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Winter Ecology of Waterfowl on the Great Salt Lake, Utah

Josh L. Vest
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WINTER ECOLOGY OF WATERFOWL
ON THE GREAT SALT LAKE, UTAH

by

Josh L. Vest

A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY
in Wildlife Biology

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2013
ABSTRACT

Winter Ecology of Waterfowl on the Great Salt Lake, Utah

by

Josh L. Vest, Doctor of Philosophy
Utah State University, 2013

Major Professor: Dr. Michael R. Conover
Department: Wildland Resources

My research provided new information regarding the ecology of waterfowl using the Great Salt Lake (GSL) during winter (November–April). Aerial survey results from winters 2004-05 and 2005-06 suggest ducks rely on hypersaline areas of GSL to a greater extent when availability of freshwater habitats is reduced. Total duck use in winter was 33% lower in 2004-05 compared to 2005-06 because of reduced freshwater habitat availability and lower GSL surface elevations resulting from persistent drought conditions. In winter 2004-05, 35% of total duck use occurred in hypersaline strata of GSL compared to only 15% in 2005-06. Occurrence of ice in freshwater and brackish strata was also associated with greater use of hypersaline strata. Common goldeneye, northern shoveler, and green-winged teal comprised ≥62% of mid-winter duck abundance and ≥94% of hypersaline use by ducks.

On average, 68% of common goldeneye diet consisted of brine fly larvae. Brine shrimp cysts comprised 52% of northern shoveler diet and 80% of green-winged teal diet
during winter. Thus, these species use halophile invertebrates to meet energetic and nutritional needs during winter at GSL.

Lipid reserves of common goldeneye were 17% lower in winter 2004-05 when aquatic habitats were reduced and indices of brine fly larvae in GSL were lower. Mean lipid reserves declined 34% during winter consistent with an endogenous pattern of lipid loss common to wintering waterfowl. Female goldeneye also exhibited a declining trend in lipids as freezing conditions persisted whereas males generally maintained greater lipid reserves at lowest observed temperatures. Regional and local environmental conditions at GSL including Ephydridae productivity, freshwater habitat availability, and effective temperature likely play a more prominent role in lipid reserve dynamics for goldeneye than energetic costs of osmoregulatory adjustments.

Wintering ducks using the GSL apparently accumulated high amounts of mercury (Hg) and selenium (Se) during winter. More than 30% of common goldeneye liver samples contained potentially harmful levels of Hg and Se. All northern shoveler liver samples contained elevated Hg concentrations and most (79%) displayed elevated Se concentrations. Further research is needed to evaluate the effect of these elements and their dynamics on GSL waterbirds.
PUBLIC ABSTRACT

Winter Ecology of Waterfowl on the Great Salt Lake, Utah

Josh L. Vest

I designed a suite of studies in coordination with Utah Division of Wildlife Resources (UDWR) to evaluate waterfowl use of the GSL in winter and ecological aspects associated with GSL use. These studies provided insight into key information gaps previously identified by UDWR regarding management of GSL resources. Population surveys indicated total duck abundance was low when GSL surface elevations were low and wetland resources diminished because of persistent drought in the system. Also, ducks appear to use hypersaline parts of GSL more when freshwater habitats are limited from either drought or ice conditions. Common goldeneye, northern shoveler, and green-winged teal exhibited the most use of hypersaline areas. Dietary evaluations indicated all three species feed on hypersaline invertebrates from GSL to meet energetic and nutritional needs in winter. Brine shrimp cysts were important foods for northern shoveler and green-winged teal. Fat levels of ducks are important determinants of survival and fitness. Fat reserves of goldeneye were generally lower in the winter when both GSL and wetland habitat resources were lower. Results suggest brine fly larvae productivity, freshwater habitat availability, and temperature and wind speed likely play a more prominent role in goldeneye fat reserves than osmoregulation. Also, common goldeneye and northern shoveler using the GSL apparently accumulated biologically concerning amounts of mercury and selenium during winter. However, further research is needed to evaluate the effect of these elements on GSL ducks.
ACKNOWLEDGMENTS

This document is not just the culmination of a suite of research endeavors. It also represents, for me, an amazing experience and journey in professional and personal growth. The remarkable people and landscapes I have encountered and engaged with during this time have forever altered my perspectives and shaped my life in ways I could not have imagined. To those friends, colleagues, and co-conspirators (who shall remain unnamed for their own protection) who shared in this journey, I will be eternally grateful.

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Project funding was provided by the Utah Division of Wildlife Resources’ Great Salt Lake Ecosystem Program (GSLEP) and U.S. Fish and Wildlife Service through Federal Aid in Restoration and Sea Duck Joint Venture.

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Josh L. Vest
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CHAPTER 1
INTRODUCTION

The Great Salt Lake (GSL) system is an important area for aquatic birds within the Western Hemisphere due to the extent and diversity of aquatic environments in a predominately xeric environment (Kadlec and Smith 1989, Jehl 1994, Cox and Kadlec 1995, Aldrich and Paul 2002). The GSL is the fourth largest terminal lake in the world and forms one of the most extensive wetland and aquatic systems in the Intermountain West. It provides a diversity of habitats ranging from ephemeral to persistent and freshwater to hypersaline (Kadlec and Smith 1989, Ratti and Kadlec 1992, Aldrich and Paul 2002). These habitats are dynamic and characterized by relatively high inter- and intra-annual variation in relation to availability, extent, and resource use by avian guilds (Aldrich and Paul 2002).

Millions of waterfowl and other waterbirds use the GSL and associated marshes annually as breeding, migratory, or wintering habitat (Kadlec and Smith 1989, Aldrich and Paul 2002). The North American Waterfowl Management Plan (NAWMP) designates the GSL and associated marshes as an area of continental significance for waterfowl (Anatidae) and a priority for habitat conservation and management actions (NAWMP 2004, 2012). An estimated 3–5 million waterfowl may migrate through the GSL region annually with a peak population during fall migration (Bellrose 1980, Aldrich and Paul 2002). However, several duck species are abundant during the breeding (e.g., cinnamon teal [Anas cyanoptera]) molting (e.g., northern pintail [A. acuta]), and wintering (e.g., common goldeneye [Bucephala clangula], northern shoveler [A. clypeata], green-winged teal [A. crecca]) periods of the annual cycle (Aldrich and Paul
Waterfowl abundance is monitored in state and federally managed wetland complexes adjacent to the GSL, but little is known about waterfowl use of the GSL outside of these areas (Aldrich and Paul 2002).

The GSL annually produces an immense biomass of halophile invertebrates consisting of brine shrimp (*Artemia franciscana*) and brine fly (Ephydridae; Belovsky et al. 2011). Several species of aquatic birds including Wilson’s phalarope (*Phalaropus tricolor*) and eared grebe (*Podiceps nigricollis*) rely on these halophile invertebrates during migration, and their populations are regularly monitored via systematic surveys (Aldrich and Paul 2002, Paul and Manning 2002, Conover and Caudell 2009, Belovsky et al. 2011). However, hypersaline use by waterfowl is relatively uncommon in North America and most reports are associated with aberrant and negative effects of hypersaline exposure (Wobeser 1997, Jehl 2001, Gordus et al. 2002, Jehl 2005). Unfortunately, lake-wide waterfowl population estimates are lacking during winter when use of hypersaline areas has been noted. Also, waterfowl use of halophile invertebrates in the GSL has not been quantified (Aldrich and Paul 2002). Waterfowl complete several nutritionally demanding processes during winter such as feather molt, courtship, and pairing (Prince 1979, Wishart 1983, Heitmeyer 1988) and insufficient energy (i.e., lipids) or nutrient reserves in winter may delay these events, spring migration, or onset of breeding activities (Hepp 1986, Heitmeyer 1988, Richardson and Kaminski 1992, Arzell et al. 2006). Consequently, the Utah Division of Wildlife Resources (UDWR) was concerned about the lack of data for wintering waterfowl populations in the GSL, especially regarding potential effects of commercial brine shrimp cyst harvesting on wintering ducks (Utah Department of Natural Resources 2000).
This document attempts to address key information gaps and uncertainties relative to waterfowl use of the GSL system during winter. Reliable estimates of waterfowl abundance are essential for population and habitat conservation and management at continental, regional, and local scales in North America (Conroy et al. 1988, Reinecke et al. 1992, Pearse et al. 2008). In Chapter 2, I report and discuss the results of an aerial-transect survey I designed to estimate abundance of wintering ducks in the GSL during winters 2004-05 and 2005-06. My primary objectives in Chapter 2 are to 1) estimate population abundance of wintering ducks, 2) evaluate temporal and spatial patterns of duck abundance, and 3) calculate duck use-days for the GSL during winter to facilitate conservation planning.

Two hypotheses potentially explain the presence of ducks on the GSL. First, use of hypersaline areas may afford security for ducks to loaf or roost and limit disturbance or predation from hunters and predators in wetland complexes. Alternatively, ducks may use these hypersaline regions of the GSL because they are foraging on the GSL’s brine shrimp cysts and brine fly larvae despite the osmoregulatory and physiological challenges that may result from hypersaline use (Nyström and Perhsson 1988, Wobeser 1997). These two hypotheses are evaluated in Chapter 3 by assessing the dietary composition of ducks collected from hypersaline areas of the GSL. The objective of Chapter 3 was to determine the extent to which wintering waterfowl utilize brine shrimp and brine fly resources from the GSL.

Unfortunately, little information exists regarding physiological condition of waterfowl using hypersaline environments such as the GSL (Kadlec and Smith 1989, Aldrich and Paul 2002, Woodin et al. 2008) despite evidence of adverse impacts to
waterfowl from hypersaline exposure (Meteyer et al. 1997, Wobeser 1997, Jehl 2001, Gordus et al. 2002, Jehl 2005). Maintenance of body condition through the use of lipid stores during the non-breeding period is an important determinant of seasonal and annual survival in waterfowl (Haramis et al. 1986, Pace and Afton 1999, Fleskes et al. 2002, Blums et al. 2005) and can have both immediate and cross-seasonal (i.e., carry-over) effects on fitness parameters (Barboza and Jorde 2002, Newton 2004, Hobson et al. 2005, Devries et al. 2008, Yerkes et al. 2008, Guillemain et al. 2008). In saline systems, osmoregulation can be an important consideration for habitat use, water balance, and bioenergetics of aquatic birds (Nyström and Perhsson 1988, Woodin et al. 2008, Gutierrez et al. 2011). Foraging ecology and osmoregulation are likely to be closely entwined in marine systems, and high salinities could impose energetically expensive osmoregulatory costs (Peaker and Linzell 1975, Woodin et al. 2008, Gutierrez et al. 2011). However, osmoregulation is generally not considered in studies of avian nutrient dynamics or energetic budgets (Woodin et al. 2008, Gutierrez et al. 2011). Although invertebrate resources in GSL are highly abundant (Collins 1980, Wurtsbaugh 2009, Belovsky et al. 2011), significant energetic and physiological costs may be associated with exploiting these hypersaline food resources. In Chapter 4, I evaluate factors influencing lipid dynamics of common goldeneye on the GSL during winter. My goal in Chapter 4 is to evaluate endogenous and exogenous (inter- and intra-annual) factors potentially influencing lipid reserves of common goldeneye using the hypersaline GSL in winter. I evaluate a set of candidate models to explain the influence of endogenous mechanisms and environmental factors on lipid dynamics.
The GSL is a closed basin, and therefore, contaminants such as lead (Pb), selenium (Se), or cadmium (Cd) that are associated with industrial and urban development or from non-local sources such as atmospheric deposition may accumulate in the GSL system (Brix et al. 2004, Naftz et al. 2008a). High concentrations of several trace elements, including arsenic (As), Cd, copper (Cu), mercury (Hg), Pb, and zinc (Zn), have been detected in sediments from the GSL and its watershed (Naftz et al. 2008b). The U. S. Geological Survey (USGS) reported water samples collected from the GSL exceeded the total Hg standard for protection of aquatic life in marine systems and were among the highest values observed for marine systems (Naftz et al. 2008a). Additionally, high Se concentrations were reported in GSL water and brine shrimp samples in relation to mining effluent into the GSL (Brix et al. 2004). Given the hemispheric importance of the GSL to migratory waterbirds and relative paucity of information regarding ecotoxicology in this system, evaluation of contaminant exposure to GSL biota is warranted. Therefore, in Chapter 5, I report and discuss the results of liver trace element concentrations from three species of overwintering waterfowl obtained from the GSL over two winters (2004-05 and 2005-06). My objectives were to 1) document selected liver trace element concentrations in common goldeneye, northern shoveler, and green-winged teal wintering on the GSL and 2) evaluate variation of selected trace elements in relation to temporal variation, sex, and age class of these waterfowl species.

My results contribute to the understanding of avian ecology and resource use by waterfowl at one of North America’s most significant aquatic systems for migratory birds. These results contribute to filling identified information gaps managers need to make wise decisions relative to GSL natural resources.
LITERATURE CITED


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ABSTRACT.— The Great Salt Lake (GSL) and its adjacent wetland complexes provide continentally significant habitat for aquatic birds in North America, including waterfowl. Although most waterfowl primarily use the extensive freshwater and brackish wetland habitats adjacent to the GSL, some species use the hypersaline GSL itself during the nonbreeding period. However, estimates of waterfowl abundance and patterns of distribution are lacking for hypersaline components of the system. I conducted aerial surveys from November through April in 2004-05 and 2005-06 to estimate abundance \((\hat{N})\) of ducks and describe their distribution on the GSL and hydrologically connected bays. I did not survey managed wetland complexes adjacent to the GSL. Peak abundance of total ducks (all species combined) occurred in November during both winters but was approximately three times higher in 2005 \((\hat{N} \pm SD = 374,800 \pm 68,600)\) than during 2004 \((100,300 \pm 32,300)\) when GSL surface elevations were 0.43 m higher and wetland availability was greater. Total duck abundance was lowest in February and estimates were generally similar between 2005 \((33,400 \pm 15,400)\) and 2006 \((30,900 \pm 7,900)\). Common Goldeneye \((Bucephala clangula)\), Northern Shoveler \((Anas clypeata)\), and Green-winged Teal \((A. crecca)\) collectively comprised \(\geq60\%\) of total duck abundance December–February; Common Goldeneye alone comprised \(\geq64\%\) of total duck abundance during February surveys both winters. No ducks were observed on GSL’s

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1 Coauthored by J. L. Vest and M. R. Conover. Published in journal Waterbirds (2011) volume 34:40–50.
North Arm transects during any survey, likely because it exhibits extreme salinity concentrations of > 25%. I calculated 13.7 million total duck use-days in 2004-05 and 20.5 million. In winter 2004-05, 35% of total duck use-days were contained in the four western hypersaline strata but only 15% were in these hypersaline strata in winter 2005-06. These results indicate the GSL is an important migration and wintering area for several duck species and GSL hypersaline resources may be important during winter, although intensity of use varies annually and within winter in response to environmental conditions such as lake surface-elevation and persistence of ice in freshwater habitats.

**INTRODUCTION**

The Great Salt Lake (GSL) is the fourth largest terminal lake in the world and a dominant water feature within the western United States (Arnow and Stephens 1990). The GSL and its associated marshes are also important resources for millions of migratory waterbirds in the western U.S. due to its size, location within a predominately xeric environment, abundant invertebrate biomass, and diversity of aquatic habitats (Kadlec and Smith 1989, Jehl 1994, Cox and Kadlec 1995, Aldrich and Paul 2002). Accordingly, the North American Waterfowl Management Plan (NAWMP) designates the GSL and associated marshes as an area of continental significance for waterfowl (i.e., ducks, geese, and swans; NAWMP 2004). An estimated 3–5 million waterfowl may migrate through the GSL region annually (Bellrose 1980, Aldrich and Paul 2002). Waterfowl populations peak during fall migration in the GSL region (Aldrich and Paul 2002). However, several duck species such as Cinnamon Teal (*Anas cyanoptera*) are abundant during the breeding season or late-summer molting period such as Northern
Pintail (*A. acuta*). Other species are also abundant in the wintering period including Common Goldeneye (*Bucephala clangula*), Northern Shoveler (*A. clypeata*), and Green-winged Teal (*A. crecca*; Aldrich and Paul 2002). Waterfowl abundance is monitored within state and federally managed wetland complexes adjacent to the GSL but little is known about waterfowl use of the GSL outside of these areas (Aldrich and Paul 2002). Lake-wide waterfowl population estimates are lacking and use of halophile food sources by waterfowl in the GSL has not been quantified (Aldrich and Paul 2002). The Utah Division of Wildlife Resources (UDWR) was concerned regarding the lack of data for wintering waterfowl populations in the GSL, especially regarding potential effects of commercial brine shrimp (*Artemia franciscana*) cysts harvesting on wintering ducks (Utah Department of Natural Resources 2000).

Reliable estimates of waterfowl abundance are essential for population and habitat conservation and management at continental, regional, and local scales in North America (Conroy et al. 1988, Reinecke et al. 1992, Pearse et al. 2008b). Calculation of cumulative duck use-days (i.e., residency of one duck for 1 day) provides a useful metric to express temporal variation in duck abundance within a given region and is commonly used in conservation planning for non-breeding waterfowl (Fleskes and Yee 2007, Petrie et al. 2011, Petrie et al 2013). Therefore, I designed an aerial-transect survey to estimate abundance of wintering ducks in the GSL during winters 2004-05 and 2005-06. Objectives of this study were to 1) estimate population abundance of wintering ducks, 2) evaluate temporal and spatial patterns of duck abundance, and 3) calculate duck use-day values for the GSL during winter.
STUDY AREA

The GSL is a hypersaline terminal lake system located in north-central Utah within the Great Basin and Range Province and is a dominant water feature within the western United States (Arnow and Stephens 1990, Stephens 1990). The Southern Pacific Railroad Causeway divides the GSL into 2 distinct areas with unique ecological characteristics (Fig. 2-1). The North Arm (Gunnison Bay) of the GSL is characterized by minimal freshwater inflow and extreme hypersaline conditions with >25% salinity (Stephens 1990, Aldrich and Paul 2002, Loving et al. 2002, Belovsky et al. 2011). The South Arm receives >90% of the freshwater surface inflow into the GSL and consequently has lower salinity (Stephens 1990, Loving et al. 2002). The South Arm is populated by green and blue-green algae, diatoms, and high biomass of halophylic macroinvertebrates consisting primarily of brine shrimp and brine fly (Ephydridae) larvae (Collins 1980, Felix and Rushforth 1980, Stephens 1990, Stephens and Birdsey 2002). Additionally, the South Arm of the GSL is bordered by approximately 1,900 km$^2$ of wetland habitats, primarily on its eastern side (Jensen 1974, Aldrich and Paul 2002).

The average annual lake elevation between the years 1847 and 1986 was 1,280.1 m above sea level, with a range of 1,277.5 to 1,283.8 m. At the mean lake elevation, the GSL encompasses approximately 4,400 km$^2$ with a range of 2,461–6,216 km$^2$ and a maximum depth of approximately 10 m (Arnow and Stephens 1990, Stephens 1990). Because of its shallow nature, a minor change in GSL surface elevation has a large impact on its surface area and volume (Arnow and Stephens 1990, Stephens 1990, Baskin 2005). On average, each 1-m change in lake elevation changes the surface area of the GSL, lakewide, by approximately 58,000 ha (Aldrich and Paul 2002). Within a recent 23
year period, the GSL has experienced both the highest and lowest lake elevations in recorded history (1847–2009) significantly altering the quality and availability of avian habitat in the GSL and adjacent wetlands (Kadlec and Smith 1989, Aldrich and Paul 2002).

Salinity concentrations are inversely related to GSL surface elevations and have changed dramatically in the South Arm ranging from a high of 27% in 1963 to 6% in the mid-1980s (Stephens 1990, Mohammed and Tarboton 2012). At the average lake surface elevation of 1,280.1 m above sea level, salinity is approximately 12% in the South Arm or three times the salinity concentration of oceans (Arnow and Stephens 1990, Stephens 1990, Gwynn 2002). Changes in lake levels, salinity, and nutrient dynamics can have cascading effects on species composition and community dynamics in hypersaline systems (Herbst 1988, 2001, 2006; Stephens 1990; Wurtsbaugh and Berry 1990; Williams 1998; Marcarelli et al. 2006; Belovsky et al. 2011). Thus, changes in GSL surface elevations may consequently influence habitat quality and availability for waterfowl and other waterbirds in the GSL system (Kadlec and Smith 1989, Aldrich and Paul 2002). Salinity also varies spatially within the GSL. Freshwater inflow to the GSL typically increases from fall through spring as precipitation increases and anthropogenic water diversions (e.g., irrigation) decline. Thus, during winter salinity is typically lower along the eastern area of the GSL between the Promontory Mountains, Fremont, and Antelope islands because of the relatively large freshwater inflows (Arnow and Stephens 1990, Marcarelli et al. 2006).

