.084 to -0.405
	Age (A)	-0.806	0.919	-2.616 to 1.004
	ICE	-4.533	0.396	-5.313 to -3.752
	ICE \times ICE	0.075	0.012	0.052 to 0.098
Common Goldeneye	Intercept	183.876	7.700	167.805 to 199.943
	Structural size	0.269	1.522	-2.731 to 3.628
	TEMP	-0.341	0.176	-0.688 to 0.006
	Age (A)	18.979	6.202	6.755 to 31.202
	Sex (F)	-20.929	10.276	-41.182 to -0.675
	Age \times sex (AF)	-13.066	5.624	-24.151 to -1.982
	ICE	-7.586	0.785	-9.134 to -6.038
	ICE \times ICE	0.077	0.018	0.041 to 0.113
	ICE \times ICE (AF)	0.052	0.018	0.016 to 0.089
	ICE \times ICE (AM)	0.058	0.012	0.034 to 0.082
	ICE \times ICE (JF)	0.052	0.015	0.023 to 0.081
	ICE \times ICE (JM)	0.026	0.016	-0.005 to 0.057
Long-tailed Duck	Intercept	189.580	27.144	136.110 to 243.050
	Structural size	7.481	1.547	4.433 to 10.529
	TEMP	-0.428	0.224	-0.869 to 0.013
	Sex (F)	14.172	5.692	2.960 to 25.384
	DATE	-0.264	0.069	-0.399 to -0.129

^aFAT = the sum of wet weights of plucked skin, abdominal fat, and visceral fat (g).

^bModel-averaged parameter estimates are reported for the Buffleheads and Common Goldeneye, whereas statistics for the Long-tailed Duck are based on the model with the lowest AIC score.

^cAbbreviations: TEMP = daily mean temperature for the day prior to specimen collection; ICE = percentage ice cover of Lake Ontario; DATE = study date (1 January = 366, etc.); A = Adult, J = Juvenile, M = Male, F = Female.

Furthermore, model-averaged parameter estimates indicated that FORAGING EFFORT increased by 5 min per day for each 10 °C decrease in TEMP (Table 5). Model-averaged FORAGING EFFORT increased by 38% (159 min) from 15 December (414 min foraging per day) through 20 February (573 min foraging per day), then remained ≥ 555 min per day through 15 March (Fig. 4).

Common Goldeneye. The top model explaining variation in FORAGING EFFORT included a linear relationship with DATE and was negatively related to TEMP (Table 4, Fig. 4). Model-averaged FORAGING EFFORT increased by 41% from 389 to 549 min foraging per day (2.7 hr) through our study period (Fig. 4). Seasonal (i.e., DATE) increases in FORAGING EFFORT were modified substantially by conditions the day preceding observations with each 10 °C decrease in TEMP increasing foraging effort by 41 min per day (Table 5).

Long-tailed Duck. Variation in FORAGING EFFORT was best explained by a linear relationship with DATE (Table 4, Fig. 4), and model-averaged parameter estimates indicated that a 10 °C decrease in TEMP increased FORAGING EFFORT by 4 min per day (Table 5). Through our study period, FORAGING

EFFORT adjusted for changes in TEMP increased by 45% from 367 to 532 min foraging per day (2.8 hr) (Fig. 4).

DISCUSSION

Exogenous factors can limit the northern limit of waterfowl ranges during winter because ice coverage, ambient temperature, and food availability can influence the ability of birds to maintain lipids for metabolic function and thus survive (Albright et al. 1983, Alerstam 1990, Morton et al. 1990, Suter and Van Eerden 1992). At our study site, lipid reserves in Buffleheads and Common Goldeneyes declined by $\geq 52\%$ as the percentage ice cover of Lake Ontario increased (from 6% to 50% in 2002–2003; from 1% to 39% in 2003–2004). Lipid reserves of Long-tailed Ducks were more stable, declining seasonally by only 18–21%. We interpreted the models of lipid reserves including study date (for the Long-tailed Duck) as endogenous lipid loss and models including percentage ice cover (for the Bufflehead and Common Goldeneye) as suggesting that environmental conditions at least