The GSL ecosystem is characterized by a temperate arid environment with an average of 38 cm of moisture near the lake’s east side and <25 cm on its west side.
(Aldrich and Paul 2002). Average winter (December – February, 1971–2000) temperature in the GSL system is approximately –0.6°C. On average, this region has 22 days with a maximum temperature ≤0°C and 77 days with a minimum temperature ≤0°C during winter (National Oceanic and Atmospheric Administration 2004, Western Regional Climate Center 2008).

**METHODS**

**Survey Design**

I attempted to conduct seven surveys annually during winters 2004-05 and 2005-06. I conducted surveys once monthly between November 2004–April 2005 (Nov. 2, Dec. 2, Jan. 14, Feb. 11, Mar. 9, Apr. 26) and October 2005–April 2006 (Oct. 19, Nov. 9, Dec 7, Jan 4, Feb. 17, Mar 13, Apr 19). The October 2004 survey could not be completed because of logistical and weather constraints; thus, a total of 13 surveys were completed during the two winters. Survey methods were generally similar to those described by Reinecke et al. (1992), and Pearse et al. (2008a). I used fixed-wing aircraft (Cessna 180) owned and operated by UDWR flown at an altitude of 150 m above ground level and speeds of 120–150 km/hr. I navigated transects using an on board Global Positioning System. Two aircraft were flown simultaneously on different portions of the GSL to reduce survey duration and minimize likelihood of waterfowl movement among survey areas (Fleskes and Yee 2007). Observers were positioned in the right front seat and left rear seat of each plane. Observers recorded species-specific numbers of ducks (Anatinae) observed within each transect only from their respective sides of the plane. Surveys began within 1 hour of sunrise and were generally completed within 5 hours.
Surveys were not conducted when adverse weather conditions existed (e.g., rain, snow, fog) or wind speeds were >13 km/hr because white-cap waves reduced visibility of waterfowl. I did not account for visibility bias because all transects were located on open expanses of water or mudflats.

I used stratified random sampling to estimate duck numbers (Fig. 2-1). I identified eight strata within the GSL ecosystem based on differing salinity gradients, juxtaposition with freshwater wetland habitats, and prior unpublished work by UDWR (Paul and Manning 2001). Managed wetland complexes adjacent to the GSL were not surveyed because the primary objective was to elucidate patterns of duck abundance and distribution on the GSL. Strata included: 1) Carrington Bay on the western side of the GSL which lacks adjacent wetland habitat; 2) north Gilbert Bay which is predominantly pelagic with little shoreline habitat and no adjacent wetlands; 3) central Gilbert Bay located between Antelope and Stansbury Islands with no adjacent wetlands; 4) south Gilbert Bay which receives freshwater inflow from Lee Creek and Goggin Drain and is adjacent to wetland habitats in the Tooele Valley, 5) Farmington Bay which has lower salinity (<7%), is shallow (≤1 m), and receives significant freshwater inflow from the Jordan River and wastewater treatment plants, and is adjacent to managed and unmanaged wetland habitat complexes; 6) Ogden Bay which receives significant freshwater inflows from the Bear and Weber rivers and is adjacent to managed and unmanaged wetland habitat complexes; 7) Bear River and Willard bays which are predominantly shallow (≤1 m), freshwater areas adjacent to managed wetland habitat complexes; and 8) the North Arm (i.e., Gunnison Bay) which has extreme hypersaline conditions (>25% salinity) and has minimal freshwater and wetland habitats adjacent to it.
(Aldrich and Paul 2002, Paul and Manning 2002, Marcarelli et al. 2006, Johnson 2007; Fig. 2-1).

I delineated all strata boundaries based on the average (years 1847–1986) GSL surface elevation of 1,280.1 m above sea level; thus, transects did not extend beyond the 1280.1 elevation mark. GSL elevations during this study ranged 1278.4–1279.5 m above sea level. Hence, transect lengths were long enough to cover the width of the GSL surface elevations during this study. I designated fixed-width transects as sample units and used Geographic Information System technology to create a sample frame by orienting transects east to west and spaced 500 m apart within each strata. I selected new sets of transects for each survey and strata to avoid the possibility an individual transect was not representative, reduce serial correlation among surveys, and increase study area coverage (Reinecke et al. 1992, Eggeman et al. 1997, Pearse et al. 2008a). I selected transects randomly, with replacement, and with probability proportional to length (Caughley 1977, Pearse et al. 2008a). I constrained adjacent transects from being selected to reduce the chance of multiple counting individual ducks (Reinecke et al. 1992, Pearse et al. 2008a).

**Estimation and Analysis**

I estimated population abundance for Common Goldeneye, Northern Shoveler, Green-winged Teal, and total ducks for all surveys. I calculated abundance \( \hat{N} \), standard deviation (SD), and coefficients of variation (CV) for total ducks, total diving ducks, and total dabbling ducks from transect sums of individuals observed and transect sample weights (i.e., [probability of selecting a transect from the sampling frame]^{-1})
using PROC SURVEYMEANS (SAS Institute 2004). These statistics were also calculated for five of the most common and abundant species identified during surveys including Common Goldeneye, Gadwall (A. strepera), Green-winged Teal, Northern Pintail, and Northern Shoveler. Cumulative duck use-days were calculated by assuming linear change in abundance between survey dates and total use-days calculated by summing those use-day estimates across surveys.

Environmental variables, such as availability or quality of habitat and climatic conditions including temperature, ice, and wind can influence waterfowl abundance and distribution during winter (Nichols et al. 1983, Jorde et al. 1984, Pearse 2007, Schummer et al. 2010). To assess climatic variability, I calculated daily average temperatures from three MESOWEST weather stations in or adjacent to the South Arm of the GSL at Hat Island, Antelope Island, and along the south shoreline of the GSL between Lake Point Junction and Saltair boat harbor (MESOWEST 2013; Fig. 2-1). All weather stations were located between 1,280–1,305 m above mean sea level and therefore within 12 m of GSL surface elevations during this study. I calculated the average temperature (°C) for a 15-day interval prior to each survey. I chose a 15-day interval because this approximated the average mid-point in days between when two consecutive surveys were conducted.

I obtained daily lake surface elevation measurements from a United States Geological Survey gauge located at Saltair boat harbor in southern Gilbert Bay. However, wind and seiche activity can influence daily measures of GSL lake surface elevations (Atwood 2002). Therefore, similar to temperature, I calculated the average GSL surface elevation for a 15-day interval prior to each survey.
RESULTS

Total Ducks

During winter 2004-05, total duck abundance estimates peaked in November (123,000 ± 28,300; \( \hat{N} \pm SD \)) declined to February (33,400 ± 15,400), and then increased from February to March (83,500 ± 42,100; Fig. 2-2). During winter 2005-06, total duck abundance was also highest in the early winter surveys of October (306,700 ± 54,300) and November (374,800 ± 68,600). The November 2005 estimate was approximately three times higher than the November 2004 estimate. Temporal patterns and estimates of total duck abundance December–March in winter 2005-06 was similar to that observed in winter 2004-05. Total duck abundance was approximately three times higher in April 2006 relative to April 2005 (Fig. 2-2). Precision of total duck abundance estimates was generally poor with coefficient of variation (CV) ranging 23–50% and 18–28% in winters 2004-05 and 2005-06, respectively.

Over the course of the winter, ducks generally shifted use from the eastern stratum to the western stratum and then back to the eastern stratum. In early surveys (October–November) during both winters, most (≥92%) of total duck abundance was distributed among the three eastern strata: Bear River Bay, Ogden Bay, and Farmington Bay. In winter 2004-05, 41–69% of total duck abundance December–February was contained in the four western hypersaline strata, primarily in Carrington (6–31%) and South Gilbert Bays (6–58%; Fig. 2-3). In winter 2005-06, 19–69% of total duck abundance was contained in the four western hypersaline strata, primarily in Carrington (5–42%) and South Gilbert Bays (3–21%; Fig. 2-3). During late winter surveys (March–
April) in both winters, ≥93% of total duck abundance occurred in the three eastern strata, primarily (≥55%) in Bear River Bay (Fig. 2-3). No ducks were observed along transects in the North Arm during any survey period.

I calculated 13.7 million total duck use-days in winter (November–April) 2004-05, 35% (4.8 million use-days) of which were contained in the four western hypersaline strata (Table 2-2). I calculated 20.5 million total duck use-days in winter (November–April) 2005-06, 15% (3.1 million use-days) of which were contained in the four western hypersaline strata (Table 2-2). There was a 15% and 33% decline in the proportion of dabbling and diving duck use-days, respectively, in the four western hypersaline stratum between 2004-05 and 2005-06. Concomitantly, 22% more diving duck use-days were calculated in Bear River Bay 2005-06. Dabbling duck use-days were 8% lower in Bear River Bay and 15% higher in Farmington Bay in 2005-06 compared to 2004-05.

Principal Duck Species

During winters 2004-05 and 2005-06, I encountered 16 species of waterfowl on survey transects (Table 2-1). Seven species of dabbling ducks comprised >70% of total duck abundance in October–December and March–April surveys during both years (Table 2-1). Diving ducks comprised 45–79% of total duck abundance in January and February surveys during both winters (Table 2-1).

Collectively, Northern Shoveler, Green-winged Teal, Northern Pintail, and Common Goldeneye comprised the majority (57–98%) of total duck abundance during all surveys except April 2005 when Gadwall comprised 63% of total duck abundance and in April 2006 when increased proportions of scaup (A. affinis and A. marila combined)
and Ruddy Ducks (*Oxyura jamaicensis*) were estimated (Table 2-1). Gadwall was an abundant species in early winter and comprised 25–26% of total duck abundance in November surveys both winters and 21% in the October 2005 (Table 2-1).

Common Goldeneye, Green-winged Teal, and Northern Shoveler combined accounted for 98% and 94% of total duck use-days in the four western hypersaline strata during winter 2004-05 and 2005-06, respectively (Table 2-2). The majority of the remaining duck use-days in the hypersaline stratum were comprised of Northern Pintail (2%) in 2004-05 whereas Gadwall and Northern Pintail each comprised 3% in 2005-06. Within the four western hypersaline stratum, Northern Pintail (abundance ≤ 2,700) and Gadwall (abundance ≤ 3,100) only occurred in South Gilbert Bay and were closely associated with the Goggin Drain freshwater flow into the GSL.

**COMMON GOLDENEYE.**—Common Goldeneye (hereafter goldeneye) abundance peaked in January both winters with estimated abundances (± SD) of 44,300 ± 12,000 and 43,600 ± 10,200 in 2005 and 2006, respectively (Fig. 2-2d). Patterns were similar between years except goldeneye abundance in March 2006 (28,400 ± 7,000) was higher relative to March 2005 (13,400 ± 3,200). Goldeneye comprised >64% of total duck abundance in February surveys and nearly half (44–46%) in January surveys in both winters (Table 2-1). However, precision of abundance estimates was generally poor and CV for December–March goldeneye abundance estimates ranged from 19–27% in winter 2004-05 and from 23–27% in winter 2005-06.

Goldeneye were observed in all four western hypersaline strata (Carrington Bay; North, Central, and South Gilbert Bays) during some portion of both winters (Fig. 2-3d). During winter 2004-05, 74% of total goldeneye use-days were distributed among the four
western hypersaline strata where 41% of the total occurred in Carrington Bay. During
winter 2005-06 only 45% of total goldeneye use-days were distributed among the four
western hypersaline strata where 23% of the total occurred in Carrington Bay (Table 2-2,
Figure 3h).

NORTHERN SHOVELER.—Northern Shoveler peak abundance in winter 2004-05 occurred in November (31,400 ± 10,800) and generally declined through winter; no
shovelers were observed during February 2005 and abundance estimates were low in
March (1,700 ± 1,000) and April 2005 (1,000 ± 600; Fig. 2-2b). Northern Shoveler
abundance estimates were similar between October (74,800 ± 17,100) and November
2005 (77,600 ± 17,500) and the November 2005 estimate was approximately three times
higher than November 2004. During winter 2005-06, Northern Shoveler abundance
decreased from November to February (5,200 ± 3,100), increased from February to March
(22,900 ± 4,000), and remained at a similar level in April (15,600 ± 8,500; Fig. 2-2b).
Precision of Northern Shoveler abundance estimates were generally poor during both
winters and CVs ranged from 34–61% and 18–61% in winters 2004-05 and 2005-06,
respectively.

Northern Shovelers were observed in all strata except Carrington and Central
Gilbert Bays. Among the hypersaline strata, Northern Shovelers occurred primarily in
South Gilbert Bay. Northern Shovelers were not observed on any transects outside of the
three eastern strata in October, March, and April surveys in winter 2005-06 (Fig. 2-3b).

Total Northern Shoveler use-days were approximately two times higher in winter
2005-06 than 2004-05 (Table 2-2). During winter 2004-05, South Gilbert Bay comprised
64% of total Northern Shoveler use-days with the remainder distributed among the three
eastern strata. However, during winter 2005-06, South Gilbert Bay comprised only 12% of total use-days (Table 2-2).

**GREEN-WINGED TEAL.**—During winter 2004-05, green-winged teal abundance generally was highest in November \((27,600 \pm 9,100)\) and December \((32,900 \pm 18,700)\). Abundance was low in March 2005 \((1,800 \pm 900; \text{Fig. 2-2d})\). During winter 2005-06, abundance estimates exhibited a “saw-blade” pattern between consecutive surveys where the peak abundance occurred in November \((64,000 \pm 22,400)\) and lowest abundance occurred in February \((800 \pm 600; \text{Fig. 2-2d})\). Precision of Green-winged Teal abundance estimates was poor for all surveys, and CVs ranged from 32–92% and 29–68% in winters 2004-05 and 2005-06, respectively.

No Green-winged Teal were observed on any transects in the four western hypersaline strata except South Gilbert Bay during this study (Fig. 2-3d). Total Green-winged Teal use-days were approximately two times higher in winter 2005-06 than 2004-05 (Table 2-2). During winter 2004-05, South Gilbert Bay comprised 58% of total Green-winged Teal use-days with the remainder distributed among the three eastern strata. However, during winter 2005-06, South Gilbert Bay comprised only 13% of total use-days and 87% were distributed among the three eastern strata (Table 2-2, Fig. 2-3d).

**NORTHERN PINTAIL.**—During winter 2004-05, Northern Pintail abundance was highest during the March \((56,560 \pm 35,890)\) survey. However, during winter 2005-06, Northern Pintail abundance was highest during the October \((121,300 \pm 28,870; \text{Fig. 2c})\). Precision of Northern Pintail abundance estimates was poor for all surveys and CVs ranged from 32–90% and 24–77% in winters 2004-05 and 2005-06, respectively. During
both winters, ≥98% of Northern Pintail total use-days were distributed among the three eastern strata (Table 2-2, Fig. 2-3c).

**GADWALL.**—Gadwall abundance was highest during November surveys in both winters but was approximately three times higher in 2005 (97,970 ± 23,750) than 2004 (30,970 ± 9,070). Precision of Gadwall abundance estimates was generally poor for all surveys, and CVs ranged from 29–59% and 19–84% in winters 2004-05 and 2005-06, respectively. During both winters, ≥ 96% of Gadwall total use-days were distributed among the three eastern strata (Table 2-2, Fig. 2-3f).

**DISCUSSION**

**Abundance and Distribution**

Abundance estimates from these aerial surveys suggest the GSL is an important migratory and wintering area in the western U.S for Common Goldeneye, Northern Shoveler, Green-winged Teal, Northern Pintail, and Gadwall. The peak goldeneye population estimate (44,300) observed in January 2005 represents 4.3% of the combined continental breeding population of Common and Barrow’s (*Bucephala islandica*) goldeneye in North America for the corresponding breeding season (i.e., summer 2004; U.S. Fish and Wildlife Service 2009). Common and Barrow’s goldeneye are not differentiated during annual continental assessments of breeding waterfowl populations in North America. Therefore, the percentage of the continental population of Common Goldeneye wintering at the GSL is likely higher than 4%. The peak goldeneye estimate at GSL also represents 94% of the Pacific Flyway winter population (common and
Barrow’s combined) based on the long-term average (1955–2012) from mid-winter inventories (Olson and Trost 2012). Peak estimates of Northern Shovelers (77,600) and Green-winged Teal (64,100) that occurred in November 2005 represented 2.2% of the continental breeding population and approximately 18% of the long-term average Pacific Flyway mid-winter population of both Northern Shoveler and Green-winged Teal (U.S. Fish and Wildlife Service 2009, Olson and Trost 2012). The peak abundance of Northern Pintail (121,500) and Gadwall (97,800) represented 4.5% and 4.7%, respectively, of their continental breeding populations and 6.5% and 86%, respectively, of their mid-winter average populations in the Pacific Flyway (U.S. Fish and Wildlife Service 2009, Olson and Trost 2012).

Extensive complexes of privately and publicly managed freshwater wetlands (> 85,000 ha) lie adjacent to the GSL and are important habitats for migratory waterfowl (Kadlec and Smith 1989, Aldrich and Paul 2002, Petrie et al. 2013). However, managed wetland complexes were not included in these surveys because the primary objective was to elucidate patterns of waterfowl use in the main body of the GSL and those bays with hydrologic connectivity that have not been surveyed by other programs. Thus, estimates of continental significance from this study should be considered conservative and may underestimate the extent of the flyway population using this system.

Habitat availability and quality likely played an important role in temporal and spatial patterns of duck abundance through winter on the GSL. Waterfowl distribution and abundance in winter generally responds positively to increases in foraging and aquatic habitat availability at multiple spatial scales (Nichols et al. 1983, Heitmeyer and Vohs 1984, Cox and Afton 2000, Fleskes et al. 2002). Drought conditions in the GSL
region extended for several years prior to the initiation of this study and persisted into 2004 causing GSL surface elevations to decline within 0.9 m of the lowest recorded elevation and reducing wetland availability (Stephens 1990, Wilkowske et al. 2003, Olson 2005). Precipitation in the GSL watershed increased in 2005, and lake elevations consequently increased 0.43 m (National Climate Data Center 2008; Fig. 2-4). Additionally, wetland habitat conditions adjacent to the GSL improved in 2005 because of greater availability of water (Olson 2006). Accordingly, total duck abundance in the GSL was approximately three times higher in both early and late winter periods of 2005-06 compared to 2004-05. Relatively few diving ducks, except goldeneye, were present in late winter 2004-05 when lake levels were low and wetlands diminished. However, diving duck abundance increased in the three eastern strata in late winter 2005-06 when lake elevations were higher (Fig. 2-4). Higher total duck abundance and use-days on the GSL during winter 2005-06 likely resulted from increased availability of wetland and lake habitat within the GSL system from greater hydrologic inputs that year (Olson 2006, Mohammed and Tarboton 2012).

The persistence and extent of ice can also reduce foraging and roosting habitat availability for waterfowl in winter (Lovvorn 1989, Schummer et al. 2012). The extent of ice in freshwater and coastal habitats is positively correlated with the cumulative number of days <0 °C (Lovvorn 1989, Assel 2003). Much of the freshwater and wetland habitats adjacent to the GSL typically experience ice conditions by late December as temperatures decline (Aldrich and Paul 2002; Fig. 2-4). Accordingly, duck species diversity and total duck abundance was lower during the mid-winter period (December–February). This pattern is likely explained by emigration out of the GSL system by many
waterfowl when temperatures decline and resource availability was reduced because of snow and ice cover in foraging habitats (Jorde et al. 1984, Aldrich and Paul 2002, Schummer et al. 2010).

However, the GSL does not freeze because of high salinity and may provide available habitat for some duck species during freezing events. Ice conditions may therefore influence spatial distribution of ducks among GSL stratum. Ice was present in the three eastern strata during the December surveys both winters but was more extensive in December 2004 when nearly all Northern Shoveler and Green-winged Teal were observed in South Gilbert Bay (J. Vest, unpublished data). Similarly, the proportion of goldeneye in the eastern strata increased from February to March surveys in both winters. During March, warming temperatures and increased freshwater inflows (Fig. 2-4) from snowmelt cause the eastern strata and adjacent freshwater marshes to become ice-free and goldeneye may seek to exploit the increased availability of these habitats. Consistent with this hypothesis, January 2006 was warmer than average and most goldeneye (67%) were observed in the three eastern strata that were free of ice. Thus, wintering ducks may rely on hypersaline areas of GSL to a greater extent as either foraging or secure loafing sites because of lower availability of freshwater habitats from reduced hydrologic inputs and extent of ice in the system.

Highly abundant food sources could explain use of hypersaline areas in winter. The South Arm of the GSL annually produces a remarkable biomass of brine shrimp and commercially harvested brine shrimp cysts (Stephens and Birdsey 2002, Kuehn 2002, Belovsky et al. 2011). Wind and lake currents can cause large streaks of cysts to form at the water surface that make them highly accessible to commercial harvesters and
waterbirds (Aldrich and Paul 2002, Stephens and Birdsey 2002, Caudell and Conover 2006, Belovsky et al. 2011). Over the course of all surveys, a total of 160 goldeneye and 80 Northern Shovelers were observed on cyst streaks within sampled transects. Aldrich and Paul (2002) speculated that wintering ducks, particularly goldeneye, Northern Shoveler, and Green-winged Teal, use brine shrimp cysts as a food source and noted that flocks of ducks have been regularly observed along cyst streaks on the lake surface, along ice edges, and against shorelines. However, neither the value of brine shrimp cysts to GSL waterfowl nor the extent of cyst use by waterfowl has been quantified. Given that brine shrimp cysts are commercially harvested and may be used as a food source by wintering waterfowl, when food availability or abundance may be low in the GSL region, efforts to quantify the use of brine shrimp, cysts, and other halophile invertebrates by waterfowl in the GSL region are warranted.

Hypersaline use varied considerably among species. Northern Shoveler, Green-winged Teal, and Common Goldeneye collectively comprised ≥62% of total duck abundance in December–February surveys and ≥94% of hypersaline stratum use in both winters. Ecomorphological traits such as lamellar density, bill shape, body size or behavioral and physiological strategies of these three species may allow them to meet thermoregulatory and energetic demands during winter when freshwater foraging resources decline. The high lamellar density of Northern Shovelers and, to a lesser degree, Green-winged Teal may allow them to use brine shrimp cysts as a forage resource if salinity is not a physiological barrier (Nyström and Perhsson 1988, Gurd 2005, Guillemain et al. 2008). Common Goldeneye used the hypersaline strata of the South Arm more extensively than other duck species. Sea ducks (Tribe Mergini) such as
Common Goldeneye may have relatively higher osmoregulatory efficiency or capacity than other ducks (Bennett and Hughes 2003). They also exhibit different foraging behavior by diving and using benthic resources compared to surface-feeding dabbling ducks such as Northern Shoveler and Green-winged Teal. Variation in osmoregulatory capacity or foraging behavior may therefore influence the more extensive use of hypersaline stratum by goldeneye compared to other species.

Carrington Bay was an important area for goldeneye in winter 2004-05 accounting for approximately 41% of all goldeneye use-days that winter. These results are interesting in that goldeneye using Carrington Bay may be up to 40 km away from the nearest reliable sources of freshwater. During this study, goldeneye flocks were observed making evening flights from Carrington Bay to the inflow of the Bear River in Ogden Bay. Based on personal observations of diurnal diving behavior in Carrington Bay and drinking behavior of arriving goldeneye flocks at the Bear River inflow of Ogden Bay at dusk, I speculate these evening flights are a function of obtaining and roosting in freshwater for osmoregulation after foraging or loafing in hypersaline stratum. However, the frequency of flights between these two areas by goldeneye is unknown.

South Gilbert Bay was an important area for Green-winged Teal and Northern Shovelers during both winters, especially during the December surveys where this stratum contained $\geq 35\%$ of these species abundance estimates (Fig. 2-3). During this study, Northern Shoveler and Green-winged Teal counted in South Gilbert Bay were typically observed in the eastern third of the stratum that is associated with the Lee Creek and Goggin Drain freshwater inflows to the GSL. Similarly, Northern Pintail and Gadwall were observed in close association of these same inflows on the few occasions
they were present in South Gilbert Bay. Thus, access to flowing freshwater could be an important requirement to use of hypersaline stratum. Consequently, abundance of Northern Shovelers, Green-winged Teal, Northern Pintail, and Gadwall may be overestimated for South Gilbert Bay as these birds were not distributed across the entire stratum. Consideration should be given to redistribution of stratum boundaries for future surveys based on areas of freshwater inflows and juxtaposition with wetland resources.

Survey results indicated the North Arm of the GSL did not provide habitat for migrating and wintering ducks. Creation of the Southern Pacific Railroad causeway in 1959 effectively removed hydrologic connection to the GSL and has dramatically altered the chemistry and ecology of the North Arm (Stephens 1990, Loving et al. 2002). The North Arm receives only minor freshwater inputs and extreme hypersaline conditions persist (> 25% salinity) which limit halophile invertebrate production (Herbst 1988, Loving et al. 2002, Stephens and Birdsey 2002, Belovsky et al. 2011). Prior to creation of the causeway, the North Arm likely provided similar habitat values to ducks as exhibited by the South Arm. Given the North Arm comprises approximately one-third of the surface area of the GSL, substantial reductions in the availability of GSL duck habitat have occurred as a result of the Southern Pacific Railroad causeway.

Although hypersaline portions of the South Arm may provide important habitat when freshwater resources are diminished, use of these areas may expose ducks to environmental contaminants. Naftz et al. (2008) reported mercury concentrations in GSL water samples were the highest reported for marine environments and mercury concentrations increased in brine shrimp samples from spring to fall. Similarly, mercury and selenium concentrations in eared grebes, which feed almost exclusively on brine
shrimp in the GSL, increased through fall suggesting bioaccumulation of these contaminants in GSL biota (Naftz et al. 2008, Conover and Vest 2009a,b). Furthermore, Naftz et al. (2008) reported selenium loading into the GSL was highest in inflows in the eastern portion of South Gilbert Bay where Northern Shoveler and Green-winged Teal were observed in winter. Thus, a clearer understanding of duck resource use of hypersaline stratum in the GSL is needed to inform management decisions and evaluate potential contaminant exposure to ducks.

**Precision**

These population indices suggest the GSL hosts a substantial number of migratory and wintering waterfowl but the precision of those estimates was generally poor. Most aerial survey programs attempting to determine population estimates of wintering waterfowl strive for a coefficient of variation of < 20% as a suitable precision metric (Conroy et al. 1988, Prenzlow and Lovvorn 1996; Pearse et al. 2008a, 2009). Several factors may lead to poor precision in aerial surveys including visibility, observer variability, flock or group size of ducks on transects, or distribution of ducks within strata (Conroy et al. 1988, Frederick et al. 2003, Pearse et al. 2008a,b). Variability in experience and estimation among observers likely reduces precision of population estimates (Caughley et al. 1976, Conroy et al. 1988, Bayliss and Yeomans 1990, Frederick et al. 2003). Four observers were used in all GSL surveys, and all of them were biologists with waterbird survey experience. Frederick et al. (2003) noted there is likely considerable variation (up to 70%) even among trained biologists in their ability to estimate large numbers of birds. However, Pearse et al. (2009) and Prenzlow and Lovvorn (1997) in studies evaluating wintering and breeding waterfowl surveys,
respectively, reported adding a second observer increased the area sampled and increased precision of population estimates.

Refinement of strata boundaries or optimal allocation of sampling effort among strata would also improve precision. Pearse et al. (2009) evaluated multiple survey designs and sampling strategies to estimate winter mallard abundance in the Mississippi Alluvial Valley and reported the largest gain in precision was from optimal allocation of sample effort and configuring the study area to include strata with consistently high densities of mallards. However, an effective and efficient sampling plan is not always apparent, especially when a priori information regarding spatial and temporal distributions of the target population is limiting such as in the GSL. Study areas are typically stratified to increase precision of overall estimates by grouping sample units into strata within which observations of the target population are less variable than among strata (Cochran 1977). I attempted to stratify the GSL study area based on expected high densities of ducks from information obtained from local experts (i.e., UDWR avian biologists) and variation in habitat attributes across the GSL study area. Data obtained from these GSL surveys should facilitate refinement of strata configuration and sampling effort allocation in future surveys. However, the non-uniform distribution of ducks within strata likely contributed to a significant amount of the observed variation. Georeferencing duck observations along transects during future surveys would provide greater insight into configuration of strata boundaries. To improve precision of estimates, I recommend future surveys on the GSL incorporate correction factors for individual observers, georeference observations, and allocate additional sampling effort to eastern
strata or use variances from previous surveys to allocate sample effort optimally among strata.

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Table 2-1. Estimated total abundance (in bold) of all ducks combined and percent of total abundance for duck foraging guilds (Dabbling ducks and Diving ducks) and individual species on the Great Salt Lake during winters (November–April) 2004-05 and 2005-06.

<table>
<thead>
<tr>
<th></th>
<th>2004-05</th>
<th>2005-06</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>November</td>
<td>December</td>
</tr>
<tr>
<td>Total Ducks</td>
<td>123,010</td>
<td>100,270</td>
</tr>
<tr>
<td>Total Dabbling ducks</td>
<td>98.4</td>
<td>70.9</td>
</tr>
<tr>
<td>Northern Pintail</td>
<td>12.6</td>
<td>0.1</td>
</tr>
<tr>
<td>Green-winged Teal</td>
<td>22.4</td>
<td>32.8</td>
</tr>
<tr>
<td>Northern Shoveler</td>
<td>25.5</td>
<td>22.9</td>
</tr>
<tr>
<td>Gadwall</td>
<td>25.2</td>
<td>7.7</td>
</tr>
<tr>
<td>Mallard</td>
<td>8.2</td>
<td>7.4</td>
</tr>
<tr>
<td>American Wigeon</td>
<td>4.3</td>
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</tr>
<tr>
<td>Cinnamon Teal</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Total Diving Ducks</td>
<td>1.6</td>
<td>29.1</td>
</tr>
<tr>
<td>Common Goldeneye</td>
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<td>25.9</td>
</tr>
<tr>
<td>Scaupa</td>
<td>1.1</td>
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<td>Redhead</td>
<td>0.1</td>
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<tr>
<td>Canvasback</td>
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</tr>
<tr>
<td>Ruddy Duck</td>
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<tr>
<td>Bufflehead</td>
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<td>Common Merganser</td>
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<td>Long-tailed Duck</td>
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<tr>
<td>White-winged Scoter</td>
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*Lesser and Greater scaup (*Aythya affinis* and *A. marila*) combined.
Table 2-2. Use-days calculated for total ducks, groups of ducks based on foraging guild, principal winter species and the percent of total use-days distributed across hypersaline strata and eastern (freshwater/brackish) strata of the Great Salt Lake during winters (November–April) 2004-05 and 2005-06 and in October 2005.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Total Use-days</th>
<th>Western Hypersaline</th>
<th>Eastern</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Carrington</td>
<td>North Gilbert</td>
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<tr>
<td>Total ducks</td>
<td>2004-05</td>
<td>13,717,150</td>
<td>11</td>
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<td>2005-06</td>
<td>20,572,920</td>
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<td>Oct. 2005</td>
<td>7,122,930</td>
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<tr>
<td>Dabbling ducks</td>
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<td>2005-06</td>
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<td></td>
<td>Oct. 2005</td>
<td>6,968,870</td>
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<td>0</td>
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<tr>
<td>Northern Pintail</td>
<td>2004-05</td>
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</tr>
<tr>
<td></td>
<td>2005-06</td>
<td>3,781,330</td>
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<td>0</td>
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<tr>
<td></td>
<td>Oct. 2005</td>
<td>2,074,860</td>
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<td>0</td>
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<tr>
<td>Green-winged Teal</td>
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<td>0</td>
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<td></td>
<td>2005-06</td>
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<td></td>
<td>Oct. 2005</td>
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<td>0</td>
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<td>Northern Shoveler</td>
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<td>0</td>
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<tr>
<td></td>
<td>2005-06</td>
<td>3,086,940</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Oct. 2005</td>
<td>1,598,390</td>
<td>0</td>
<td>0</td>
</tr>
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</table>
Table 2-2 continued.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Total Use-days</th>
<th>Western Hypersaline</th>
<th>Eastern</th>
<th>Bear River</th>
<th>Total Eastern</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Carrington</td>
<td>North Gilbert</td>
<td>Central Gilbert</td>
<td>South Gilbert</td>
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<tr>
<td>Gadwall</td>
<td>2004-05</td>
<td>1,341,880</td>
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<td>0</td>
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<td></td>
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<td>2</td>
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<tr>
<td></td>
<td>Oct. 2005</td>
<td>1,695,560</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
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<tr>
<td>Diving ducks</td>
<td>2004-05</td>
<td>4,082,260</td>
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<td>11</td>
<td>4</td>
<td>14</td>
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<td></td>
<td>2005-06</td>
<td>6,225,940</td>
<td>16</td>
<td>7</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Oct. 2005</td>
<td>154,050</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Common Goldeneye</td>
<td>2004-05</td>
<td>3,595,100</td>
<td>41</td>
<td>12</td>
<td>4</td>
<td>16</td>
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<td>2005-06</td>
<td>4,288,920</td>
<td>23</td>
<td>10</td>
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<td>9</td>
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<td></td>
<td>Oct. 2005</td>
<td>3,200</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>56</td>
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Fig. 2-1. Geophysical location and strata designation (gray areas) of the Great Salt Lake, Utah that I used to estimate abundance of wintering ducks during winters 2004-05 and 2005-06.
Fig. 2-2a-d. Abundance (± SD) of total ducks combined (a), total dabbling ducks (b), Northern Pintail (c), and Green-winged Teal estimated from aerial surveys across seven strata of the Great Salt Lake, Utah during winters 2004-05 (solid line, filled circle) and 2005-06 (dashed line, open circle).
Fig. 2-2e-h. Abundance (± SD) of Northern Shoveler (e), Gadwall (f), total Diving ducks (g), and Common Goldeneye (h) estimated from aerial surveys across seven strata of the Great Salt Lake, Utah during winters 2004-05 (solid line, filled circle) and 2005-06 (dashed line, open circle).
Fig. 2-3a-d. Estimated abundance of total ducks (a), total Diving ducks (b), Northern Pintail (c), and Green-winged Teal (d) in seven strata of the Great Salt Lake, Utah including Bear River Bay, Farmington Bay, Ogden Bay, South Gilbert Bay, Central Gilbert Bay, North Gilbert Bay, and Carrington Bay during winters 2004-05 and 2005-06.
Fig. 2-3e-h. Estimated abundance of Northern Shoveler (e), Gadwall (f), total Diving ducks (g), and Common Goldeneye (h) in seven strata of the Great Salt Lake, Utah including Bear River Bay, Farmington Bay, Ogden Bay, South Gilbert Bay, Central Gilbert Bay, North Gilbert Bay, and Carrington Bay during winters 2004-05 and 2005-06.
Fig. 2-4. Mean (± SD) temperature (°C; y1 axis) for a 15-day interval prior to aerial surveys conducted on the Great Salt Lake, Utah winters 2004-05 (filled bars) and 2005-06 (open bars); asterisks (*) indicate average monthly temperatures at Salt Lake City International Airport between 1971–2000. Circles and line indicate the mean Great Salt Lake surface elevation for a 15-day interval prior to aerial surveys conducted winters 2004-05 (filled circles, solid line) and 2005-06 (open circles, dashed line). An aerial survey was not conducted October 2004.
CHAPTER 3
FOOD HABITS OF WINTERING WATERFOWL
ON THE GREAT SALT LAKE, UTAH

Abstract.—Two invertebrates, brine shrimp (*Artemia franciscana*) and brine flies (Ephydridae), occur in great densities in the Great Salt Lake (GSL) but it is unknown whether ducks forage extensively on them during winter or rely on freshwater food. Common Goldeneye (*Bucephala clangula*), Northern Shoveler (*Anas clypeata*) and Green-winged Teal (*Anas crecca*) were collected from the GSL during winters 2004-05 and 2005-06 to evaluate their food habits. Brine shrimp and brine flies comprised more than 70% of the winter diet of these ducks. Common Goldeneye consumed mainly brine fly larvae (68% based on dry weight biomass), which live primarily along the substrate. Northern Shovelers fed on brine shrimp cysts (52%) and adult brine shrimp (20%) while Green-winged Teal consumed mainly brine shrimp cysts (80%). In some years, up to half of the brine shrimp cysts in the GSL are commercially harvested. Care should be taken so that this commercial harvest does not adversely impact ducks that depend on these brine shrimp cysts for winter food.

INTRODUCTION

Saline systems provide important habitat for many waterbirds worldwide (Collazo *et al.* 1995; Owino *et al.* 2002; Shuford *et al.* 2002). Within the western hemisphere, the Great Salt Lake (GSL) and associated marshes are an important resource for millions of migratory waterbirds (Kadlec and Smith 1989; Cox and Kadlec 1995; Aldrich and Paul
An estimated 3–5 million waterfowl annually migrate through the GSL area (Bellrose 1980; Aldrich and Paul 2002).

Tens of thousands of waterfowl have been observed using the GSL during winter, primarily Common Goldeneye (*Bucephala clangula*), Northern Shoveler (*Anas clypeata*) and Green-winged Teal (*A. crecca*). Two hypotheses potentially explain the presence of ducks on the GSL. Firstly, GSL is a safe place to loaf or roost due to the absence of waterfowl hunters and predators. This hypothesis argues that these ducks are either fasting or are flying, perhaps at night, to the distant freshwater and brackish marshes to forage. The second hypothesis is that these ducks over-winter in the pelagic regions of the GSL because they are foraging on the GSL’s brine shrimp (*Artemia franciscana*) cysts and brine fly (Ephydridae) larvae despite the osmoregulatory and physiological challenges that result from consuming them (Nyström and Perhsson 1988; Wobeser 1997). These two hypotheses were tested by assessing the diet of these ducks during the winter. The objective of this study was to determine the extent to which wintering waterfowl utilize brine shrimp and brine fly resources from the GSL.

**METHODS**

**Study Area**

The GSL is a hypersaline terminal lake located in north-central Utah within the Great Basin and Range Province and is a dominant water feature within the western United States (Arnow and Stephens 1990; Stephens 1990). When the GSL is at its average lake elevation of 1,280 m above sea level, it encompasses approximately 4,400 km² with a maximum depth of approximately 10 m (Arnow and Stephens 1990; Stephens 1990).
1990). The Southern Pacific Railroad Cause-way divides the GSL into two distinct areas with unique ecological characteristics (Fig. 3-1). The North Arm of the GSL is characterized by minimal freshwater inflow, extreme hypersaline conditions (>20% salinity) and is rarely used by waterfowl (Stephens 1990; Aldrich and Paul 2002; Loving et al. 2002). The South Arm receives >90% of the freshwater surface inflow into the GSL and consequently has lower salinity than the North Arm (Stephens 1990; Loving et al. 2002). Salinity varies inversely with lake levels in the GSL but has generally averaged 13% salinity in the South Arm, approximately three times the salinity concentration of seawater (Arnow and Stephens 1990; Stephens 1990). The South Arm is populated by green and blue-green algae, diatoms and high biomass of halophile macroinvertebrates consisting of brine shrimp and brine flies (Collins 1980; Stephens and Birdsey 2002). Additionally, the GSL is bordered by approximately 1,900 km² of freshwater and brackish habitats, primarily on the east side of the lake (Johnson 2007).

I obtained daily and monthly GSL surface elevation data from a U.S. Geological Survey gauging station located at Saltair Boat Harbor (U.S. Geological Survey 2009) and monthly salinity concentrations from Utah Division of Wildlife Resources’ (UDWR) Great Salt Lake Ecosystem Program. South Arm surface elevations ranged from 1,278.4-1279.2 m, and salinity varied from 17–13% over the course of this study (Fig. 3-2).

I calculated daily and monthly average temperatures and wind speeds using data from 3 MESOWEST weather stations in or adjacent to the South Arm of the GSL at Hat Island, Antelope Island and on the south shore between Saltair Boat Harbor and Lake Point Junction (Fig. 3-3). All weather stations were located between 1,280–1,305 m above sea level and were within 12 m of GSL surface elevations during this study.
Data Collection

Common Goldeneye were collected from portions of the South Arm of the GSL, including Ogden, Farmington, Gilbert and Carrington Bays during winters 2004-05 and 2005-06 (Fig. 3-1). Collections began soon after Common Goldeneye arrived in the GSL system (late November) and were suspended once birds departed the GSL (early April). Winter was divided into three periods: 1) early winter (November 19–December 20), 2) mid-winter (January 1–February 22) and 3) late winter (February 28–April 5). Northern Shoveler samples were obtained from Farmington Bay in November 2004 and October 2005 and from Ogden and Farmington Bays in November 2005. Northern Shoveler and Green-winged Teal samples were obtained in December 2004 and 2005 and February 2006 from southeastern Gilbert Bay near the Lee Creek and Goggin Drain outflows into the GSL (Fig. 3-1). Additionally, a small number (n < 10 per species) of Northern Shoveler and Green-winged Teal samples were obtained from Ogden Bay in Decembers 2004 and 2005.