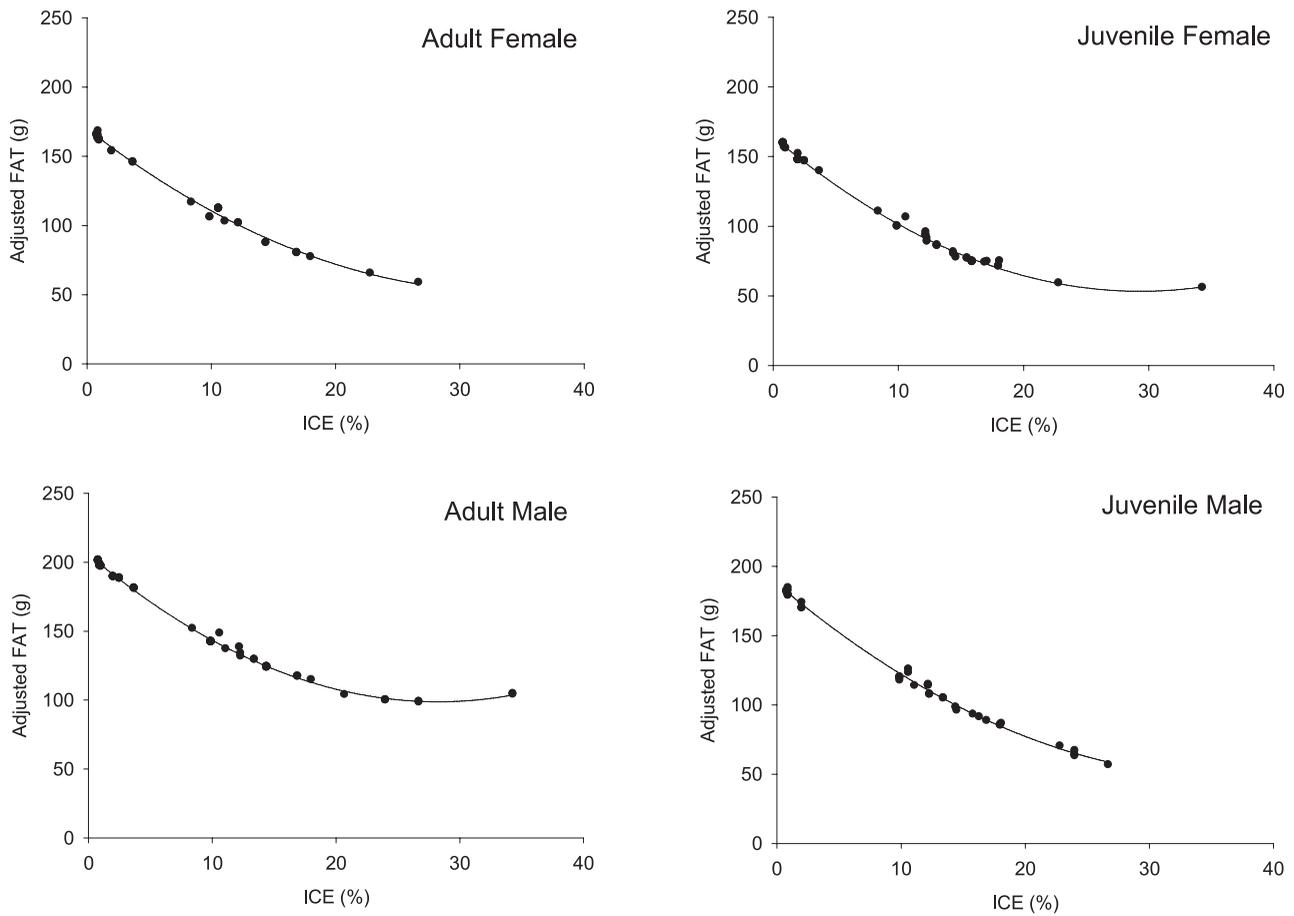


FIGURE 2. Lipid-reserve index (FAT) in relation to percentage ice cover of Lake Ontario (ICE) for Common Goldeneyes collected on northeastern Lake Ontario, December–March 2002–2003 and 2003–2004, adjusted for variation explained by model parameters; thus plot residuals represent variation remaining unexplained after modeling.

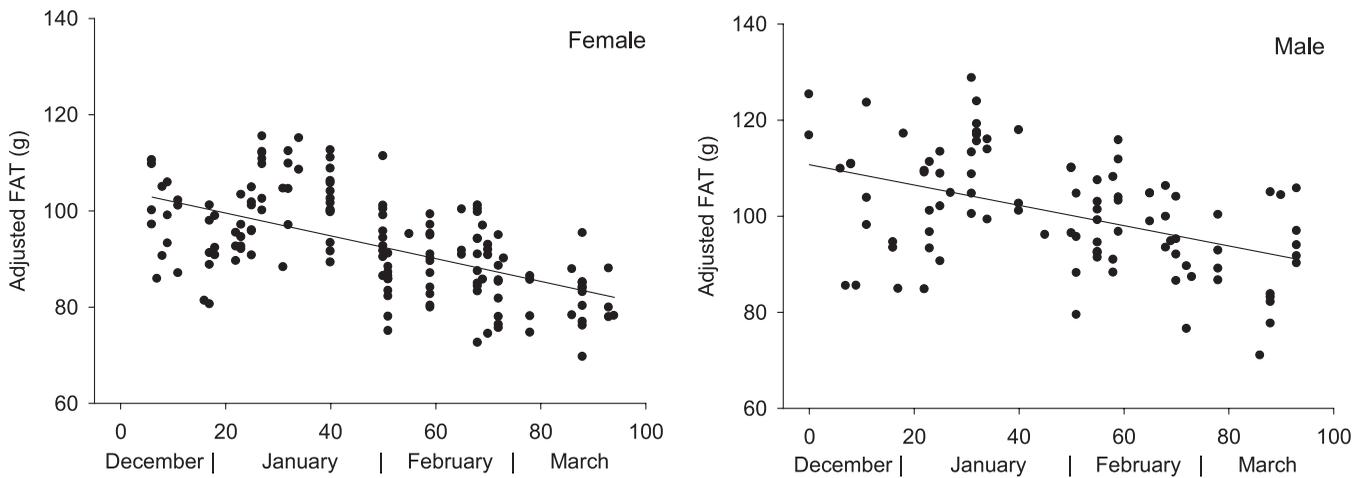


FIGURE 3. Lipid-reserve index (FAT) in relation to date for Long-tailed Ducks collected on northeastern Lake Ontario, December–March 2002–2003 and 2003–2004, adjusted for variation explained by model parameters; thus plot residuals represent remaining variation unexplained after modeling. Day 1 = 14 December.