Collection locations were selected based on areas of high bird concentrations that were observed during monthly aerial surveys of the GSL for waterbirds. All waterfowl samples were collected by pass shooting over decoys from layout boats (99%), jump shooting (<1%), and shooting into flocks from a scull boat (<1%) under authority of federal (no. MB693616) and state (no. COLL6550) scientific collection permits and protocol approved by Utah State University Institutional Animal Care and Use Committee (approval no. 1117). Collected birds were labeled (species, date and location), placed in plastic bags, frozen at –10°C within six hours of collection and later transported frozen to Utah State University.
Birds were sexed and aged (i.e. adult or juvenile and subadult; Hochbaum 1942; Carney 1992). Contents of the esophagus (including proventriculus) were removed from each bird and rinsed through a 150 μm sieve. I collected food samples from the esophagus rather than from the gizzard or intestines because soft foods (e.g. adult brine shrimp) are digested faster than hard foods (e.g. seeds) causing hard foods to be over-represented in gizzard samples (Swanson and Bartonek 1970).

I stored the contents of the esophagus in labeled containers containing a 70% ethyl alcohol solution. A dissection microscope (10x ocular lens) was used to identify and sort all dietary taxa to the lowest taxonomic level possible (Wirth et al. 1987; Thorp and Covich 2001; DiTomaso and Healy 2003; U.S. Department of Agriculture 2009). I used these data to determine how often a particular food item was found in ducks (frequency of occurrence).

Individual taxonomic food groupings for each bird were then kept in a drying oven set at 60°C for at least 24 hours to obtain their dry masses (±0.0001 g). Dry weights are preferred over wet weights because dry weights eliminate biases caused by differential water evaporation (Sugden 1973). Dry masses of each food item were converted into aggregate percent dry mass values for each bird (Swanson et al. 1974).

Data Analyses

Frequency of occurrence and mean aggregate percent dry mass of all food items were calculated for each waterfowl species to identify important food groups. Although brine shrimp cysts were observed in most bird samples, percent occurrence of cysts was quantified only when a bird’s esophagus contained ≥0.0001 g of cysts because of the ubiquitous nature of cysts in the GSL and the potential for incidental ingestion by birds.
Aggregate percent dry mass of each food item per bird was converted into proportions, and the latter values were used as dependent variables in subsequent analyses (Afton et al. 1991; Badzinski and Petrie 2006). An arcsine square-root transformation was performed on proportions to create a normal distribution of data (Zar 1999; Badzinski and Petrie 2006).

Multivariate analyses of variance (MANOVA) was used to evaluate variation in aggregate percent biomass of major food items consumed by Common Goldeneye, including brine fly larvae, brine shrimp cysts, freshwater or brackish macroinvertebrates, and plant seeds or achenes from freshwater or brackish habitats (PROC GLM; SAS Institute 2005). Vegetative parts were not included in food groupings for statistical analyses because these food items comprised a minor proportion of dietary biomass (<0.5% aggregate biomass) in all bird species (Table 3-1). Additionally, adult brine shrimp were not included into food groupings for statistical analyses of Common Goldeneye diets because they comprised a minor (0.2%) proportion of dietary biomass and were generally unavailable during winter. Waterfowl food habits may vary in relation to gender, age, time and space. Therefore, effects of gender, age, winter time period and year of collection were evaluated; year × period and gender × age interactions were included as effects of biological interest for Common Goldeneye dietary analyses. Additionally, the bay (Ogden Bay, Farmington Bay, South Gilbert Bay and Carrington Bay [Fig. 3-1]) from which Common Goldeneye were collected was specified as a random variable in all Common Goldeneye models (PROC GLM; SAS Institute 2004).

MANOVAs were used to evaluate variation in major food groups consumed by Northern Shoveler and Green-winged Teal, including brine fly larvae, adult brine shrimp,
brine shrimp cysts, freshwater or brackish invertebrates and seeds or achenes. Overall variation in diet between Northern Shoveler and Green-winged Teal was first evaluated using only samples from December and February (across years) to limit potential bias associated with variation in collection location; most Northern Shoveler and Green-winged Teal samples (97%) were obtained from the same location (Gilbert Bay) in December and February. For each Anas species, I assessed effects of gender and age, including the gender × age interaction, on consumption of major food groups using MANOVAs (PROC GLM; SAS Institute 2004). Differences in dietary composition between years were tested in the December samples and between December and February collection periods in winter 2005-06 for each Anas species using MANOVAs (PROC GLM; SAS Institute 2004). Differences in Northern Shoveler diets between October and November time periods were not evaluated because few samples with food present (n = 2) were obtained in 2004 and all October 2005 samples were obtained from Farmington Bay whereas November 2005 samples were obtained from both Farmington and Ogden Bays.

For analyses of all three waterfowl species, final reduced models were obtained by sequentially removing interaction terms and then main effects (P ≥ 0.10; Type III sums of squares) based on Wilks’ criterion (Hair et al. 1998; Badzinski and Petrie 2006). I then conducted a posteriori contrasts using least-square means of response variables on effects of interest from the reduced model and multiple comparisons were adjusted using the Tukey-Kramer method (PROC GLM; SAS Institute 2004). For Common Goldeneye, I reported least squares means and standard errors of non-transformed data for more meaningful interpretation of results (Badzinski and Petrie 2006). However, raw means of
Northern Shoveler and Green-winged Teal dietary compositions are graphically presented given the temporal and spatial limitations of those data.

RESULTS

Overall, 602 Common Goldeneye were collected from throughout the South Arm of the GSL during winters 2004-05 and 2005-06; of which 355 (59%) contained food in their esophageal tracts (Table 3-1). Eighteen food item types were detected in Common Golden-eye diets. For those Common Goldeneyes that contained food, 86% contained animal material and 35% contained plant material; 77% had food from saline areas (73% contained brine fly larva and 19% brine shrimp cysts) and 16% contained freshwater or brackish water invertebrates. Aggregate percent biomass of food was dominated by animal matter (81%); particularly brine fly larvae (68%; Table 3-2). Other important foods based on percent biomass included wetland plant seeds (19%) and freshwater/brackish invertebrates (9%) (primarily corixids; Table 3-1).

The final reduced MANOVA model evaluating variation in Common Goldeneye diets included the gender main effect ($F_{4,341} = 2.09$, $P = 0.08$) and the year × period interaction ($F_{8,682} = 3.84$, $P = 0.0002$); the age main effect and all other interaction terms were removed from the model ($P > 0.10$). A posteriori contrasts from the reduced MANOVA indicated female Common Goldeneye consumed 6% more ($P = 0.01$) freshwater invertebrates, primarily corixids, than males but similar proportions of other food groups relative to males ($P \geq 0.28$; Table 3-2). Contrasts of the year × period interaction indicated Common Goldeneye consumed 31–41% less ($P \leq 0.002$) brine fly larvae and concomitantly more ($P \leq 0.0003$) wetland plant seeds during late winter 2004-
05 than in other time periods during the same year or during late winter 2005-06 (Table 3-3). Widgeon Grass (*Ruppia maritima*) and Alkali Bulrush (*Scirpus maritimus*) seeds comprised 38% and 10%, respectively, of aggregate percent biomass during late winter 2004-05 when seed biomass was highest in Common Goldeneye diets. Common Goldeneye consumed 16% more (*P* = 0.001) freshwater invertebrates during early winter 2005-06 relative to 2004-05 and aggregate percent biomass of freshwater invertebrates declined (*P* = 0.09) 15% from early to late winter 2005-06 (Table 3-1). During early winter 2005-06, freshwater invertebrates in Common Goldeneye were comprised mostly of corixids, accounting for 22% of the overall mean aggregate percent biomass.

Overall, 312 Northern Shoveler and 218 Green-winged Teal were collected of which 241 (77%) and 137 (63%), respectively, contained food items in their esophageal tracts. Twenty-four and 17 food item types were detected in Northern Shoveler and Green-winged Teal diets, respectively, and biomass composition was dominated by animal matter (≥88%), particularly brine shrimp cysts (>51%; Table 3-1). Other important food groups included adult brine shrimp (≤20%), brine fly larvae (≤11%), wetland plant seeds (≤11%), and freshwater and brackish invertebrates (≤9%), primarily corixids.

During the December and February time periods, Northern Shovelers consumed 5%, 6% and 19% more (*P* ≤ 0.02) seeds, freshwater invertebrates and brine shrimp, respectively, than Green-winged Teal but 28% fewer cysts based on aggregate percent biomass (*P* < 0.0001; Fig. 3-4). Amounts of brine fly larvae did not vary (*P* = 0.29) between Green-winged Teal and Northern Shoveler (Table 3-1). Aggregate percent biomass did not vary between genders or ages in either Northern Shovelers (*F* < 0.001; Fig. 3-4).
1.22, \( P \geq 0.30 \) or Green-winged Teal \( (F_{5,129-130} \leq 0.80, P \geq 0.56) \). Northern Shovelers consumed 11% and 34% more \( (P \leq 0.001) \) brine fly larva and adult brine shrimp, respectively, but 40% fewer \( (P < 0.0001) \) cysts during December 2005 relative to December 2004 (Fig. 3-4). Based on aggregate percent biomass, Green-winged Teal consumed 37% and 4% more \( (P \leq 0.04) \) brine fly larvae and adult brine shrimp, respectively, but 54% fewer \( (P < 0.0001) \) cysts during December 2005 relative to December 2004 (Fig. 3-4). Additionally, Green-winged Teal consumed 14% more \( (P = 0.0004) \) seeds in December 2005 relative to 2004 (Fig. 3-4). During December 2005 and February 2006, Northern Shovelers consumed 16% fewer brine fly larva and 48% fewer adult brine shrimp and increased their consumption of cysts by 59% \( (P < 0.0001; \text{Fig. 3-4}) \). During winter 2005-06, brine fly larvae comprised approximately 40% of the diet of Green-winged Teal in December but were absent in February when they were replaced by fresh-water invertebrates (Fig. 3-4). In December 2005, seeds of Alkali Bulrush and Widgeon Grass each comprised 7% of dietary biomass. In February 2006, Chenopodium, Alkali Bulrush and Widgeon Grass seeds comprised 10%, 9%, and 4%, respectively, of dietary biomass whereas corixids and Chironomidae larvae comprised 19% and 9%, respectively.

**DISCUSSION**

I tested two hypotheses to explain why large numbers of Common Goldeneye, Northern Shoveler and Green-winged Teal are over-wintering on the GSL. These results support the hypothesis that these ducks are there because they are foraging on the GSL’s brine shrimp and brine fly larva. Adult brine shrimp, brine shrimp cysts and brine fly
larva constituted >70% of the winter diet of Common Goldeneyes, Northern Shovelers and Green-winged Teal based on aggregate percent biomass.

The only invertebrates that can survive the GSL’s hyper-saline conditions are brine shrimp and brine flies (Stephens 1990). Brine flies overwinter as pupae and larvae which are located on the substrate. They can occur in densities >5,000 per m$^2$ in preferred habitats, including stromatolites (i.e. bioherms) and fine alluvial deposits above the GSL deep brine layer (Collins 1980). Brine shrimp occur in the water column; adult densities normally range from 250 and 2,500 adults/m$^3$ and cyst densities exceed 20,000/m$^3$ in the fall (Conover and Caudell 2009). Wind and lake currents concentrate cysts into large streaks at the water surface. During the fall, these streaks also contain adult brine shrimp but adults die during November when the water temperature drops and are no longer available after December (personal observation).

While all three duck species forage on brine flies and brine shrimp, I found that they exploit different species based on their foraging behaviors. Common Goldeneye are diving ducks, and I found that they foraged mainly on brine fly larvae, which are located on the bottom substrate. Concomitantly, I found that brine shrimp cysts comprised a small proportion of their overall diet. The bill morphology of Common Goldeneyes could limit their ability to forage on small food items such as cysts, which are only 0.2 mm in diameter (Kehoe and Thomas 1987; Gurd 2007). Alternatively, cysts may be a less profitable food source than brine fly larvae because cysts are difficult to digest (Mac-Donald 1980; Caudell and Conover 2006).

Northern Shovelers and Green-winged Teal are dabbling ducks, and I found that these ducks forage primarily on adult brine shrimp and their cysts. Brine shrimp and
their cysts are located throughout the water column and concentrated in streaks along the water surface where these ducks typically forage. Brine fly larvae are not physically attached to benthic substrates and seiches from wind and storm events cause some larvae to become mixed in the water column (Collins 1980). The movement of brine fly larvae into the water column could explain why I found that brine fly larvae made up 8–11% of the winter diet of Green-winged Teal and Northern Shovelers.

I observed Northern Shovelers foraging more along streaks than Green-winged Teal while the latter foraged more frequently in the shallow water along beaches. In early winter, adult brine shrimp are often incorporated into streaks along with the cysts, where they would both be available to Northern Shovelers while cysts are concentrated along beaches (Kuehn 2002). The interspecific differences in foraging areas may explain why Northern Shovelers consumed more adult shrimp than Green-winged Teal while the latter consumed more cysts.

Freshwater and brackish habitats adjacent to the GSL are frozen during the mid-winter period but become important foraging habitat for waterfowl during spring. I found that in late-winter (i.e. March) when ice in freshwater habitats begins to melt, ducks increased their consumption of wetland plant seeds, primarily widgeon grass and alkali bulrush. Plant seeds are carbohydrate-rich food resource (Baldassarre and Bolen 2006; Smith 2007), and may be preferred over brine shrimp cysts and brine fly larvae as birds prepare for the physiological demands of spring migration.

The amount of fresh and saline water available in the GSL and associated wetlands is primarily determined by amounts of winter snow pack within the Great Basin, runoff and diversion of freshwater for anthropogenic uses (Arnow and Stephens 1990;
Aldrich and Paul 2002). Hence, the size of the GSL varies annually. An extended drought period caused GSL surface elevations in 2004 to decline to within 0.9 m of the lowest recorded elevation (Stephens 1990; Wilkowske et al. 2003). A 1-m decrease in lake elevation causes the surface area of the entire GSL to decrease by approximately 58,000 ha (Aldrich and Paul 2002). Increased precipitation during 2005-06 caused the GSL to rise in elevation (National Climate Data Center 2008; Figs. 3-2 and 3-3). This may explain the greater amounts of freshwater and brackish invertebrates, primarily corixids, in Common Goldeneye diets during early winter 2005-06. Corixids cannot survive in the main body of the GSL due to its high salinity but are abundant in brackish marshes around the GSL (Huener and Kadlec 1992; Wurtsbaugh 1992). Caudell and Conover (2006) reported corixids have higher energetic content (21.2 kJ/g) than brine fly larvae (13.6 kJ/g). Hence, Common Goldeneye may prefer to forage on corixid when the marshes are not covered with ice.

I found that female Common Goldeneyes consumed more corixid than males. I am unsure why there was a sexual difference in diet. Being smaller, females may need to devote more calories to thermoregulation. This may lead them to seek a more nutritious diet than males despite the risks of foraging in the marshes that are frequented by both duck hunters and predators.

Although the GSL may serve as important habitat for wintering ducks, several potential threats exist including: high levels of selenium and mercury, diversion of freshwater for irrigation and commercial harvest of brine shrimp cysts. I found high concentrations of mercury and selenium in the same sample population of GSL waterfowl reported in Chapter 5 and in Eared Grebes (Podiceps nigricollis) that feed almost
exclusively on GSL brine shrimp (Conover and Vest 2009). It is unknown whether ducks that overwinter on the GSL suffer any ill effects from the high levels of mercury and selenium in their tissues. However, a health advisory has been issued warning people about consuming Common Goldeneyes and Northern Shovelers harvested near the GSL (see Chapter 5).

Many saline lake systems around the world have experienced increased salinities and reductions in lake levels via anthropogenic forces, primarily water diversions (Williams 2002; Timms 2005). Many governing and international conservation bodies have failed to recognize salt lakes as important inland aquatic systems, thereby hampering effective conservation strategies for these systems (Williams 2002). The GSL faces identical threats as freshwater is diverted for irrigation and other uses (Kadlec and Smith 1989; Aldrich and Paul 2002; Naftz et al. 2008). The GSL is a terminal basin and a reduction in the quantity of freshwater flowing into it will lead to an increase in salinity concentrations as lake levels decline (Stephens 1990). These results indicate that ducks wintering on the GSL would lose an important food source if salinity levels increase to levels above the tolerance of brine flies or brine shrimp (Herbst 1988; Dana et al. 1993; Stephens and Birdsey 2002).

Two million kilograms of brine shrimp cysts are commercially harvested annually from the GSL (Conover and Caudell 2009). This harvest is regulated by the Utah Division of Wildlife Resources so that the commercial harvest of cysts will have minimal impact on birds. Up to now, the main concern has been the impact of the cyst harvest on Eared Grebes (Conover and Caudell 2009). These results indicate that wintering population of Green-winged Teal and Northern Shovelers also are dependent upon brine
shrimp and their needs should be considered when determining how many brine shrimp cysts can be commercially harvested. This could be accomplished by stopping the commercial harvest of cysts annually whenever their densities in the GSL reach a particular level.

LITERATURE CITED


Table 3-1. Percent occurrence and aggregate percent dry biomass of food items consumed by Common Goldeneye, Northern Shoveler, and Green-winged Teal during winters (October–March) 2004-05 and 2005-06 on the Great Salt Lake, Utah.

<table>
<thead>
<tr>
<th>Food Item</th>
<th>Common Goldeneye (n = 355)</th>
<th>Northern Shoveler (n = 241)</th>
<th>Green-winged Teal (n = 137)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Occurrence</td>
<td>Aggregate % Biomass</td>
<td>% Occurrence</td>
</tr>
<tr>
<td><strong>ANIMAL</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Saltine</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Artemiidae</td>
<td>77</td>
<td>71.5</td>
<td>84</td>
</tr>
<tr>
<td><em>Artemia franciscana</em> (adult)</td>
<td>3</td>
<td>0.2</td>
<td>44</td>
</tr>
<tr>
<td><em>Artemia franciscana</em> (cysts)</td>
<td>19</td>
<td>3.7</td>
<td>70</td>
</tr>
<tr>
<td>Ephydridae</td>
<td>73</td>
<td>67.6</td>
<td>56</td>
</tr>
<tr>
<td>Adult</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Larvae</td>
<td>73</td>
<td>67.6</td>
<td>56</td>
</tr>
<tr>
<td>Egg</td>
<td>&lt; 1</td>
<td>Trace</td>
<td>&lt; 1</td>
</tr>
<tr>
<td><strong>Freshwater/Brackish</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arachnidae</td>
<td>1</td>
<td>0.3</td>
<td>3</td>
</tr>
<tr>
<td>Hydracnida</td>
<td>&lt; 1</td>
<td>Trace</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Unidentified</td>
<td>&lt; 1</td>
<td>0.3</td>
<td>2</td>
</tr>
<tr>
<td>Crustacea</td>
<td>2</td>
<td>0.3</td>
<td>3</td>
</tr>
<tr>
<td>Cladocera ephippia</td>
<td>2</td>
<td>0.3</td>
<td>2</td>
</tr>
<tr>
<td>Copepoda</td>
<td>0</td>
<td>&lt; 1</td>
<td>0</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>0</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>1</td>
<td>0.3</td>
<td>0</td>
</tr>
<tr>
<td>Insecta</td>
<td>13</td>
<td>8.3</td>
<td>26</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>&lt; 1</td>
<td>Trace</td>
<td>1</td>
</tr>
<tr>
<td>Diptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chironomidae</td>
<td>0</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>Adults</td>
<td>0</td>
<td>1</td>
<td>Trace</td>
</tr>
<tr>
<td>Larvae</td>
<td>1</td>
<td>0.2</td>
<td>9</td>
</tr>
<tr>
<td><strong>Hemiptera</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corixidae</td>
<td>12</td>
<td>8.1</td>
<td>20</td>
</tr>
<tr>
<td>Adults</td>
<td>12</td>
<td>7.6</td>
<td>15</td>
</tr>
<tr>
<td>Eggs</td>
<td>3</td>
<td>0.4</td>
<td>8</td>
</tr>
<tr>
<td>Odonata</td>
<td>0</td>
<td>2</td>
<td>Trace</td>
</tr>
<tr>
<td>Unknown invertebrate</td>
<td>0</td>
<td>4</td>
<td>Trace</td>
</tr>
<tr>
<td><strong>PLANT</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetation</td>
<td>35</td>
<td>19.4</td>
<td>54</td>
</tr>
<tr>
<td><em>Lemma</em> spp</td>
<td>1</td>
<td>Trace</td>
<td>14</td>
</tr>
<tr>
<td>Unknown (fragments, algae)</td>
<td>1</td>
<td>0.2</td>
<td>9</td>
</tr>
<tr>
<td><strong>Seeds/achenes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chenopodium spp.</td>
<td>&lt; 1</td>
<td>Trace</td>
<td>3</td>
</tr>
<tr>
<td>Cyperus</td>
<td>0</td>
<td>1</td>
<td>Trace</td>
</tr>
<tr>
<td>Hordeum jubatum</td>
<td>0</td>
<td>2</td>
<td>Trace</td>
</tr>
<tr>
<td>Phragmites australis</td>
<td>7</td>
<td>0.4</td>
<td>31</td>
</tr>
<tr>
<td>Rumex spp.</td>
<td>0</td>
<td>&lt; 1</td>
<td>Trace</td>
</tr>
</tbody>
</table>
Table 3-1 continued.