TABLE 4. Mixed models of foraging effort (min day⁻¹) of Buffleheads ($n = 124$), Common Goldeneyes ($n = 135$), and Long-tailed Ducks ($n = 124$) wintering on northeastern Lake Ontario, December–March 2002–2003 and 2003–2004.

Taxon	Models ^a	K	ΔAIC^b	w_i
Bufflehead	DATE, DATE \times DATE	3	0.00	0.38
	TEMP, DATE	2	0.70	0.27
	TEMP, DATE, DATE \times DATE	4	1.30	0.20
	Null	1	17.00	0.00
Common Goldeneye	TEMP, DATE	2	0.00	0.41
	TEMP, DATE, DATE \times DATE	4	1.80	0.17
Long-tailed Duck	Null	1	7.80	0.01
	DATE	2	0.00	0.42
	TEMP, DATE	2	1.70	0.18
	Null	1	7.20	0.00

^aModels incorporated parameters of percent ice cover on Lake Ontario (ICE), daily mean temperature for the day prior to behavioral observations (TEMP), and study date (DATE). Collection PERIOD (2002–2003 or 2003–2004) was included as a random variable and observation location as the repeated measure.

^bModels are sorted by AIC and models with $\Delta AIC \leq 2.0$ and null models are shown. The AIC values for the top models were 1504.5, 1654.7, and 1585.8 for the Bufflehead, Common Goldeneye, and Long-tailed Duck, respectively.

partially influenced the ability of these ducks to maintain lipid reserves. In waterfowl, endogenous lipid loss is often accompanied by reductions in foraging effort even when food and foraging time are readily available (Baldassarre et al. 1986, Loesch et al. 1992). For example, Green-winged Teal (*Anas crecca*) wintering in the High Plains of Texas have been found to spend only 15–20% of the day foraging

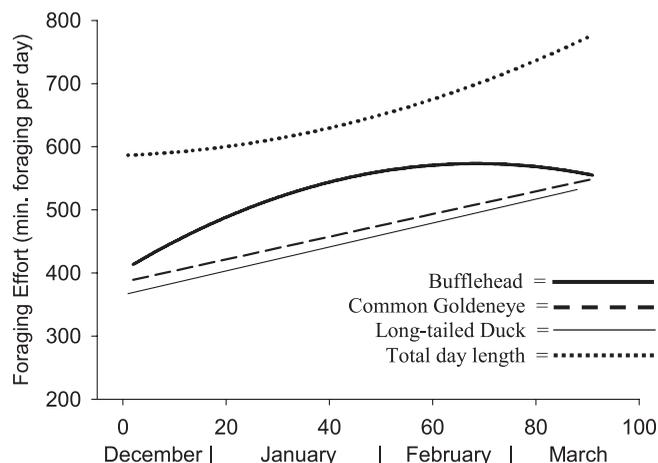


FIGURE 4. Model-averaged fit lines in foraging effort (minutes foraging per day) in relation to date for the Bufflehead (thick solid line), Common Goldeneye (thick dashed line), and Long-tailed Duck (thin solid line) on northeastern Lake Ontario, December–March 2002–2003 and 2003–2004. Dotted line = total day length. Day 1 = 15 December

despite declines in lipid reserves and high-carbohydrate foods such as corn being relatively abundant (Baldassarre and Bolen 1984). The ducks we studied foraged the majority of daylight hours, with Buffleheads to a greater degree (81%) than Common Goldeneyes (71%) and Long-tailed Ducks (69%), suggesting that conditions at our study site necessitated foraging over resting. Furthermore, increased foraging in response to declining temperatures suggests a behavioral response to proximate environmental cues. Overall, our results suggest that environmental conditions at Lake Ontario influenced lipid reserves and behavior of wintering

TABLE 5. Model-averaged parameter estimates (θ), standard errors, and 95% confidence intervals derived from candidate models ($\Delta AIC \leq 2$) for foraging effort (min. foraging per day) in Buffleheads ($n = 124$), Common Goldeneyes ($n = 135$), and Long-tailed Ducks ($n = 124$) during winter at northeastern Lake Ontario, December–March, 2002–2003 and 2003–2004.

Taxon ^a	Parameter ^b	θ	SE	95% CI
Bufflehead	Intercept	-5059.550	2657.370	-10318.900 to 200.146
	TEMP	-0.506	0.557	-1.616 to 0.590
	DATE	26.941	13.512	0.197 to 53.684
	DATE \times DATE	-0.032	0.017	-0.066 to 0.002
Common Goldeneye	Intercept	-23.904	174.810	-372.630 to 324.820
	TEMP	-4.130	1.672	-7.435 to -0.822
	DATE	1.190	0.437	-0.324 to 2.060
Long-tailed Duck	Intercept	-203.127	203.793	-606.521 to 200.263
	TEMP	-0.404	0.594	-1.580 to 0.772
	DATE	1.617	0.520	0.587 to 2.647

^aModel averaged parameter estimates are reported for Long-tailed Ducks, whereas statistics for Buffleheads and Common Goldeneyes are based on the model with the lowest AIC score.

^bAbbreviations: TEMP = daily mean temperature for the day prior to behavioral observations; DATE = study date (1 January = 366, etc.).

Buffleheads and Common Goldeneyes, whereas ice coverage and ambient temperature influenced these variables less in the Long-tailed Duck.

Percentage ice cover of the Great Lakes varies positively with the cumulative number of days $<0^{\circ}\text{C}$ (Assel 1980, 2003, 2005c). Typically, ice first forms near shore, then extends farther from shore over deeper water as the temperature of the lake decreases and the number of days $<0^{\circ}\text{C}$ accumulates (Assel 2003, 2005c). As reported by Gauthier (1993), Eadie et al. (1995), and Robertson and Savard (2002), Long-tailed Ducks feed in water up to 31 m deep, whereas Buffleheads and Common Goldeneyes also forage at the ice–water interface in shallow water (≤ 1 m deep) but not in deeper water (maximum depths 5 and 10 m, respectively; Schummer 2005). Because percentage ice cover on Lake Ontario best explained lipid reserves in shallower-diving species (i.e., Bufflehead and Common Goldeneye) but not the Long-tailed Duck, our results suggest that the differences of these species in maximum foraging depth have consequences for energy acquisition and lipid reserves during winter at the northern latitude of our study site.

Decreasing foraging time during winter relative to that at other seasons is thought to be adaptive in waterfowl because lipid reserves are not needed for migration during this period and the chance of an energy deficit decreases as spring approaches (Paulus 1988). Also, foraging effort during winter generally increases in response to declining temperatures but then declines or is interrupted when temperatures are below a critical threshold, when resting becomes beneficial (Albright 1983, Quinlan and Baldassarre 1984). In contrast, at our study site sea ducks increased foraging effort through the winter, and foraging effort did not decline even when temperatures were less than -20°C . We suggest that ducks foraged the majority of the day to store energy reserves for use during potential food shortages, periods of extended cold temperatures, and night roosting over water without foraging. Because macroinvertebrate prey were relatively abundant, did not decline appreciably in most of our study area through the winter (Schummer et al. 2008a, b), and some were high-energy foods (e.g., Amphipoda, Chironomidae; Sugden 1973, Driver et al. 1974), we do not think foraging effort was influenced by declines in food abundance through the winter. Furthermore, increased foraging effort related to decreases in ambient temperature also coincided with short-term increases in lipid reserves (Tables 3 and 5), suggesting that ducks were reacting to proximate temperature cues and able to reduce rates of lipid loss at least temporarily. Last, extensive diurnal foraging may have been necessary if ducks did not forage in our study area nocturnally. Therefore, it appeared that food resources were abundant enough to make diurnal foraging more advantageous than resting (*sensu* Brodsky and Weatherhead 1985), and

such behavior may have been necessary for homeostasis and survival at this northern latitude (Systad et al. 2000).

The three sea ducks we studied appear to have evolved different strategies to maximize winter survival. The proportion of daylight Common Goldeneyes and Long-tailed Ducks spent foraging did not increase substantially through the winter (Schummer 2005), so the seasonal increase in foraging effort (minutes foraging per day) was due mainly to increasing photoperiod. Foraging effort of Buffleheads exceeded that of Common Goldeneyes and Long-tailed Ducks, especially from December to February, which could be an attempt by Buffleheads to reduce loss of lipid reserves through this period in preparation for the peak in ice coverage at Lake Ontario that normally occurs in late February (Assel 2003). In contrast, Long-tailed Ducks may not need to maintain substantial lipid reserves because their ability to dive deeper than the other species reduces the probability that food will be unavailable when ice persists near shore for extended periods (Bednekoff et al. 1994, Barboza and Jorde 2001, Newton 2008). Like Buffleheads, Common Goldeneyes foraged in shallow areas near shore, and their lipid reserves were also best explained by percentage ice cover. However, the Common Goldeneye, being larger than the Bufflehead and Long-tailed Duck, has greater capacity to store lipids (Calder 1974, Bellrose 1980), which may provide it with an advantage in surviving the winter. For Common Goldeneyes, the increase in foraging effort in response to declining temperature was 7 times greater than that of Buffleheads and Long-tailed Ducks suggesting that Common Goldeneyes restrict increased foraging effort and related exposure to periods of declining temperatures (Lima 1986). For Buffleheads, increasing foraging effort seems an unlikely energy-acquisition strategy because the proportion of the day spent foraging was relatively high ($\bar{x} = 81.3\% \pm 15.5$) and remaining time was spent in other necessary activities such as preening and moving between foraging locales (Schummer 2005). Overall, our findings suggest that ice cover has the potential to affect survival and limit the winter range of Buffleheads to a greater extent than those of other larger-bodied or deeper-diving sea ducks wintering at the lower Great Lakes.