<table>
<thead>
<tr>
<th>Food Item</th>
<th>Common Goldeneye $(n = 355)$</th>
<th>Northern Shoveler $(n = 241)$</th>
<th>Green-winged Teal $(n = 137)$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Occurrence</td>
<td>Aggregate % Biomass</td>
<td>% Occurrence</td>
</tr>
<tr>
<td>Ruppia maritima</td>
<td>12</td>
<td>8.3</td>
<td>2</td>
</tr>
<tr>
<td>Salicornia rubra</td>
<td>1</td>
<td>Trace</td>
<td>12</td>
</tr>
<tr>
<td>Scirpus acutus</td>
<td>1</td>
<td>0.1</td>
<td>1</td>
</tr>
<tr>
<td>Scirpus maritimus</td>
<td>14</td>
<td>7.7</td>
<td>18</td>
</tr>
<tr>
<td>Stuckenia pectinatus</td>
<td>4</td>
<td>2.1</td>
<td>4</td>
</tr>
<tr>
<td>Typha spp.</td>
<td>1</td>
<td>0.3</td>
<td>11</td>
</tr>
<tr>
<td>Zannichellia palustris</td>
<td>1</td>
<td>0.3</td>
<td>3</td>
</tr>
<tr>
<td>Unknown seed fragments</td>
<td>&lt; 1</td>
<td>Trace</td>
<td>1</td>
</tr>
</tbody>
</table>

*Trace = trace amounts of food item (≤ 0.1 aggregate percent biomass).
Table 3-2. Results of a posteriori contrasts of the gender main effect evaluating variation in the aggregate percent dry biomass (least-square means ± SE) of major food groups consumed by Common Goldeneye wintering on the Great Salt Lake, Utah. Means with similar letters in each row do not differ ($P \geq 0.10$).

<table>
<thead>
<tr>
<th>Food Item</th>
<th>Female ($n = 191$)</th>
<th>Male ($n = 164$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brine shrimp cysts</td>
<td>3.9 ± 1.7 a</td>
<td>6.2 ± 1.2 a</td>
</tr>
<tr>
<td>Ephydridae larvae</td>
<td>62.5 ± 3.5 a</td>
<td>62.7 ± 3.6 a</td>
</tr>
<tr>
<td>Freshwater invertebrates</td>
<td>16.8 ± 2.0 a</td>
<td>10.5 ± 2.0 b</td>
</tr>
<tr>
<td>Seeds</td>
<td>16.7 ± 3.1 a</td>
<td>20.6 ± 3.2 a</td>
</tr>
</tbody>
</table>
Table 3-3. Results of a posteriori contrasts of year × season interaction evaluating variation in the aggregate percent dry mass (least-square means ± SE) of major food groups consumed by Common Goldeneye wintering on the Great Salt Lake, Utah. Early winter = November 19–December 22, Mid-winter = January 1–February 22, Late winter = February 28–March 31. Means with similar letters in each row do not differ ($P \geq 0.10$).

<table>
<thead>
<tr>
<th>Food Item</th>
<th>2004-05</th>
<th>2005-06</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early Winter ($n = 78$)</td>
<td>Mid-winter ($n = 41$)</td>
</tr>
<tr>
<td>Brine shrimp cysts</td>
<td>3.8 ± 2.3 a</td>
<td>10.2 ± 3.2 a</td>
</tr>
<tr>
<td>Ephydridae larvae</td>
<td>76.6 ± 5.0 a</td>
<td>73.0 ± 6.9 a</td>
</tr>
<tr>
<td>Freshwater invertebrates</td>
<td>9.0 ± 2.8 a</td>
<td>13.6 ± 3.9 a</td>
</tr>
<tr>
<td>Seeds</td>
<td>10.6 ± 4.4 a</td>
<td>3.2 ± 6.0 a</td>
</tr>
<tr>
<td></td>
<td>Early Winter ($n = 67$)</td>
<td>Mid-winter ($n = 67$)</td>
</tr>
<tr>
<td>Brine shrimp cysts</td>
<td>5.3 ± 2.6 a</td>
<td>4.3 ± 2.7 a</td>
</tr>
<tr>
<td>Ephydridae larvae</td>
<td>64.8 ± 5.5 a</td>
<td>58.5 ± 5.9 a</td>
</tr>
<tr>
<td>Freshwater invertebrates</td>
<td>24.9 ± 3.2 b</td>
<td>17.5 ± 3.4 ab</td>
</tr>
<tr>
<td>Seeds</td>
<td>5.0 ± 4.9 a</td>
<td>19.7 ± 5.2 a</td>
</tr>
</tbody>
</table>
Figure 3-1. Geophysical location and features of the Great Salt Lake, Utah. Dark shading represents state and federal wetland management complexes. Dotted shading represents commercial solar evaporation complexes. Gray lines represent 1277.1, 1278.6, and 1279.5 m surface elevation contours.
Figure 3-2. Great Salt Lake surface elevations (m above sea level) and salinity concentrations (%) during winters 2004-05 (elevation = solid line; salinity = filled diamond) and 2005-06 (elevation = dashed line; salinity = open diamond).
Figure 3-3. Average monthly temperatures (°C; ± SE) and wind speeds (km/hour; ± SE) at the Great Salt Lake during winters 2004-05 (temperature = white bars, wind speed = white triangles) and 2005-06 (temperature = gray bars, wind speed = gray triangles). Average temperatures and wind speeds calculated from three MESOWEST weather stations in or adjacent to the South Arm of the Great Salt Lake; refer to Methods and Fig. 1.
Figure 3-4. Food items consumed by Northern Shoveler and Green-winged Teal during winters (October–February) 2004-05 and 2005-06 on the Great Salt Lake, Utah. Shrimp = adult *Artemia franciscana*, Cysts = *A. franciscana* cysts, Ephydridae = larval Ephydridae, Fw. Invert = freshwater/brackish invertebrates, Seeds = seeds/achenes from wetland plants.
CHAPTER 4
FACTORS AFFECTING LIPID RESERVE DYNAMICS OF WINTERING
COMMON GOLDENEYE AT GREAT SALT LAKE

ABSTRACT The Great Salt Lake (GSL) is important to millions of migratory waterbirds including wintering common goldeneye (Bucephala clangula) harboring as much as 4% of the combined common and Barrow’s goldeneye (B. islandica) continental population. Unfortunately, little information exists regarding physiological condition of waterfowl within the GSL system or other hypersaline environments in winter. I collected common goldeneye (hereafter goldeneye) from the GSL during winters (late November–early April) 2004-05 and 2005-06 to evaluate endogenous and exogenous factors influencing lipid reserves. I modeled change in lipid mass as a function of seven independent variables including: structural size, sex, age, date, effective temperature, salt gland mass, and year. Lipid reserves were, on average, 17% lower in winter 2004-05 when regional and local wetland and aquatic habitat conditions at GSL were diminished because of an extended drought and indices of the primary halophile food resource, brine fly (Ephydridae) larvae, were low. On average, lipid reserves declined 34% through winter. Lipid reserves appeared to follow a quadratic relationship with effective temperature ($T_{ef}$; ambient temperature adjusted for wind speed); this pattern was relatively stronger in females than males. Female lipids were highest at average $T_{ef}$ of 6.8 °C, or 0 °C ambient temperature, and declined at a rate of 6% and 14% per 5°C change below and above this threshold, respectively. Male lipids were highest at the lowest $T_{ef}$ ($\leq 5$ °C) and declined 10% per 5 °C increase in $T_{ef}$ (22% overall). Salt gland mass was used as an index of relative hypersaline exposure, and was the least important factor
influencing lipid reserves interpreted from cumulative parameter weights ($\sum w_i = 0.71$). However, adult male lipid reserves generally did not vary in relation to changes in salt gland mass. Overall, female and juvenile male lipid reserves declined 2% per 0.1 g increase in salt gland mass, were lowest when salt gland mass approached 0.7 g for females and 0.8 g for juvenile males, then increased 3% and 4% per 0.1 g increase above this threshold for females and males, respectively. These results suggest regional and local foraging habitat conditions were important influences on lipid dynamics of goldeneye during winter. Although acclimation to and use of hypersaline resources likely incurred additional energetic costs, goldeneye at GSL were able to maintain lipid reserves similar to levels reported in freshwater systems. The availability and high abundance of brine fly larvae likely played a key role in maintenance of lipid reserves through winter.

**INTRODUCTION**

Lipid reserves are directly correlated with avian body condition and are important determinants of fitness parameters in waterfowl (Blem 1976, Owen and Cook 1977, Ankney and MacInnes 1978, Johnson et al. 1985, Blums et al. 2005). Lipids supply energy for homeostasis and during periods of fasting (i.e., migration, roosting, food shortages) and provide insulation (Blem 1976, Newton 2008, Schummer et al. 2012). Thus, lipid reserves and resulting body condition are typically positively correlated with seasonal and annual survival in waterfowl (Haramis et al. 1986, Pace and Afton 1999, Fleskes et al. 2002, Blums et al. 2005), though this relationship may vary seasonally or geographically (e.g., Dugger et al. 1994, Cox et al. 1998). Also, lipid reserves acquired
during winter are both directly and indirectly related to subsequent breeding performance in waterfowl through factors such as clutch formation and competitive advantage, respectively (Ankney and MacInnes 1978, Krapu 1981, Esler and Grand 1994, Esler et al. 2001, Hobson et al. 2005, Guillemain et al. 2008). Thus, acquisition and maintenance of lipid reserves during winter can have immediate and cross-seasonal or carry-over effects on fitness parameters in waterfowl (Barboza and Jorde 2002, Newton 2004, Hobson et al. 2005, Devries et al. 2008, Yerkes et al. 2008, Guillemain et al. 2008).

Lipid reserves in waterfowl generally increase through autumn and decline through winter into early spring, particularly for those wintering at mid- and northern latitudes (Ryan 1972, Reinecke et al. 1982, Baldassarre et al. 1986, Baldassarre and Bolen 2006). The pattern of lipid reserve declines through winter may be an adaptive response to winter conditions influenced by an endogenous mechanism which could have evolved in response to reduced probability of energy deficits with the onset of spring (Baldassarre et al. 1986, Loesch et al. 1992, Baldassarre and Bolen 2006). However, the degree of lipid reserve change can be influenced by exogenous factors such as prolonged periods of cold or food shortages that influence energy expenditure and acquisition (King and Farner 1966, Owen and Cook 1977, Baldassarre et al. 1986, Lovvorn 1994, Baldassarre and Bolen 2006, Schummer et al. 2012). Also, energy expenditure by diving homeotherms such as diving ducks increases with dive duration and with decreasing ambient temperatures below a critical threshold (Lovvorn et al. 1991, McKinney and McWilliams 2005). Thus, long- and short-term fluctuations in ambient temperatures and habitat conditions influence the energy economy of birds and their strategies to maintain adequate lipid reserves for survival and subsequent annual cycle events (Newton 2004,
The Great Salt Lake (GSL) system is an important area for aquatic birds within the Western Hemisphere because of the extent and diversity of aquatic environments within a predominately xeric environment (Aldrich and Paul 2002). The GSL system is one of the most extensive wetland and aquatic systems in the Intermountain West and provides a diversity of habitats ranging from ephemeral to persistent and freshwater to hypersaline (Kadlec and Smith 1989, Ratti and Kadlec 1992). These habitats are dynamic and characterized by relatively high inter- and intra-annual variation in relation to availability, extent, and resource use by avian guilds (Aldrich and Paul 2002). Millions of waterfowl and other waterbirds use the GSL and associated marshes annually as breeding, migratory, or wintering habitat (Kadlec and Smith 1989, Aldrich and Paul 2002). Avian abundance at GSL is lowest during winter (Aldrich and Paul 2002) but it is an important wintering area for common goldeneye (*Bucephala clangula*) in the western U.S. and Pacific Flyway, harboring approximately 4% of the combined continental Barrow’s (*B. islandica*) and common goldeneye population (Chapter 2). Waterfowl complete several nutritionally demanding processes during winter such as feather molt, courtship, and pairing (Prince 1979, Wishart 1983, Heitmeyer 1988) and insufficient energy in the form of lipids or nutrient reserves may delay these events, spring migration, and onset of breeding activities (Hepp 1986, Heitmeyer 1988, Richardson and Kaminski 1992, Arzell et al. 2006). Common goldeneye on the GSL forage extensively on halophile invertebrates, primarily brine fly (Ephyridae) larvae, to meet their energy needs during winter (see Chapter 3). However, little information exists regarding

Osmoregulation can be an important consideration for habitat use, water balance, and bioenergetics of aquatic birds (Nyström and Perhsson 1988, Woodin et al. 2008, Guiterrez et al. 2011). Foraging ecology and osmoregulation are likely to be closely entwined in marine systems, and high salinities could impose energetically expensive osmoregulatory costs (Peaker and Linzell 1975, Woodin et al. 2008, Gutierrez et al. 2011). However, osmoregulation is generally not considered in studies of avian nutrient dynamics or energetic budgets (Woodin et al. 2008, Gutierrez et al. 2011). Most studies involving salt loading and osmoregulatory mechanisms in birds have been conducted in laboratory settings and usually at salinities consistent with marine environments which are approximately three times lower than GSL salinities (Schmidt-Nielsen and Kim 1964, Bøkenes and Mercer 1995, Bennett and Hughes 2003, Hughes and Bennett 2004). Also, energetic costs associated with foraging may be increased for diving ducks in hypersaline systems because of greater water density and resulting increased buoyancy relative to freshwater and marine environments (Lovvorn and Jones 1991a, Lovvorn et al. 1991, Lovvorn et al. 2001). Although the benthic invertebrates (i.e., Ephydridae) that goldeneye forage on in GSL are highly abundant, reaching densities of 49 g (dry weight) per m² (Collins 1980, Wurtsbaugh 2009, Belovsky et al. 2011), significant energetic and physiological costs may be associated with exploiting these hypersaline food resources.
My goal was to evaluate endogenous and exogenous (inter- and intra-annual) factors potentially influencing lipid reserves of common goldeneye using the hypersaline GSL in winter. I evaluated a set of candidate models to explain the influence of endogenous regulation, short-term ambient temperature combined with wind speed and relative use of saline resources as indexed by individual salt gland masses, both of which are intra-annual and exogenous factors, inter-annual variation in environmental conditions, or some combination of these factors on lipid reserves.

**STUDY AREA**

The GSL is a terminal and shallow hypersaline lake located in north-central Utah within the Great Basin and Range Province and is a dominant water feature within the western United States (Stephens 1990; Fig. 4-1). The GSL is bordered by an extensive complex of wetland habitats of approximately 1,900 km², primarily on its eastern side (Jensen 1974, Aldrich and Paul 2002). The Southern Pacific Railroad Causeway divides the GSL into two distinct areas with unique ecological characteristics. The North Arm (Gunnison Bay) of the GSL is characterized by minimal freshwater inflow, extreme hypersaline conditions with >25% salinity and near halite saturation) and is rarely used by waterfowl (Stephens 1990, Aldrich and Paul 2002, Belovsky et al. 2011; Chapter 2). Lake and wetland extents are highly dynamic in the GSL system in response to inter- and intra-annual variation in climatic patterns influencing precipitation, which directly impacts the quantity, quality, and availability of avian habitats within the system (Kadlec and Smith 1989, Aldrich and Paul 2002, Mohammed and Tarboton 2012). Between 1847 and 1986, the average annual lake elevation was 1,280.1 m above sea level and ranged
1,277.5–1,283.8 m. At this average surface elevation, the GSL encompasses approximately 4,400 km² and ranges 2,461–6,216 km² with a maximum and average depth of approximately 13.7 m and 5.5 m, respectively (Stephens 1990, Baskin 2005, Belovsky et al. 2011). On average, each 1-m change in lake elevation changes the surface area of the GSL, by approximately 58,000 ha lakewide (Aldrich and Paul 2002). The South Arm receives >90% of the freshwater surface inflow into the GSL and consequently has lower salinity than the North Arm (Stephens 1990, Loving et al. 2002). Salinity concentrations vary inversely to lake levels in the GSL ranging 6–28% or 60–280 ppt between a historic low in 1963 and high in 1986 in the South Arm. At the average lake surface elevation of 1,280 m above sea level, salinity is approximately 12% which is roughly four times the salinity concentration of oceans (Arnow and Stephens 1990, Stephens 1990, Gwynn 2002). The South Arm is populated by numerous species of phytoplankton and algae, several zooplankton species, and high biomass of halophile macroinvertebrates consisting primarily of brine shrimp (*Artemia franciscana*) and brine fly (Ephydridae; Collins 1980, Stephens 1990, Belovsky et al. 2011). The GSL ecosystem is characterized by a temperate arid environment with an average of 38 cm of precipitation near the lake’s east side and < 25 cm on its west side (Aldrich and Paul 2002). Average December–February temperature in the GSL system between 1977 and 2000 is –0.6°C. On average, this region has 22 days with a maximum temperature ≤ 0°C and 77 days with a minimum temperature ≤ 0°C during winter (National Oceanic and Atmospheric Administration 2004, Western Regional Climate Center 2008).
METHODS

Specimen Collections

I collected common goldeneye (hereafter goldeneye) throughout the South Arm of the GSL, including Farmington Bay (Fig. 4-1), during winters 2004-05 and 2005-06 under authority of federal (no. MB693616) and state (no. COLL6550) scientific collection permits and protocol approved by Utah State University Institutional Animal Care and Use Committee (approval no. 1117). I did not collect goldeneye from the North Arm because they were not observed using this area, likely because of the extreme hypersaline conditions which do not support halophile macroinvertebrates (Aldrich and Paul 2002, Chapter 2). I began collections soon after goldeneye arrived in the GSL system in late November and suspended collections once birds departed the GSL, typically the first week of April. I divided winter into 3 periods: 1) early winter, November 15–December 20, 2) mid-winter, December 21–February 22, and 3) late winter, February 23–April 5. Early-winter dates are characterized by declining ambient and lake temperatures; freezing of freshwater habitats typically occurs by mid-December. Mid-winter dates included the period of coldest annual ambient and lake temperatures in the GSL system and peak goldeneye abundance. Late winter dates reflect the time interval when ambient and lake temperatures begin increasing, GSL biological productivity increases, and adjacent freshwater areas are thawed or infrequently frozen (Arnow and Stephens 1990, Aldrich and Paul 2002, Stephens and Birdsey 2002, National Oceanic and Atmospheric Administration 2004, Western Regional Climate Center 2008, Crosman and Horel 2009, Belovsky et al. 2011). Nearly all goldeneye samples (99%) were collected by pass shooting over decoys from layout boats. Upon collection, all birds
were labeled (species, sex, date, location), placed in plastic bags, kept cool, and frozen at –10°C within 12 hours.