To interpret and compare fasting potential among species, we estimated the number of days until lipid reserves were zero (i.e., fasting days), which represents a hypothetical situation when food is depleted below foraging thresholds or functionally unavailable (e.g., ice cover; see Suter and van Eerden 1992). We estimated lipid reserves (g) of an individual from the equations in Table 1, then converted them to energy (kJ) by assuming 37.7 kJ g^{-1} of lipid (Ricklefs 1974, Blem 1976) and reduced estimates by 10% to account for lipids not available as an energy source (Ricklefs 1974, Navarro 1992). We assumed the bird was resting and using energy at 1.4 times the basal metabolic rate (BMR; Wooley and Owen 1978), where $\text{BMR} = 3.56(\text{body mass in grams})^{0.73}$ and $4.40(\text{body mass in}$

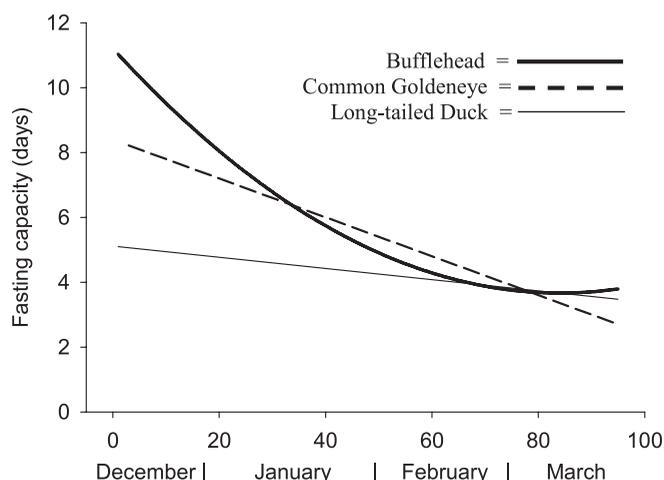


FIGURE 5. Estimated fasting capacity (number of days until lipid reserves are zero) of Buffleheads, Common Goldeneyes, and Long-tailed Ducks wintering at Lake Ontario. Estimated from metabolizable energy of lipid reserves (lipid = 37.7 kJ g^{-1}) and energetic cost of resting (basal metabolic rate $\times 1.4$; Wooley and Owen 1978). Day 1 = 15 December.

grams)^{0.73} at night and by day, respectively (Kendeigh et al. 1977). We used AIC scores (Littell et al. 2007) to fit data to either a linear or quadratic regression (Fig. 5). Although the lipid reserves and behavior dynamics of the three species differed, by March their resulting fasting capacities were similar (i.e., ~4 days) suggesting their survival strategies differed during similar winter conditions. Because we made our observations during near-normal ice conditions (see Assel 2005), we cannot be certain how greater-than-normal ice coverage or food depletion during late winter may influence lipid reserves and survival. Nonetheless, the ducks we studied were most susceptible to starvation during late winter, which is consistent with the timing of mass mortalities of diving ducks wintering at similar latitudes (Trautman et al. 1939, Boyd 1964, Suter and Van Eerden 1992).

Lipid reserves can influence survival within a season and in successive seasons and can have cross-seasonal effects on reproductive potential of birds (Haramis et al. 1986, Lindström and Piersma 1993, Barboza and Jorde 2002). The Great Lakes are near the northern limit of the winter ranges of the Bufflehead and Common Goldeneye (Bellrose 1980), but how wintering at such a northern locale influences subsequent survival and reproductive output remains poorly known. The abundance of sea ducks wintering on the lower Great Lakes increased after increases in macroinvertebrate prey (Hamilton and Ankney 1994, Petrie and Knapton 1999). Receiving less attention is how the interaction between increased food availability and ice coverage may influence the functional availability of macroinvertebrate prey and subsequent abundance of sea ducks wintering at the lower Great Lakes. Investigating and modeling spatial and temporal patterns (i.e., annual and long-term) of ice coverage of the lower Great Lakes to identify ice-free areas with water shallow enough for sea ducks and other waterfowl could

be used to forecast how climatic variability may influence the suitability of habitat for wintering waterfowl in this region.