**Lab Measurements and Proximate Analyses**

I determined sex and aged each specimen as either adult or subadult/juvenile by examining combinations of internal characteristics such as the syrinx, testes, ovaries, and cloacal characters, and external morphological characteristics such as rectrices, wing, and body plumage (Hochbaum 1942, Bellrose 1980, Carney 1992, Eadie et al. 1995). I thawed all specimens and measured the following lengths (± 1 mm): total body (from end of the most distal rectrix to tip of bill with the bird gently stretched on its back), rectral (from base to tip of the most distal rectrix), and wing chord (flattened; from the carpus to the tip of the longest primary). I also measured the following lengths (± 0.1 mm): total head (from the distal parietal to bill’s most distal point) and tarsometatarsus (from the notch at the proximal caudal tarsometatarsus to the articulation of the middle tarsometatarsus/phalangeal joint). I plucked each specimen and weighed plucked body mass (± 0.1 g). I removed ingesta items from the entire gastrointestinal tract and weighed (± 0.001 g) intestinal, gizzard, and esophageal masses with and without ingesta to determine ingesta-free body mass (BODY MASS). I excised both left and right supraorbital salt glands from each bird and weighed them (± 0.001 g). I removed 10 g (± 0.5 g) of breast muscle and 5 g (± 0.5 g) of liver tissues from each carcass for other analyses (see Chapter 5) and to archive tissue samples. I weighed (± 0.001 g) abdominal fat (ABDOMINAL), which lies in the abdominal cavity under the subcutaneous fat and is partially surrounded by the pubic bone, and fat from the large intestine, caecum, and
small intestine (VISCERAL; Chappel and Titman 1983, Schumer et al. 2012). A sub-set of carcasses were selected to quantify total body lipids of goldeneye. I randomly selected 15 carcasses per sex and age class from each of the three time periods each winter. If <15 carcasses were available within each sex-age-period-winter category, I randomly selected additional carcasses from the other age category within the same sex-period-winter group to obtain at least 30 samples within sex-period-year categories where possible. Selected carcasses \( n = 343 \) were shipped frozen to the Avian Energetics Laboratory (AEL) at Bird Studies Canada (Port Rowan, Ontario, Canada) for proximate analyses under authority of federal (USA–MB130293, Canada–POS202) import/export permits. Total body lipid mass \( (g; \text{LAB FAT}) \) estimates for each bird were derived from proximate analyses of carcass homogenate at AEL using standardized procedures (Horwitz 1975, Ankney and Afton 1988, Afton and Ankney 1991). To account for the removal of muscle and liver tissues in total carcass composition (see above), I obtained lipid mass estimates from 10-g muscle and 5-g liver samples \( (± 0.5 \, g; \, n = 10 \, \text{per tissue}) \) from proximate analyses at AEL. Mean values for each tissue were then added to each carcass estimate prior to statistical analyses.

A small number (1%) of goldeneye samples were obtained from the GSL opportunistically throughout the study period by either jump shooting \( (n = 5) \), or shooting into a flock from a scull boat \( (n = 3) \). Birds collected by varying methods may display corresponding variation in body condition (Reinecke and Shaiffer 1988, Pace and Afton 1999, Szymanski et al. 2013). Thus, I used simple t-tests to evaluate if the individual body mass (plucked, ingesta-free) of a bird not collected over decoys differed \( (P < 0.10) \) from mean body mass of birds collected over decoys within the same sex-age-winter
cohort within the same 14-day interval. One female sample collected by jump shooting exhibited a higher body mass ($t_{11} = -3.04, P = 0.01$) consistent with collection bias theory; therefore, I removed this sample from all statistical analyses. Body mass of all other samples not collected over decoys were generally lower than ($n = 2; t_{3-14} = 2.42, P \leq 0.09$) or did not vary with ($n = 5; -0.48 \leq t_{3-14} \leq 1.93, P > 0.10$) mean body mass of their cohorts collected over decoys. These samples were retained for all subsequent analyses.

**Environmental Conditions**

I obtained GSL surface elevations from a U.S. Geological Survey (USGS) gauging station located in the South Arm at Saltair Boat Harbor (USGS 2013; Fig. 4-1). Estimates of average monthly salinity and invertebrate biomass in the South Arm were obtained from samples collected throughout the South Arm weekly by Utah Division of Wildlife Resources (UDWR) and described in more detail by Belovsky et al. (2011). Physical and biological factors of the GSL varied between years during this study. Surface elevations were 0.4 m lower, on average, in winter 2004-05 compared to 2005-06 and, conversely, average salinity concentrations were 1.5% higher in 2004-05 compared to 2005-06 (Fig. 4-2). On average, the GSL surface area and volume was 5% (87 km$^2$) and 7% (0.6 km$^3$) larger, respectively, in 2005-06 compared to 2004-05 (Baskin 2005).

Invertebrate halophile biomass was generally greater in 2005 compared to 2004 based on estimates from UDWR samples over the five months prior to peak goldeneye abundance in GSL (August–December; Fig. 4-3; Chapter 2; Belovsky et al. 2011). *Artemia* biomass is intensively monitored by UDWR via water column samples.
throughout the South Arm (Belovsky et al. 2011). *Artemia* are a small component of
goldeneye diets (≤ 10%) but Ephydridae larvae comprise 35–76% of goldeneye diet
during winter on the GSL (see Chapter 3). The only Ephydridae biomass estimates
available during this study were by-catch from UDWR water column samples for
*Artemia*, and it is unknown how water column densities correlate to Ephydridae biomass
on benthic substrates where goldeneye forage. Regardless, these data suggest a general
pattern of greater halophile invertebrate biomass in 2005 for the time periods prior to
peak goldeneye abundance.

I obtained daily measures of mean temperature and wind speeds in the South Arm
from 3 MESOWEST weather stations in or adjacent to the South Arm of the GSL at Hat
Island, Antelope Island, and along the south shoreline of the GSL between Lake Point
Junction and Saltair boat harbor (MESOWEST 2013; Fig. 4-1). All weather stations
were located within 12 m of GSL surface elevations during this study.

**Statistical Analyses**

*Lipid-reserve index.*— I developed a suite of models to determine whether BODY
MASS, ABDOMINAL, VISCERAL, or a combination of these weights best
approximated the actual lipid content of each bird. I used an information-theoretic
approach for model selection and to calculate Akaike’s information criterion (AIC) for
each model (Burnham and Anderson 2002). I used ∆AIC and AIC weights ($w_i$) to assess
relative support for linear and non-linear relationships of LAB FAT with ABDOMINAL,
VISCERAL, BODY MASS or the sum of these measures (PROC MIXED, SAS Institute
2009). Three samples exerted a high degree of influence (Cook’s D > 4/n; Hamilton
(1992:132]) across models and were removed from analyses. The best model that explained considerable variation in LAB FAT contained quadratic effects of BODY MASS plus quadratic effect for summed ABDOMINAL + VISCERAL mass (AVFat; Table 4-1). Thus, parameter estimates from this model were used as a proxy for total lipid reserves and used as the response variable (FAT) in subsequent analyses.

Model development.—I included main effects of Sex and Age as categorical variables in each candidate hierarchical regression model to account for influences of physiological and behavioral variation associated with sex and age classes such as sexual dimorphism, courtship, and feather molt (Bellrose 1980, Sayler and Afton 1981, Eadie et al. 1995). I also included a Sex × Age interaction term as a fixed effect in a subset of models to evaluate if amount and rates of change in FAT varied with sex-age class. Intraspecific variation in structural size can significantly influence carcass components (Ankney and Afton 1988, Sedinger et al. 1997). Therefore, the first principal component (PC1) from principal component analyses (PCA; PROC PRINCOMP; SAS Institute 2009) of four morphological measurements (wing, tarsus, head length, and body length [total body length – rectrix length]) was used to index individual structural size. All correlations between morphometrics were positive, PC1 eigenvectors ranged between 0.46–0.52, and PC1 accounted for 80% of the variation in morphometrics. Thus, PC1 was included as a covariate in all models to control for individual differences in structural size and enable better interpretation of results by sex and age class (Schummer et al. 2012).

I developed a candidate set of 11 primary models that represented endogenous and intra- and inter-annual exogenous factors that likely influence lipid reserve (FAT)
dynamics of goldeneye at GSL. These models were comprised of seven independent variables.

(1) Wintering waterfowl may experience considerable thermoregulatory and energetic costs due to low ambient temperatures and wind effects (Smith and Prince 1973, Reinecke et al. 1982, Lovvorn 1994, McKinney and McWilliams 2005). Thus, I calculated the average daily ambient temperature adjusted for the effect of wind speed, \( T_{ef} \) from McKinney and McWilliams (2005):

\[
T_{ef} = T_b - (T_b - T_a) \times (0.474 + 0.239 \times \sqrt{u} - 0.023 \times u)
\]

Where \( T_{ef} \) is the effective temperature (°C), \( T_b \) is duck body temperature (41.5 °C; Irving and Krog [1954]), \( T_a \) is ambient temperature (°C) and \( u \) is wind speed (m/second). I then calculated the average \( T_{ef} \) for the 10-day period prior to when each bird was collected each year. I chose a 10-day interval because I believed it to be long enough to dampen daily weather fluctuations but short enough to express short-term weather patterns within years (Lovvorn 1994). Additionally, 10 days was the approximate limit of estimated fasting endurance provided by lipid stores for several waterfowl species in natural conditions, including goldeneye (Reinecke et al. 1982, Suter and Van Eerden 1992, Lovvorn 1994, Schummer et al. 2012).

(2) I used total salt gland mass (g; SALT) of individual goldeneye as an index of exposure to saline resources. The salt glands of aquatic birds are capable of eliminating sodium chloride as a highly concentrated solution. As birds are exposed to and consume saline water or food their salt glands hypertrophy, enhancing their capacity to excrete salt (Schmidt-Nielson and Kim 1964). Habitat salinity and dietary salt are major influences on the size and excretory capacity of salt glands (Peaker and Linzell 1975, Gutierrez et al.
2011). The rapid increase in size and secretion rate of salt glands (< 3 days) is primarily a function of salt loading to which birds are subjected (Hildebrandt 2001, Bennett and Hughes 2003, El-Gohary et al. 2013). Conversely, salt glands atrophy once saline ingestion is diminished (Fletcher et al. 1967, Holmes and Stewart 1968). Additionally, Bennett and Hughes (2003) reported the closely related Barrow’s goldeneye excreted all of the experimentally infused salt via the salt glands. Thus, salt gland mass provides a useful index of relative saline resource use (Tietje and Teer 1988, Jehl 2005, Woodin et al. 2008).

(3) Additive inter-annual effects of $T_{ef}$ plus SALT; $T_{ef}$ and exposure to saline resources may act in tandem to influence lipid reserves through winter.

(4) Inter-annual variation may occur because of correlations among several physical and biological attributes between years within the GSL system. For example salinity, habitat extent, and biological productivity are correlated (Fig. 4-2–3). I use YEAR (2004-05 or 2005-06) as a categorical variable to evaluate inter-annual variation on goldeneye fat reserves.

(5) The continuous variable DATE was included either alone or as an additive effect with intra-annual factors of $T_{ef}$ and SALT in three primary models or as an additive effect with intra- and inter-annual (YEAR) factors in three additional primary models because lipid dynamics for many waterfowl are often explained by a seasonal, endogenous mechanism of decline through winter irrespective of environmental conditions (Reinecke et al. 1982, Loesch et al. 1992, Baldassarre and Bolen 2006). I evaluated Pearson correlation coefficients (PROC CORR, SAS Institute 2009) of all pairwise combinations of continuous explanatory variables. I determined that no primary explanatory variables
were strongly confounded with each other \((-0.27 \leq r \leq 0.48)\) and subsequently did not restrict their co-occurrence in any models.

I used an information-theoretic approach for model selection and to calculate Akaike’s information criterion (AIC) and AIC weights \((w_i)\) for each model (Burnham and Anderson 2002). I calculated cumulative parameter weights \((\Sigma w_i)\) for each variable to evaluate the level of support for variables within the candidate model set. I used \(\Delta\)AIC and \(w_i\) to assess support for linear or quadratic effects of \(\text{DATE}\), \(T_{ef}\), and \(\text{SALT}\) in explaining variation in \(\text{FAT}\) (PROC Mixed, SAS Institute 2009). I included quadratic terms to account for nonlinear increases in photoperiod \((\text{DATE}^2)\) and potential nonlinear effects of effective temperature \((T_{ef}^2)\) and saline resource use \((\text{SALT}^2)\) on \(\text{FAT}\). I centered each variable \((\text{DATE}, T_{ef}, \text{SALT})\) from their respective means prior to squaring to provide independence between the linear and quadratic terms and improve interpretability of parameter estimates (Schielzeth 2010). I considered models \(\leq 2.0\) \(\Delta\)AIC units from top ranked models as competitive (Burnham and Anderson 2002). For variables identified in competing models, I used model averaging (across all models) to estimate parameters, cumulative parameter weights, 85% confidence intervals, and model-adjusted \(\text{FAT}\) (Burnham and Anderson 2002, Arnold 2010). Both linear and quadratic effects of \(\text{DATE}\), \(T_{ef}\), and \(\text{SALT}\) occurred in equal number models (22 each) and \(\text{YEAR}\) was included in an additional two models (24 total) in order to balance the occurrence of each variable, including linear and quadratic effects, across candidate models to facilitate interpretation of variable importance (Burnham and Anderson 2002).
RESULTS

The top ranked (i.e., most parsimonious) model explaining variation in FAT included the Sex×Age interaction, YEAR, and quadratic functions of DATE, $T_{ef}$, and SALT (Table 4-2). The closest model was only 0.6 AIC units from the top model and did not include SALT (Table 4-2). Considerable uncertainty existed among candidate models relative to the top model ($w = 0.21$) and the influence of linear versus quadratic effects for DATE, $T_{ef}$, and SALT (Table 4-2). Summed Akaike weights ($\Sigma w_i$) across all models indicated that YEAR ($\Sigma w_i = 1.0$) was the most important variable influencing FAT along with DATE ($\Sigma w_i = 1.0$; summed linear [0.41] and quadratic terms [0.59]; Table 4-3). Model averaged parameter estimates indicated that goldeneye, overall, contained 24 g less FAT (17%) in winter 2004-05 relative to 2005-06 (Table 4-3, Fig. 4-4). Juvenile females and adult and juvenile males had 16–20 g less (11–13%) FAT, on average, in 2004-05 relative to 2005-06; adult females displayed a generally consistent pattern of less fat in 2004-5 but FAT only varied by 7 g (6%) between winters (Fig. 4-4).

On average, goldeneye FAT declined 34% through winter. Females and males displayed varying patterns of FAT reserves through winter. Female FAT reserves generally declined through winter from an early winter peak with total loss in FAT of 41% in adults and 34% in juveniles from peak mean mass (Fig. 4-5). Average male FAT peaked by the second week of December and then declined 25% and 36% through winter in adults and juveniles, respectively (Fig. 4-5).

The third most important variable influencing FAT was $T_{ef}$ ($\Sigma w_i = 0.94$; summed linear [0.42] and quadratic terms [0.52]; Table 4-3). Mean $T_{ef}$ over the course of this study was 8.8°C (SD = 2.5). Overall, mean FAT was highest (157.6 g) at 6.6 °C $T_{ef}$ and
declined 10g (6%) per 5°C decrease below 6.6 °C $T_{ef}$, and declined 22g (14%) per 5 °C increase above 6.6 °C $T_{ef}$ within the range of environmental conditions experienced during this study. Patterns in FAT mass relative to $T_{ef}$ generally varied between sex classes (Fig. 4-6). On average, Female FAT was highest (137g) at 6.8 °C $T_{ef}$ and declined 8g (6%) and 19g (14%) per 5 °C change below and above 6.8 °C $T_{ef}$, respectively (Fig. 4-6). However, average male FAT mass was highest (adult = 199 g, juvenile = 167 g) when $T_{ef}$ was lowest and male FAT declined 19g (10%) with every 5 °C increase in $T_{ef}$ (Fig. 4-6).

SALT was the least important variable influencing FAT ($\Sigma w_i = 0.71$; summed linear [0.22] and quadratic terms [0.49]; Table 4-3). Overall, goldeneye FAT increased 2 g (2%) per 0.1 g increase in SALT until mean SALT approached 0.7 g, then FAT increased 6 g (4%) per 0.1 g increase in SALT. However, considerable variation in patterns of FAT mass relative to SALT was exhibited between adult males and other sex-age classes (Fig. 4-7). On average, female FAT declined 3g (2%) per 0.1 g increase in SALT until SALT approached 0.7 g, then FAT increased 3g (3%) per 0.1 g increase in SALT (Fig. 4-7). Similar to the pattern exhibited by females, juvenile male goldeneye FAT declined 4 g (2%) per 0.1 g increase in SALT until SALT approached 0.8 g, then FAT increased 6 g (4%) per 0.1 g increase in SALT (Fig. 4-7). Adult male FAT generally did not vary with respect to SALT (Fig. 4-7).

**DISCUSSION**

Most (99%) of the goldeneye in this study were collected by use of decoys and therefore samples may reflect a condition bias (Hepp et al. 1986, Reinecke and Shaiffer
1988, Dufour et al. 1993, Pace and Afton 1999, Szymanski et al. 2013). However, Schummer (2005:101) reported no difference in lipid mass between goldeneye collected randomly without decoys and those collected over decoys during winter on Lake Ontario, Canada. A similar condition-bias may exist for waterfowl collected as singles rather than from flocks (Olson 1965, Bain 1980). Although I did not collect data to evaluate the potential influence of flock size on lipid reserves, Schummer (2005:103) found no relationship in lipid mass between goldeneye collected as singles or from flocks during winter. I collected goldeneye from flocks and as singles throughout this study, and acknowledge limitations of inference by not accounting for flock size in analyses. However, comparisons of lipid estimates to those of wintering goldeneye from Schummer (2005) and Schummer et al. (2012) do not suggest an obvious pattern of condition bias in GSL samples. Thus, I believe these samples likely reflect the range of natural variation within the wintering population at GSL.

Inter-annual variation was an important factor influencing goldeneye lipid reserves at GSL and, overall, lipid reserves were 17% lower during winter 2004-05. Between 1999–2004, much of the West experienced recurrent drought conditions (Wilkowske et al. 2003, Cook et al. 2004, Hughes and Diaz 2008). Within the 11 western states comprising the Intermountain West, 14–25% of the region experienced extreme drought conditions and an additional 20–30% experienced severe drought conditions in calendar year 2004 (National Drought Mitigation Center 2013). Thus, the extent and availability of wetland and aquatic habitats throughout much of the Intermountain West was likely reduced in 2004 (Kadlec and Smith 1989, McKinstry 2004, Hughes and Diaz 2008). Reduced habitat availability and drought conditions have
been related to poor body condition and fitness in waterfowl (Rogers 1964, Heitmeyer 1988, Miller 1986, Ballard et al. 2006). Recurrent regional drought conditions between 1999–2004 resulted in low inflows to GSL and the lake level in early winter 2004-05 was within 0.8 m of the historic (post-1847) low elevation and the lowest since 1963 (Stephens 1990, Mohammed and Tarboton 2012). Similarly, the extent of wetland habitats adjacent to the GSL was also markedly reduced in 2004 (Olson 2005). However, regional drought and hydrologic conditions improved in 2005 resulting in higher GSL surface elevation and improved wetland conditions in adjacent complexes (Olson 2006, National Drought Mitigation Center 2013). Also, Ephydridae abundance was likely higher in winter 2005-06 at GSL based on water column samples (Fig. 4-3). Thus, lower lipid reserves in goldeneye during 2004-05 are likely a function of both regional and local habitat conditions in the GSL system. I speculate goldeneye likely arrived at GSL with relatively lower lipid reserves in early winter 2004-05 and because of diminished wetland habitat conditions and lower Ephydridae food resources lipids remained relatively lower during winter.

Temporal variation was also an important factor influencing lipid reserves. In winter, body mass fluctuations are primarily a function of lipid dynamics because they are the primary source of energy for homeostasis (Baldassarre and Bolen 2006). Diving ducks, including goldeneye, at other mid-latitude wintering sites display a pattern of body mass and lipid declines through winter consistent with those observed in this study (Ryan 1972, Peterson and Ellarson 1979, Kaminsky and Ryan 1981, Schummer 2005, Schummer et al. 2012). The observed temporal pattern at GSL is consistent with an endogenous rhythm of decline through winter reported for other waterfowl as an
adaptation to winter conditions (Reinecke et al. 1982, Baldassarre and Bolen 2006). For example, diving (*Aythya* sp.) and dabbling (*Anas* sp.) ducks in captive studies have displayed declines in body mass through winter despite being provided with unlimited food (Perry et al. 1986, Loesch et al. 1992, Barboza and Jorde 2002). Field studies of dabbling ducks in environments with abundant and energy-rich foods have also displayed declines in body mass through winter (Baldassarre et al. 1986, Miller 1986). Throughout their annual cycle, birds are thought to maintain optimal levels of endogenous lipid reserves, but not necessarily maximum levels, driven by trade-offs associated with costs and benefits of building and maintaining reserves (Lima 1986, Bond and Esler 2006). Decisions on how to balance these trade-offs are influenced by their environment(s) where predictability and accessibility of food resources may reduce the need for endogenous reserves (Rogers 1987, Tamisier et al. 1995, Bond and Esler 2006). The GSL annually produces an immense biomass of Ephydridae that have relatively high net-energy content, and there is little competition from benthic predators other than goldeneye during winter (Collins 1980, Caudell and Conover 2006, Wurtsbaugh 2009, Belovsky et al. 2011, Chapter 3). Ephydridae are also likely a more available and predictable food resource for goldeneye than freshwater foods in winter because of ice conditions (Chapter 3, Schummer et al. 2012). If food resources are abundant, available, and energetically profitable to forage on through winter, it becomes an adaptive advantage to use lipid reserves progressively through winter to minimize the energetic costs (e.g., mass-dependent foraging costs) and risks (e.g., predation from reduced agility) of maintaining high lipid levels.
Alternatively, lipid declines through time may simply reflect turnover in the wintering population from early to late winter. If birds with higher lipid reserves (i.e., better body condition) departed the GSL earlier than those with lower lipid reserves (Serie and Sharp 1989, Prop et al. 2003, Bridge et al. 2010), then lipid estimates in late winter would be biased low, resulting in an inverse relationship with DATE as I observed. Monthly aerial surveys conducted on the GSL concurrent with this study indicated goldeneye populations declined from a peak in mid-winter (January) to late winter; although goldeneye abundance remained high in late winter 2005-06 when lake levels were higher and temperatures colder relative to late winter 2004-05 (see Chapters 2 and 3). This pattern suggests emigration of goldeneye from the study area before the end of winter and it is therefore plausible those remaining into late winter are individuals in poorer condition. Consequently, higher lipid reserves in 2005-06 may also be explained by a higher proportion of birds in good condition remaining into late winter because of lower temperatures or other environmental factors. However, comparisons of these data to lipid estimates of wintering goldeneye from a similar study in the Great Lakes region at Lake Ontario suggest late winter samples at GSL were not substantially biased low. At Lake Ontario, collection of goldeneye was suspended in late winter when a significant change in duck population abundance occurred (Schummer et al. 2012). Lipid estimates between these studies were very similar during early winter and during late winter GSL samples were generally similar or higher than those reported for Lake Ontario goldeneye (Schummer 2005, Schummer et al. 2012). I therefore posit the observed lipid declines through winter at GSL are more likely influenced by an endogenous pattern to optimize
energy and nutrient reserves but a condition-bias sample in late winter cannot be fully dismissed.

Environmental factors such as temperature and wind speed can be important proximate factors affecting the amplitude of an endogenous pattern in lipid reserves during winter (King and Farner 1966, Whyte and Bolen 1984, Baldassarre et al. 1986, McKinney and McWilliams 2005, Schummer et al. 2012). Declining temperatures and high winds increase energetic costs of thermoregulation either directly or through altered behavior such as increased foraging activity (Nilsson 1970, Bennett and Bolen 1978, Paulus 1984, McKinney and McWilliams 2005). Cumulative parameter weights of $T_{ef}$ indicated temperature and wind were also important factors influencing lipid dynamics at GSL. Overall, lipid reserves varied in a nonlinear fashion with average $T_{ef}$ 10 days prior to collection where lowest lipid estimates occurred at the highest $T_{ef}$. Evaluation of sex-specific patterns suggests this nonlinear relationship is more pronounced in females where highest lipids were estimated at approximately 6.8°C $T_{ef}$ (about 2°C below the overall average) but then generally declined below and above this threshold. In contrast, male lipid estimates were, on average, highest at lowest $T_{ef}$ and declined with increasing $T_{ef}$. Male goldeneye are considerably larger than females, both in structural size and body mass (Bellrose 1980, Eadie et al. 1995), and therefore have a higher capacity to store lipids (Calder 1974; Figs. 4-4–5). This confers an adaptive advantage at northern latitudes and provides greater flexibility for males to adjust to thermoregulatory stresses or food shortages (Calder 1974, Sayler and Afton 1981). Because of their smaller size, female goldeneye have higher metabolic rates, store fewer lipids per unit mass, are less efficient at insulating themselves, and have a higher heat conductance per unit body mass.
than larger males (Calder 1974, Goudie and Ankney 1986). Consequently, the combined effects of declining temperature and higher winds would have relatively greater impact on females. For example, Nilsson (1970) reported feeding intensity of wintering goldeneye in southern Sweden was negatively correlated with mean temperature and more pronounced in females. Also, Campbell (1977) reported a higher proportion of wintering female goldeneye at wind-protected areas in coastal Scotland. Thus, variation in thermoregulatory responses resulting from size differences between sexes likely played an important role in the observed patterns of lipid dynamics. When future energetic demands are anticipated from proximal cues to exceed daily energy intake, foraging is increased to store lipids (Lima 1986, Rogers 1987). However, when temperatures decline below a critical threshold, foraging effort may decline or be suspended in favor of energy-conserving behaviors (Albright et al.1983, Quinlan and Baldassarre 1984).

Schummer et al. (2012) demonstrated increased foraging effort in wintering goldeneye at Lake Ontario was related to declining ambient temperatures and coincided with short-term increases in lipid reserves; thus, goldeneye responded to proximate temperature cues and reduced rates of lipid loss, at least temporarily. Thus, a pattern of declining lipid reserves at low $T_{ef}$ for female goldeneye suggests that either cost of increased foraging effort or thermoregulatory costs (or both) exceeded energy acquisition rates.

Reduced availability of foraging habitat due to ice conditions can be an important factor influencing habitat selection and lipid dynamics of diving ducks and other waterfowl in winter (Lovvorn 1989, Schummer et al. 2012). For example, lipids of goldeneye wintering at Lake Ontario declined > 50% as percent ice cover increased up to 39–50% (Schummer et al. 2012).
The extent of ice in freshwater and coastal habitats is positively correlated with the cumulative number of days < 0 °C (Lovvorn 1989, Assel 2003, Schummer et al. 2012).

Linear regression of average 10 day $T_{ef}$ and ambient temperatures at GSL over this study ($R^2 = 0.64$) indicated 6.8 °C $T_{ef}$ approximated 0 °C ambient temperature (Fig. 6). Thus, females exhibited a declining trend in lipids as freezing conditions (i.e., ≤0 °C) persisted in the GSL system (Fig. 4-6). The GSL does not freeze because of its high salinity and benthic Ephydridae are therefore available throughout winter whereas freshwater food resources become limited due to ice conditions. However, ephemeral ice can form at the surface of GSL. The thin freshwater lens that overrides denser hypersaline water can freeze and form extensive (several km$^2$), thin (≤ 2.5 cm), and temporary sheets of ice. These events typically occur in association with exceptionally cold and calm conditions and nearest Ogden Bay where most freshwater inflows occur though ice sheets have been observed several km west of Fremont Island (J. Vest, Utah State University, unpublished data). These ice sheet events typically exist for only a few days and cover only a small portion of the lake, although they typically occur in areas closest to the largest amount of freshwater habitats (i.e., Bear River, Ogden, Farmington Bays; Fig. 4-1). Thus, goldeneye may have to travel farther, and expend more energy, to find foraging sites on GSL during these ice events. Thus, the pattern of female lipid decline at low $T_{ef}$ could be a function of reduced forage availability due to ice conditions in adjacent freshwater habitats and increased costs of thermoregulation and foraging behavior.

During extended periods of low ambient temperatures, goldeneye likely rely more heavily on hypersaline food resources because of reduced access to freshwater foods from ice conditions (see Chapter 3). The major energetic cost associated with foraging
for diving ducks is overcoming buoyancy (Lovvorn et al. 1991, Lovvorn and Jones 1991a). These energetic costs are likely magnified at GSL because of the higher density of hypersaline water. Buoyancy in aquatic birds is positively correlated with overall body mass (Lovvorn and Jones 1991b). Higher lipid levels associated with increased body mass could increase buoyancy of individual birds and thus increase energetic costs of foraging (Witter and Cuthill 1993). Consequently, declines in lipid reserves during winter at GSL may also be an adaptive response to high energy costs of hypersaline use by lowering individual buoyancy and enhancing foraging efficiency (Bond and Esler 2006, Gutiérrez et al. 2011). Conversely, Lovvorn and Jones (1991a) reported that maximal increases in lipid mass of another diving duck, lesser scaup (*Aythya affinis*), had minimal energetic costs of diving to shallow depths, that most energetic changes could be compensated for by altering air volumes or length of time spent at the bottom, and therefore the effect of diving in marine versus freshwater was negligible. Because the large air volumes in the plumage and air-sacs are compressible, buoyancy declines via increased ambient pressure as the bird dives deeper (Lovvorn and Jones 1991b). However, the GSL is shallow (maximum depths range 7.6–13.7 m with annual conditions) and Ephydridae larvae are generally not present at deepest depths because of the presence of a deep brine layer or chemocline (Collins 1980, Baskin 2005, Belovsky et al. 2011). The most productive habitats for Ephydridae larvae typically occur at shallower depths (Collins 1980). Interpretation of GSL bathymetry (Baskin 2005) and the distribution of GSL substrates related to Ephydridae productivity from Collins (1980) suggests that the most productive habitats for Ephydridae larvae were, on average, at a depth of about 2 m during the course of this study. Consequently, the substantial
differences in buoyancy between marine and hypersaline waters and the shallow foraging depths at GSL may have more significance for optimization of body mass and lipid dynamics for diving ducks than previously evaluated. I posit such a body mass optimization strategy could have also played a role in the observed pattern of declining female lipids with low $T_{ef}$. As females respond to cues from declining temperatures they may also seek to lower body mass to make foraging in hypersaline conditions more energetically profitable when availability of other freshwater food sources was low because of ice conditions.

The index of relative hypersaline use via salt gland mass was the least important of variables attempting to explain variation in lipids. However, cumulative parameter weights were, overall, high with more support for a quadratic relationship. On average, lipid reserves were lowest at intermediate salt gland mass except for adult males which displayed little relationship when adjusted for other model parameters (Fig. 4-7). The process of acclimating to varying salinities and maintaining osmotic homeostasis by developing and maintaining active salt glands and other osmoregulatory mechanisms is energetically costly (Nelhs 1996, Peaker and Linzell 1975, Guitérrez et al. 2011). The cost of salt gland development, secretory activity, or other physiological adjustments for osmoregulation use may increase basal metabolic rates (BMR) 7–17% in aquatic birds (Peaker and Linzell 1975, Guitérrez et al. 2011). Several studies have demonstrated body mass declines (5–42%) during an adjustment period to saline (i.e., marine/saltwater) conditions in several species of aquatic birds and some attributed body mass loss to osmotic stress (Mahoney and Jehl 1985, Klaassen and Ens 1990, Bennett et al. 2003, Guitérrez et al. 2011). Goldeneye from the GSL displayed a similar pattern where
average lipid mass declined 11% in females and 14% in juvenile males as salt glands increased from low to intermediate masses within the range observed in this study. However, maintaining a relatively lower body mass could be an adaptive strategy to lower energy demand and cope with costs of existing in saline environments (Guitérrez et al. 2011). As energetic demands increase from osmoregulatory challenges, it is likely advantageous to employ strategies that mitigate overall energetic demands. Lowering individual BMR through body mass reductions could be accomplished by catabolizing lipid reserves. However, females and juvenile males displayed a nonlinear relationship with higher average lipid masses as salt glands increased from intermediate to high masses. Increased salt gland mass is positively correlated with excretory capacity in sea ducks (i.e., Mergini Tribe) and other aquatic birds (Bøkenes and Mercer 1995, Bennett and Hughes 2003, Guitérrez et al. 2011). Thus, at higher salt gland masses, goldeneye may have been able to more efficiently use hypersaline resources and mitigate energetic costs associated with osmoregulation. By extension, foraging on hypersaline foods should become more energetically profitable once initial physiological and energetic costs are alleviated through enhanced osmoregulatory efficiency.

Adult male goldeneye exhibit a number of competitive advantages at northern wintering latitudes over females and sub-adult males including social and competitive dominance, more efficient use of deeper foraging sites, access to larger prey items, larger fat stores, and lower rates of energy use (Sayler and Afton 1981, Eadie et al. 1995). Although absolute food requirements increase with increasing body size, larger individuals can use lipid reserves more efficiently while fasting (Calder 1974). Thus, any additional energetic costs associated with osmoregulation could be more efficiently
mitigated by adult males than smaller females or sub-adult males either through use of endogenous reserves or acquisition of exogenous resources. Additionally, birds with higher body mass have an increased sensitivity to osmotic challenges and salt gland secretions are stimulated at lower sodium concentrations (Peaker et al. 1973, Hammel et al. 1980, Hughes and Bennett 2004). Thus, salt glands of larger adult males may respond differentially to hypersaline exposure. Large renal mass and high rates of body fluid filtration are also adaptations to saline environments so other organs such as kidneys and intestines also likely played an important role in osmoregulation of goldeneye and sex related differences in salinity acclimation could be related to these organ functions as well (Bennett and Hughes 2003, Hughes and Bennett 2004). Thus, larger adult males may have adjusted differentially to hypersaline exposure through either behavioral or physiological mechanisms or combinations of both.

The size of salt glands may not be proportional to environmental salinity but may also be influenced by the prey type consumed (Mahoney and Jehl 1985). Hypersaline invertebrates such as Ephydridae possess physiological adaptations which allow them to osmoregulate and maintain water balance similar to freshwater invertebrates (~80% freshwater; Nemenz 1960, Mahoney and Jehl 1985, Herbst et al. 1988, Herbst and Bradley 1989). Thus, Ephydridae larvae provide goldeneye a source of hypo-osmotic fluids while foraging in hypersaline water. Goldeneye undoubtedly ingest some hypersaline water during foraging bouts but Mahoney and Jehl (1985) identified eared grebes foraging on brine shrimp in hypersaline lakes could minimize saline ingestion because of bill morphology and mechanical manipulation of prey with their tongues prior to ingestion. They also noted eared grebe salt gland masses at hypersaline Mono Lake
were not of maximal size despite extended periods of stay (2–3 months). Similarly, I do not believe goldeneye salt gland masses achieved maximal mass as my estimates were generally lower than salt gland masses (either absolute or per unit body mass) reported for other wild waterfowl (Tietje and Teer 1988, Bøkenes and Mercer 1995, Woodin et al. 2008). Additionally, a thin freshwater lens typically occurs at the surface of GSL due to the higher density of saline water. Thus, goldeneye could have used this freshwater source between foraging bouts on the GSL to further mitigate saline ingestion. Also, goldeneye were frequently observed making flights between hypersaline bays of GSL and freshwater sources (i.e., rivers, marsh), some flights in excess of 30 km (J. Vest, Utah State University, personal observation). Consequently, these strategies likely influenced the high variability in salt gland masses observed in this study (Fig. 4-7) and likely explain, at least partly, the lower overall importance (i.e., low cumulative parameter weights) of hypersaline use on lipid dynamics as indexed by salt glands.

Although goldeneye likely experienced energetic costs during acclimation to hypersaline resources, my data suggest those adaptations did not impose a significant barrier to maintenance of lipid reserves through winter. Regional environmental conditions in conjunction with local habitat conditions at GSL such as Ephydridae productivity, freshwater and wetland availability, and climate likely play a more prominent role in lipid reserve dynamics for goldeneye than osmotic stress. Persistence of the abundant and available halophile food resource through winter at GSL likely played an important role in maintaining energy reserves during inclement winter weather and energetic stress.
My findings are of particular interest in light of projected future demands on water resources and changes in hydrologic patterns in the GSL watershed and throughout western North America. Climate analyses indicate the western U.S. has experienced substantial decline in precipitation and sustained warming over the past several decades resulting in less snowfall, earlier snowmelt, changes in hydrology, and greater evaporative loss (Cayan et al. 2001, Mote et al. 2005, Regonda et al. 2005, Barnett et al. 2008, Hughes and Diaz 2008). These same hydrologic alterations have also occurred within the GSL watershed (Bedford and Douglass 2008). Climate models generally predict that these patterns will continue in the western U.S. over much of this century (Barnett et al. 2004, 2005; Seager et al. 2007; Hughes and Diaz 2008). Superimposed on these alterations will be the burgeoning demand for water resources from a growing human population in the western U.S. (Hansen et al. 2002, Service 2004). In Utah alone, the human population is projected to double to nearly 6 million by 2050 (Bennett 2008). Thus, water resource managers throughout the West and within the GSL watershed face significant challenges in the coming decades (Barnett et al. 2004, 2005; Bedford and Douglass 2008; Milly et al. 2008; Welsh et al. 2013). Water diversions for irrigation, public supply, and other uses have led to a steady increase in consumptive water use within the GSL watershed since 1847 and further diversions are planned from important water sources to the GSL (Arnow and Stephens 1990, Bennett 2008, Downard 2010). Given these hydrological patterns and increasing human demands for water resources in this region, it is likely the GSL will experience lower lake levels, higher salinities, and higher water temperatures because of anthropogenic pressures, as have occurred for hypersaline systems worldwide (Williams 2001, 2002; Mohammed and Tarboton 2012).
These modifications will have direct impacts on nutrient and food web dynamics and halophile invertebrate productivity (Belovsky et al. 2011). Low abundance of Ephydridae would likely have immediate ramifications for wintering goldeneye lipid dynamics, survival, and carry-over effects into subsequent annual-cycle events for a substantial portion of the Pacific Flyway population.

MANAGEMENT IMPLICATIONS

The GSL is a unique and important wintering area for common goldeneye in western North America and of hemispheric importance for other waterbirds. Despite this ecological significance, the GSL faces considerable anthropogenic threats to the quality and quantity of avian habitats (Kadlec and Smith 1989, Aldrich and Paul 2002, Naftz et al. 2008, Chapter 5). Many governing and international conservation bodies fail to recognize salt lakes as important inland aquatic systems, thereby hampering effective conservation strategies for these systems (Williams 2002). Water delivery and quality will be important wildlife management and conservation concerns in the GSL system because of increased human demand for water resources in western North America and the terminal nature of the GSL. Conservation and management strategies for water resources that 1) sustain halophile productivity at GSL and wetland function in associated wetland complexes and 2) improve resiliency to climate and anthropogenic induced modifications will be important to sustain goldeneye and other aquatic bird populations in the Pacific Flyway. I encourage managers to further elucidate patterns of benthic Ephydridae productivity and food web relationships to inform GSL management decisions.
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USA.


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Table 4-1. General linear models used to estimate total lipids (g) in common goldeneye ($n = 339$) collected from the Great Salt Lake, Utah November–April, 2004–2005 and 2005–2006. Models were evaluated using change in Akaike’s Information Criteria ($\Delta$AIC) and model weights ($w_i$).

<table>
<thead>
<tr>
<th>Lipid index$^a$</th>
<th>df</th>
<th>Intercept</th>
<th>$\beta_1$</th>
<th>$\beta_2$</th>
<th>$\beta_3$</th>
<th>$\beta_4$</th>
<th>$\Delta$AIC$^b$</th>
<th>$w_i$</th>
<th>$R^2$</th>
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<tr>
<td>Body Mass + Body Mass$^2$ + AVFat + AVFat$^2$</td>
<td>4, 335</td>
<td>90.04</td>
<td>$-0.205_{body mass}$</td>
<td>$0.0002_{body mass}^2$</td>
<td>$10.69_{AVFat}$</td>
<td>$-0.195_{AVFat}^2$</td>
<td>0.0</td>
<td>1.00</td>
<td>0.88</td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>15.6</td>
<td>0.00</td>
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<tr>
<td>Body Mass + AVFat</td>
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<td></td>
<td></td>
<td></td>
<td>89.6</td>
<td>0.00</td>
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<td>Abdominal + Abdominal$^2$</td>
<td>2, 337</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>315.0</td>
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<tr>
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<td>316.9</td>
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<tr>
<td>Abdominal</td>
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<td></td>
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<td>348.3</td>
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<td>366.9</td>
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<td>442.3</td>
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<td>Visceral</td>
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<td>511.2</td>
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$^a$Body Mass = ingesta-free plucked body mass wet weight; Visceral = visceral lipid wet weight; Abdominal = abdominal lipid wet weight; AVFat = Visceral + Abdominal.

$^b$The AIC values for the top model = 2892.9.
Table 4-2. Model selection results evaluating variation in lipid mass (g; FAT\(^a\)) of common goldeneye (n = 600) collected from the Great Salt Lake, Utah during winters (November–April) 2004-05 and 2005-06. Models were evaluated using change in Akaike’s Information Criteria (\(\Delta AIC\)) and model weights (\(w_i\)); \(K\) = number of parameters. Models with \(w_i <0.2\) are not reported, except the Null model.

<table>
<thead>
<tr>
<th>Model Structure(^b)</th>
<th>(\Delta AIC)(^c)</th>
<th>(w_i)</th>
<th>(K)</th>
<th>Deviance</th>
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<td>(PC_1 + Sex + Age + Sex\times Age + Date + Date^2 + T_{ef} + T_{ef}^2 + Salt + Salt^2 + Year)</td>
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<td>13</td>
<td>6103.18</td>
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<tr>
<td><strong>Null</strong></td>
<td><strong>280.44</strong></td>
<td><strong>0.00</strong></td>
<td><strong>2</strong></td>
<td><strong>6405.62</strong></td>
</tr>
</tbody>
</table>

\(^a\)FAT = function of abdominal and visceral fat and body masses (see Table 1)

\(^b\)Models included parameters of structural size (\(PC_1\)), Sex, Age (adult or juvenile), winter of collection (Year), and linear and quadratic terms (respectively) for study date (Date, Date\(^2\)), effective temperature (\(T_{ef}, T_{ef}^2\)), and salt gland mass (Salt, Salt\(^2\)).