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LITERATURE CITED

- ALERSTAM, T. 1990. Bird migration. Cambridge University Press, Cambridge, England.
- ALBRIGHT, J. J., R. B. OWEN JR., AND P. O. CORR. 1983. The effects of winter weather on the behavior and energy reserves of Black Ducks in Maine. *Transactions of the Northeast Section of the Wildlife Society* 40:118–128.
- AFTON, A. D., AND C. D. ANKNEY. 1991. Nutrient-reserve dynamics of breeding Lesser Scaup: a test of competing hypotheses. *Condor* 93:89–97.
- ASSEL, R. A. 1980. Maximum freezing degree days as a winter severity index for the Great Lakes, 1897–1977. *Monthly Weather Review* 108:1440–1445.
- ASSEL, R. A., AND S. RODIONOV. 1998. Atmospheric teleconnections for annual maximum ice cover on the Laurentian Great Lakes. *International Journal of Climatology* 18:425–442.
- ASSEL, R. A. 2003. Great Lakes ice cover, first ice, last ice and ice duration: winters 1973–2002. NOAA Technical Memorandum GLERL-125.
- ASSEL, R. A. 2005a. Classification of annual Great Lakes ice cycles: winters 1973–2002. *Journal of Climate* 18:4895–4905.
- ASSEL, R. A. 2005b. Great Lakes ice cover climatology update: winter 2003, 2004, 2005. NOAA Technical Memorandum GLERL-135.
- ASSEL, R. A. 2005c. Conditional probability of December and January ice cover at selected Great Lakes shore sites. NOAA Technical Memorandum GLERL-134.
- BAIN, G. A. C. 1980. The relationship between preferred habitat, physical condition, and hunting mortality of Canvasbacks (*Aythya valisineria*) and Redheads (*Aythya americana*) at Long Point, Ontario. M. Sc. thesis, University of Western Ontario, London, Ontario.
- BALDASSARRE, G. A., AND E. G. BOLEN. 1984. Field feeding ecology of waterfowl wintering on the southern High Plains of Texas. *Journal of Wildlife Management* 48:63–71.
- BALDASSARRE, G. A., R. J. WHYTE, AND E. G. BOLEN. 1986. Body weight and carcass composition of nonbreeding Green-winged Teal on the southern high plains of Texas. *Journal of Wildlife Management* 50:420–426.
- BALDASSARRE, G. A., AND E. G. BOLEN. 2006. Waterfowl ecology and management. Kreiger, Malabar, FL.
- BARBOZA, P. S., AND D. G. JORDE. 2002. Intermittent fasting during winter and spring affects body composition and reproduction

- of a migratory duck. *Journal of Comparative Physiology and Biology* 172:419–434.
- BARTON, D. R. 1986. Nearshore benthic invertebrates of the Ontario waters of Lake Ontario. *Journal of Great Lakes Research* 12:270–280.
- BEDNEKOFF, P. A., AND A. I. HOUSTON. 1994. Dynamic models of mass-dependent predation, risk-sensitive foraging, and premigratory fattening in birds. *Ecology* 75:1131–1140.
- BEDNEKOFF, P. A., H. BIEBACH, AND J. R. KREBS. 1994. Great Tit fat reserves under unpredictable temperatures. *Journal of Avian Biology* 25:156–160.
- BELLROSE, F. C. 1980. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA.
- BIEBACH, H. 1996. Energetics of winter and migratory fattening, p. 280–323. *In* C. Carey [ED.], *Avian energetics and nutritional ecology*. Chapman and Hall, London.
- BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. *American Zoologist* 16:171–184.
- BLEM, C. R. 2000. Energy balance, p. 327–341. *In* G. C. Whittow [ED.], *Sturkie's avian physiology*, 5th ed. Academic Press, New York.
- BOYD, H. 1964. Wildfowl and other waterbirds found dead in England and Wales January–March 1963. *Wildlife Trust Annual Report* 15:20–22.
- BRADY, C. M. 2009. Effects of dietary selenium on the health and survival of wintering Lesser Scaup. M. Sc. thesis, University of Western Ontario, London, Ontario.
- BRODSKY, L. M., AND P. J. WEATHERHEAD. 1985. Variability in behavioural response of wintering Black Ducks to increased energy demands. *Canadian Journal of Zoology* 63:1657–1662.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York.
- CALDER, W. A. 1974. The consequences of body size for avian energetics, p. 86–151. *In* R. A. Paynter [ED.], *Avian energetics*. Nuttall Ornithological Club Publication 15.
- CHAPPELL, W. A., AND R. D. TITMAN. 1983. Estimating reserve lipids in Greater Scaup (*Aythya marila*) and Lesser Scaup (*A. affinis*). *Canadian Journal of Zoology* 61:35–38.
- CUTHILL, I. C., S. A. MADDOCKS, C. V. WEALL, AND E. K. M. JONES. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. *Behavioral Ecology* 11:189–195.
- DENNIS D. G., G. B. MCCULLOUGH, N. R. NORTH, AND R. K. ROSS. 1984. An updated assessment of migrant waterfowl use of Ontario shorelines of the southern Great Lakes, p. 37–42. *In* G. Curtis, D. G. Dennis, and H. Boyd [EDS.], *Waterfowl studies in Ontario*. Canadian Wildlife Service Occasional Paper 54.
- DOBUSH, G. R., C. D. ANKNEY, AND D. G. KREMETZ. 1985. The effect of apparatus, extraction time, and solvent type on lipid extractions of Snow Geese. *Canadian Journal of Zoology* 63:1917–1920.
- DRIVER, E. A., L. G. SUGDEN, AND R. J. KOVACH. 1974. Calorific, chemical and physical values of potential duck foods. *Freshwater Biology* 4:281–292.
- DUFOR, K. D., C. D. ANKNEY, AND P. J. WEATHERHEAD. 1993. Condition and vulnerability to hunting among Mallards staging at Lake St. Clair, Ontario. *Journal of Wildlife Management* 57:209–215.
- DUGAN, P. J., R. R. EVANS, L. R. GOODYEAR, AND N. C. DAVISON. 1981. Winter fat reserves in shorebirds: disturbance of regulated levels by severe weather conditions. *Ibis* 123:359–363.
- DZUBIN, A., AND E. G. COOCH. 1992. Measurements of geese: general field methods. California Waterfowl Association. Sacramento, CA.
- EADIE, J. M., M. L. MALLORY, AND H. G. LUMSDEN. 1995. Common Goldeneye (*Bucephala clangula*), no. 170. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Academy of Natural Sciences, Philadelphia.
- ERSKINE, A. J. 1971. Buffleheads. Canadian Wildlife Service Monographs Series 4. Information Canada, Ottawa.
- GAUTHIER, G. 1993. Bufflehead (*Bucephala albeola*), no. 67. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Academy of Natural Sciences, Philadelphia.
- GOUDIE, R. I., AND C. D. ANKNEY. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475–1482.
- GREENWOOD, H., R. G. CLARK, AND P. J. WEATHERHEAD. 1986. Condition bias of hunter-shot Mallards. *Canadian Journal of Zoology* 64:599–601.
- GWINNER, E. 1977. Circannual rhythms in bird migration. *Annual Review of Ecology and Systematics* 8:381–405.
- HAMILTON, D. A., AND C. D. ANKNEY. 1994. Consumption of zebra mussels *Dreissena polymorpha* by diving ducks in Lakes Erie and St. Clair. *Wildfowl* 45:159–166.
- HARAMIS, G. M., J. D. NICHOLS, K. H. POLLOCK, AND J. E. HINES. 1986. The relationship between body mass and survival of wintering Canvasbacks. *Auk* 103:506–514.
- KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GAVRILOV. 1977. Avian energetics, p.127–204. *In* J. Pinowski and S. C. Kendeigh [EDS.], *Granivorous birds in ecosystems*. Cambridge University Press, New York.
- KERR, D. C., C. D. ANKNEY, AND J. S. MILLAR. 1982. The effect of drying temperature on extraction of petroleum ether soluble fats of small birds and mammals. *Canadian Journal of Zoology* 60:470–472.
- KESTENHOLZ, M. 1994. Body mass dynamics of wintering Tufted Duck *Aythya fuligula* and Pochard *A. ferina* in Switzerland. *Wildfowl* 45:147–158.
- KING, J. R., AND D. S. FARNER. 1966. The adaptive role of winter fattening in the White-crowned Sparrow comments on its regulation. *American Naturalist* 100:403–418.
- LILLIENDAHL, K., A. CARLSON, J. WELANDER, AND J. B. EKMAN. 1996. Behavioral control of daily fattening in Great Tits (*Parus major*). *Canadian Journal of Zoology* 74:1612–1616.
- LIMA, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377–385.
- LINDSTRÖM, A., AND T. PIERSMA. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* 135:70–78.
- LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, R. D. WOLFINGER, AND O. SCHABENBERGER. 2007. SAS for mixed models, 2nd ed. SAS Institute, Cary, NC.
- LOESCH, C. R., R. M. KAMINSKI, AND D. M. RICHARDSON. 1992. Endogenous loss of body mass by Mallards in winter. *Journal of Wildlife Management* 56:735–739.
- LOVVORN, J. R. 1989. Food dependability and antipredator tactics: implications for dominance and pairing in Canvasbacks. *Condor* 91:826–836.
- LOVVORN, J. R., D. R. JONES, AND R. W. BLAKE. 1991. Mechanics of underwater locomotion in diving ducks: drag, buoyancy and acceleration in a size gradient of species. *Journal of Experimental Biology* 159:89–108.
- MCNAMARA, J. M., AND A. I. HOUSTON. 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheoretica* 38:37–61.
- MORTON, J. M., R. L. KIRKPATRICK, AND M. R. VAUGHN. 1990. Changes in body composition of American Black Ducks wintering at Chincoteague, Virginia. *Condor* 92:598–605.

- NAVARRO, R. A. 1992. Body composition, fat reserves, and fasting capability of Cape Gannet chicks. *Wilson Bulletin* 104:644–655.
- NEWTON, I. 2008. *The migration ecology of birds*. Academic Press, San Diego.
- 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.
- PAULUS, S. L. 1988. Time activity budgets of nonbreeding Anatidae: a review, p. 135–152. *In* M. W. Weller [ED.], *Waterfowl in winter*. University of Minnesota Press, Minneapolis.
- PETERSON, S. R., AND R. S. ELLARSON. 1979. Changes in Oldsquaw weight. *Wilson Bulletin* 91:288–300.
- PETRIE, S. A., AND KNAPTON, R. W. 1999. Rapid increase and subsequent decline of zebra and quagga mussels in Long Point Bay, Lake Erie: possible influence of waterfowl predation. *Journal of Great Lakes Research* 25:772–782.
- PETRIE, S. A., AND M. L. SCHUMMER. 2002. Waterfowl response to zebra mussels on the lower Great Lakes. *Birding* 34:346–351.
- PETRIE, S. A., S. S. BADZINSKI, AND K.G. DROUILLARD. 2007. Contaminants in Lesser and Greater Scaup staging on the lower Great Lakes. *Archives of Environmental Contamination and Toxicology* 52:580–589.
- POULTON, V. K., J. R. LOVVERN AND J. Y. TAKEKAWA. 2002. Clam density and scaup feeding behavior in San Pablo Bay, California. *Condor* 104:518–527.
- PRINCE, H. H., P. I. PADDING, AND R. W. KNAPTON. 1992. Waterfowl use of the Laurentian Great Lakes. *Journal of Great Lakes Research* 18:673–699.
- QUINLAN, E. E., AND G. A. BALDASSARRE. 1984. Activity budgets of nonbreeding Green-winged Teal on playa lakes in Texas. *Journal of Wildlife Management* 48:838–845.
- RAVE, D. P., AND G. A. BALDASSARRE. 1991. Carcass mass and composition of Green-winged Teal wintering in Louisiana and Texas. *Journal of Wildlife Management* 55:457–461.
- RAVELING, D. G. 1968. Weights of *Branta canadensis* during winter. *Journal of Wildlife Management* 32:412–414.
- REINECKE, K. J., T. L. STONE, AND R. B. OWEN JR. 1982. Seasonal carcass composition and energy balance of female Black Ducks in Maine. *Condor* 84:420–426.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds, p. 152–291. *In* R. A. Paynter [ED.], *Avian energetics*. Nuttall Ornithological Club Publication 15.
- ROBERTSON, G. J., AND J. L. SAVARD. 2002. Long-tailed Duck (*Clangula hyemalis*), no. 651. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- ROGERS, C. M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* 68:1051–1061.
- RYAN, R. A. 1972. Body weight and weight changes of wintering diving ducks. *Journal of Wildlife Management* 36:759–765.
- SAS INSTITUTE. 2009. *SAS/STAT user's guide*. SAS Institute, Cary, NC.
- SCHUMMER, M. L. 2005. Resource use by diving ducks during winter on northeastern Lake Ontario. Ph. D. dissertation, University of Western Ontario, London, Ontario.
- SCHUMMER, M. L., S. A. PETRIE, AND R. C. BAILEY. 2008a. Interaction between macroinvertebrate abundance and habitat use by diving ducks during winter on northeastern Lake Ontario. *Journal of Great Lakes Research* 34:54–71.
- SCHUMMER, M. L., PETRIE, S.A., AND R.C. BAILEY. 2008b. Dietary overlap of sympatric diving ducks during winter on northeastern Lake Ontario. *Auk* 125:425–433.
- SCHUMMER, M. L., S. S. BADZINSKI, S. A. PETRIE, Y.-W. CHEN, AND N. BELZILE. 2010. Selenium accumulation in sea ducks wintering at Lake Ontario. *Archives of Environmental Contamination and Toxicology* 58:854–862.
- SCHUMMER, M. L., I. FIFE, S. A. PETRIE, AND S. S. BADZINSKI. 2011. Artifact ingestion in sea ducks wintering at northeastern Lake Ontario. *Waterbirds* 34:51–58.
- STOKKAN, K. A., S. HARVEY, H. KLANDORF, AND A. S. BLIX. 1985. Endocrine changes associated with fat deposition and mobilization in Svalbard Ptarmigan (*Lagopus mutus hyperboreus*). *General and Comparative Endocrinology* 58:76–80.
- SUGDEN, L. G. 1973. Metabolizable energy of wild duck foods. *Canadian Wildlife Service Progress Notes* 35.
- SUTER, W., AND M. R. VAN EERDEN. 1992. Simultaneous mass starvation of wintering diving ducks in Switzerland and the Netherlands: a wrong decision in the right strategy? *Ardea* 80:229–242.
- SYSTAD, G. H., J. O. BUSTNESS, AND K. E. ERIKSTAD. 2000. Behavioral responses to decreasing day length in wintering sea ducks. *Auk* 117:33–40.
- TRAUTMAN, M. B., W. E. BILLS, AND W. L. WICKLIFF. 1939. Winter losses from starvation and exposure of waterfowl and upland game birds in Ohio and other northern states. *Wilson Bulletin* 51:86–104.
- WARE, L. L. 2008. Selenium uptake and effects in Greater Scaup (*Aythya marila*) wintering on western Lake Ontario. M. Sc. thesis, University of Western Ontario, London, Ontario.
- WHYTE, R. J., AND E. G. BOLEN. 1984. Variation in winter fat depots and condition indices in Mallards. *Journal of Wildlife Management* 48:1370–1373.
- WITTER, M. S., AND I. C. CUTHILL. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London B* 340:73–92.
- WOOLEY, J. B. JR., AND R. B. OWEN JR. 1977. Metabolic rates and heart rate-metabolism relationships in the Black Duck (*Anas rubripes*). *Comparative Biochemistry and Physiology A* 57:363–367.
- WORMINGTON, A., AND J. H. LEACH. 1992. Concentrations of diving ducks at Point Pelee, Ontario, in response to invasion of zebra mussels, *Dreissena polymorpha*. *Canadian Field Naturalist* 106:376–380.