\(^c\)AIC value for the top ranked model = 6129.18.
Table 4-3. Cumulative parameter weights ($\Sigma w_i$), model-averaged parameter estimates ($\theta$), standard errors (SE), and 85% confidence intervals (CI; Arnold 2010) of variables from competitive models (\(\Delta AIC < 2.0\)) explaining variation in lipid mass (FAT\(^a\)) of common goldeneye (n=600) collected from the Great Salt Lake, Utah winters (November–April) 2004-05 and 2005-06.

<table>
<thead>
<tr>
<th>Parameter(^b)</th>
<th>$\Sigma w_i$(^c)</th>
<th>$\theta$</th>
<th>SE</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>6.41</td>
<td>164.16</td>
<td>182.63</td>
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<tr>
<td>PC(_1)</td>
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<td>2.66</td>
<td>11.52</td>
<td>19.18</td>
</tr>
<tr>
<td>Sex (F)</td>
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<td>10.18</td>
<td>-18.63</td>
<td>10.70</td>
</tr>
<tr>
<td>Age (J)</td>
<td>-</td>
<td>-29.92</td>
<td>5.15</td>
<td>-37.34</td>
<td>-22.50</td>
</tr>
<tr>
<td>Sex $\times$ Age (FJ)</td>
<td>-</td>
<td>27.65</td>
<td>6.65</td>
<td>18.08</td>
<td>37.22</td>
</tr>
<tr>
<td>Date</td>
<td>0.41</td>
<td>-0.47</td>
<td>0.05</td>
<td>-0.54</td>
<td>-0.40</td>
</tr>
<tr>
<td>Date(^2)</td>
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<td>0.001</td>
<td>-0.002</td>
<td>0.0002</td>
</tr>
<tr>
<td>$T_{ef}$</td>
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<td>1.87</td>
<td>0.81</td>
<td>0.71</td>
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</tr>
<tr>
<td>$T_{ef}^2$</td>
<td>0.52</td>
<td>-0.15</td>
<td>0.09</td>
<td>-0.28</td>
<td>-0.03</td>
</tr>
<tr>
<td>Salt</td>
<td>0.22</td>
<td>-5.31</td>
<td>6.60</td>
<td>-14.81</td>
<td>4.19</td>
</tr>
<tr>
<td>Salt(^2)</td>
<td>0.49</td>
<td>20.47</td>
<td>9.90</td>
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<td>34.72</td>
</tr>
<tr>
<td>Year (2004-05)</td>
<td>1.00</td>
<td>-23.94</td>
<td>4.07</td>
<td>-29.79</td>
<td>-18.08</td>
</tr>
</tbody>
</table>

\(^a\)FAT = function of abdominal and visceral lipid and body masses (Table 1).
\(^b\)Abbreviations: PC\(_1\) = structural size; F = female, J = juvenile; Date = study date (15 November = 1), Date\(^2\) = quadratic Date; $T_{ef}$ = daily mean effective temperature for 10 days prior to collection, $T_{ef}^2$ = quadratic $T_{ef}$; Salt = salt gland mass, Salt\(^2\) = quadratic Salt.
\(^c\)Cumulative parameter weights not calculated for PC\(_1\), Sex, or Age because they were included in all models.
Figure 4-1. Geographic location, extent, and primary regions of the Great Salt Lake, Utah (gray shading). Black polygons represent general areas of managed wetland complexes.
Figure 4-2. Average monthly surface elevation (calculated from daily measurements) and salinity (calculated from weekly samples) of the Great Salt Lake during winters (November–April) 2004-05 (elevation = solid line; salinity = filled diamond) and 2005-06 (elevation = dashed line; salinity = open diamond). Salinity expressed as %; thus, values ranged from 132–175 parts per thousand (ppt).
Figure 4-3. Box plots for monthly (August–December; $n = 5$) density estimates of brine fly (Ephydridae) larvae and brine shrimp (*Artemia franciscana*; juveniles and adults) from lakewide water column samples in the Great Salt Lake, Utah during 2004 and 2005. Box boundaries represent 10th and 90th percentiles, median = solid line, mean = dashed line. Data derived from Belovsky et al. (2011).
Figure 4-4. Box plots of lipid-reserve index (FAT) relative to winter of collection and age (adult, juvenile) of female (A) and male (B) common goldeneye collected from the Great Salt Lake, Utah during winters (November–April) 2004-05 and 2005-06, adjusted for variation explained by model parameters. Box boundaries represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, and circles represent extreme observations.
Figure 4-5. Lipid-reserve index (FAT) in relation to date for female (A) and male (B) and adult (filled circle, solid line) and juvenile (open circle, dashed line) common goldeneye collected from the Great Salt Lake, Utah during winters (November–April) 2004-05 and 2005-06, adjusted for variation explained by model parameters; thus plot residuals represent remaining variation unexplained after modeling. Day 1 = 15 November.
Figure 4-6. Lipid-reserve index (FAT) in relation to effective temperature \( (T_{ef}) \) daily mean ambient temperature adjusted for wind speed for 10 days prior to collection) for female (A) and male (B) and adult (filled circle, black solid line) and juvenile (open circle, black dashed line) common goldeneye collected from the Great Salt Lake, Utah during winters (November–April) 2004-05 and 2005-06, adjusted for variation explained by model parameters; thus plot residuals represent remaining variation unexplained after modeling. Vertical-solid gray line represents the lower critical temperature for females (14.4 °C) and males (13.5 °C). Vertical-dashed gray line represents ambient temperature of 0 °C as predicted from linear relationship between the 10 day average of \( T_{ef} \) and ambient temperature.
Figure 4-7. Lipid-reserve index (FAT) in relation to salt gland mass for female (A) and male (B) and adult (filled circle, solid line) and juvenile (open circle, dashed line) common goldeneye collected from the Great Salt Lake, Utah during winters (November–April) 2004-05 and 2005-06, adjusted for variation explained by model parameters; thus plot residuals represent remaining variation unexplained after modeling.
CHAPTER 5
TRACE ELEMENT CONCENTRATIONS IN WINTERING WATERFOWL FROM THE GREAT SALT LAKE, UTAH

Abstract  The Great Salt Lake (GSL) is an important region for millions of migratory waterbirds. However, high concentrations of some trace elements, including Hg and Se, have been detected within the GSL and baseline ecotoxicological data are lacking for avian species in this system. I collected common goldeneye (Bucephala clangula), northern shoveler (Anas clypeata), and green-winged teal (A. crecca) from the GSL during the winters of 2004-05 and 2005-06 to evaluate sources of variation in liver trace element concentrations. Hg concentrations were among or exceeded the highest values reported in the published literature for common goldeneye, northern shoveler and green-winged teal. Average Hg (total) concentrations of common goldeneye peaked in mid-winter whereas average Se concentrations peaked during late winter. During late winter, 100% and 88% of female goldeneye contained elevated concentrations of Hg (≥ 1.0 µg/g wet weight [ww]) and Se (≥ 3.0 µg/g ww), respectively, and 5% and 14% contained potentially harmful amounts of Hg (≥ 30.0 µg/g ww) and Se (> 10.0 µg/g ww), respectively. Similarly, 30% and 16% of male goldeneye contained potentially harmful concentrations of Hg and Se, respectively. Concentrations of Hg and Se were elevated in 100% and 79%, respectively, of northern shoveler samples (sexes combined) collected during February. I suggest waterfowl contain biologically concerning amounts of Hg and

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Se during winter while on the GSL and further research is needed to evaluate the effect of these elements on GSL waterbirds.

**Introduction**

The Great Salt Lake (GSL) is the fourth largest terminal lake in the world and a dominant water feature within the western United States (Arnow and Stephens 1990). The GSL is also a dynamic system but at the average lake level of 1280 m above sea level (range: 1278–1284 m) the GSL encompasses approximately 4400 km$^2$ with a maximum depth of approximately 10 meters (Arnow and Stephens 1990). Additionally, the GSL is bordered by approximately 1,900 km$^2$ of wetland habitats (Johnson 2008). Accordingly, the GSL and associated marshes are used annually by millions of waterbirds and therefore is of continental and hemispheric importance to these diverse populations of migratory and breeding waterbirds (Aldrich and Paul 2002; Kadlec and Smith 1989).

The GSL is a closed basin and therefore contaminants (e.g., Hg, Se, Cd) associated with industrial and urban development or from non-local sources (e.g., atmospheric deposition) may accumulate in the GSL system (Brix et al. 2004, Naftz et al. 2008a). High concentrations of several trace elements, including As, Cd, Cu, Hg, Pb, and Zn, have been detected in sediments from the GSL and its watershed (Naftz et al. 2008b). The U. S. Geological Survey (USGS) reported water samples from the GSL exceeded the total mercury (Hg) standard for protection of aquatic life in marine systems and were among the highest values observed for marine systems (Naftz et al. 2008a). Additionally, high Se concentrations were reported in GSL water and brine shrimp
(Artemia franciscana) samples in relation to mining effluent into the GSL (Brix et al. 2004).

Given the hemispheric importance of the GSL to migratory waterbirds and relative paucity of information regarding ecotoxicology in this system, evaluation of contaminant exposure to GSL biota is warranted. Therefore, I obtained liver trace element concentrations from three species of waterfowl that were collected from the GSL over two winters (2004-05 and 2005-06). My objectives were to 1) document selected liver trace element concentrations in common goldeneye (Bucephala clangula), northern shoveler (Anas clypeata), and green-winged teal (A. crecca) wintering on the GSL and 2) evaluate variation of selected trace elements in relation to temporal variation, sex, and age class of these waterfowl species.

**Materials and Methods**

Sample Collection

Common goldeneye (COGO) were collected throughout the South Arm of the GSL, including Farmington Bay, during winters (November–April) 2004-05 and 2005-06 (Fig. 5-1). I divided winters into 3 collection periods: 1) early winter (November 20–December 31), 2) mid winter (January 1–February 27) and 3) late winter (February 28–April 5). Northern shovelers (NSHO) were collected in November and December 2004 and October 27–February 22 during winter 2005–2006 from the South Arm of the GSL including Farmington Bay. NSHO samples were pooled across years and samples from late October and November were combined so that I evaluated temporal dynamics of elements among three time periods classified as November, December, and February. Green-winged teal (GWT) were collected December 2004. Birds were shot with
shotguns over decoys using steel shot. No birds were collected from wetlands adjacent to the GSL. Sex, collection date, and location were recorded for each bird. Birds were labeled, placed in double plastic bags, and then frozen at –10°C.

In the laboratory, birds were thawed and dissected to determine age by wing feather characteristics and presence of the bursa of Fabricius (Carney 1992; Hochbaum 1942) and to obtain a 5 g (± 0.5) liver tissue sample. Each liver tissue sample was placed separately in labeled Whirl-Pak® sample bags then placed in double plastic bags and frozen at –10°C. Liver tissue samples were hand delivered frozen to the Utah Veterinary Diagnostic Laboratory for trace element analyses.

Trace Element Analyses

Liver sample tissues were analyzed for the following major and trace elements – Ag, Al, As, B, Ba, Be, Ca, Cd, Co, Cr, Cu, Fe, Hg (total), K, Li, Mg, Mn, Mo, Na, Ni, P, Pb, Sb, Se, Si, Sn, Sr, Tl, V, and Zn. One g (± 0.001 g) of liver tissue from the original 5 g sample was digested with 2.5 ml of trace mineral grade nitric acid (Fisher Scientific, Pittsburgh, PA) in 10-ml Oak Ridge Teflon digestion tubes (Nalge Nunc International, Rochester, NY) for 1 hour at 90°C on a heat block (VWR Scientific IV 949038). The final digest volume was then brought to 3 ml with trace mineral grade nitric acid. Analytical samples were prepared by adding 0.5 ml of the digest to 9.5 ml of 18.3 MOhm water in a 15-ml polypropylene trace metal free tube (ELKAY, Mansfield, MA). This provided a 5% nitric acid matrix for the analysis, which was matrix matched for all standard curves and quality control samples. Mineral content analysis was performed using an ELAN 6000 inductively coupled plasma mass spectrometer (ICP-MS; Perkin Elmer, Shelton, CT). For all elements except Se, five-point standard curves from 0.01 to
0.50 mg/L were used to quantify minerals. For Se analysis, a four-point standard addition curve was used to prevent analytical interference. Sequential dilutions, using 5% nitric acid, were made for minerals exceeding the standard curve. Standard curves and quality control samples were analyzed every five samples. NIST standards were analyzed to verify accuracy of the analytical results.

Statistical Analyses

Statistical analyses were limited to eight trace elements (As, B, Cd, Cu, total Hg, Pb, Se, Zn) perceived to be of greatest biologic and environmental relevance to avifauna in the GSL system. The chosen subset of elements have either been related to avian fitness parameters in other studies (e.g., B, Cd, Hg, Pb, Se; Furness 1996; Hamilton and Hoffman 2003; Ohlendorf 2003; Pain 1996; Wiener et al. 2003) or detected in high concentrations within the GSL or it’s watershed (e.g., As, Cd, Cu, Hg, Pb, Se, Zn; Naftz et al. 2008a,b). Concentrations of the remaining 22 trace elements for each waterfowl species are reported in Tables 5-3, 5-4, and 5-5.

Species specific data matrices of analytes were assessed for frequencies of nondetection values and to identify which analytes had ≥ 60% detection rates. All eight trace elements of concern (As, B, Cd, Cu, Hg, Pb, Se, Zn) had 100% detection rates (Tables 5-1, 5-2, 5-3). For all other 22 analytes with ≥ 60% detection rates, nondetection values were replaced with the corresponding minimal detection limit (Tables 5-3, 5-4, 5-5). All data were natural log-transformed to normalize error distributions of data and meet assumptions of normality and homogeneity of variance for statistical analyses.

Multivariate analysis of variance (MANOVA; PROC GLM SAS 2004) was conducted to evaluate variation in concentrations of eight trace elements of concern (As,
B, Cd, Cu, Hg, Pb, Se, Zn) in relation to winter collection period, sex, and age classes of COGO including the interaction terms period×sex, period×age, and sex×age. Data were combined across winters (2004-05 and 2005-06) for COGO and NSHO because temporal variation of trace elements throughout winter was deemed of greater concern than variation between years. Backward elimination procedures (α = 0.05) were used to obtain final models and Wilks’ lambda as the test statistic for MANOVAs. A significant sex×age interaction (MANOVA: Wilks’ λ = 0.919, $F_{8,225} = 2.47, p = 0.014$) was detected for COGO. Thus, sex specific MANOVAs for COGO were used to evaluate differences in trace element concentrations in relation to collection period, age, and the interaction term to simplify interpretation and because COGO differ in physiological patterns (e.g., nutrient reserve, organ mass, & molt dynamics) during winter on the GSL with respect to sex (J. Vest unpublished data). Age was omitted from NSHO MANOVAs because age could not be confidently assigned for the February collection period. Post hoc comparisons of means for effects included in all final models were made using Tukey-Kramer tests (Petrie et al. 2007; Zar 1999,). Sample sizes of GWT were insufficient to evaluate differences in trace element concentrations between sex and age classes with MANOVA. Thus, independent analyses of variance (ANOVA; PROC GLM, SAS 2004) were conducted for each of the eight trace elements of concern between sex and age classes. The interaction term was not allowed in the model because of small sample sizes for each sex×age combination ($n \leq 7$).

Concentrations of Hg (total) and Se in COGO were further analyzed separately to assess temporal trends because these elements: 1) have been detected at high concentrations in water, sediment and/or other GSL biota, 2) were elevated in most
COGO samples, and 3) pose potential risks to bird fitness parameters. Exploratory evaluation of Hg and Se scatter plots suggested a non-linear relationship likely existed between collection day and both Hg and Se. Collection day was calculated by subtracting the annual day (day 1 = November 20) from the median number of collection days for each sex of COGO (female collection interval = 137 days; male collection interval = 127 days). Sex- and element-specific ANOVAs (PROC GLM, SAS 2004) were used to assess age and collection date related variation (age + day + day^2 + day×age + day^2×age) in Hg and Se concentrations. Backward elimination procedures (α = 0.05) were used to select final models (Zar 1999). Temporal trends of Hg and Se concentrations in NSHO were not further evaluated because these birds were collected over short time intervals (≤ 4 days) in both the December and February collection periods.

All natural log-transformed concentrations were back-transformed for presentation of summary statistics. Geometric means with lower and upper 95% confidence intervals and ranges of trace element concentrations are reported for summary statistics. Unless otherwise stated, trace element concentrations are reported as µg/g wet liver mass (ww). To facilitate comparisons with other studies, liver tissue samples (5 g, N = 10 per species) were dried to a constant mass in a drying oven at 60°C. Moisture content averaged (\( \bar{x} \ ± \ SE \)) 66.4% ± 0.5, 68.1% ± 0.5, and 66.4% ± 0.4 for COGO, NSHO, and GWT, respectively.
Results

Common Goldeneye

Female COGOs

Several trace element concentrations of concern varied by winter collection period (MANOVA: Wilks’ $\lambda = 0.362$, $F_{16,218} = 9.01$, $p < 0.001$) and age (Wilks' $\lambda = 0.598$, $F_{8,109} = 9.14$, $p < 0.001$) in female COGO. Female concentrations of Cd, Hg, Pb, and Se increased between early and late winter (T-K $p \leq 0.002$). Mean Cu concentrations increased between mid and late winter (T-K $p = 0.036$). Mean B concentrations declined between early and late winter (T-K $p = 0.038$). Mean concentrations of As and Zn in female COGO displayed no among winter period differences (Table 5-1). Juvenile female concentrations ($n = 59$, $\bar{x}$ [95% CI]) of Cd (0.15 [0.13–0.18], Cu (11.8 [10.8–12.9]), and Zn (38.5 [36.9–40.1]) were lower (T-K $p \leq 0.008$) than those of adult female COGO ($n = 61$, Cd = 0.37 [0.31–0.44], Cu = 14.1 [12.9–15.4], Zn = 41.6[36.9–40.1]). All other trace elements of concern in female COGO displayed no age related variation (T-K $p > 0.05$).

Male COGOs

Several trace element concentrations of concern varied by winter collection period (MANOVA: Wilks’ $\lambda = 0.440$, $F_{16,218} = 6.92$, $p < 0.001$) and age (Wilks’ $\lambda = 0.409$, $F_{8,109} = 19.69$, $p < 0.001$) in male COGO. Concentrations of Hg, Pb, and Se increased between early and late winter (T-K $p < 0.001$). However, mean concentrations of Zn declined between early and late winter (T-K $p = 0.001$). Mean concentrations of As, B, Cd, and Cu displayed no among winter period variation in male COGO (Table 5-1).
Juvenile male concentrations (n = 56, \( \bar{x} [95\% CI] \)) of Cd (0.15 [0.12–0.17]) and Pb (0.25 [0.21–0.30]) were lower (T-K \( p \leq 0.035 \)) than those of adult male COGO (n = 64, Cd = 0.62 [0.53–0.73], Pb = 0.33 [0.28–0.38]). All other trace elements of concern in male COGO displayed no age related variation (T-K \( p > 0.05 \)).

\textit{Hg and Se dynamics}

Analyses of female COGO indicated that neither Hg nor Se concentrations varied in relation to age class (Hg: \( F_{3,116} = 1.56, p = 0.214 \); Se: \( F_{3,116} = 3.33, p = 0.071 \)) or the age×day interaction (Hg: \( F_{4,115} = 0.17, p = 0.679 \); Se: \( F_{4,115} = 1.18, p = 0.279 \)). However, the quadratic (i.e., nonlinear) collection day term was an important source of variation in both Hg (Hg model: \( r^2 = 0.33, F_{2,117} = 28.33, P < 0.001 \)) and Se (Se model: \( r^2 = 0.40, F_{2,117} = 39.14, P < 0.001 \)) concentrations in female COGO (Fig. 5-2). Mercury concentrations in female COGO increased between late November and early February but then declined through early April. Concentrations of Se in female COGO increased between late November and mid-March and then remained relatively stable through early April.

Analyses of male COGO indicated date, the quadratic date term, and the interaction age×date were important sources of variation for both Hg (\( r^2 = 0.32, F_{4,119} = 13.61, p < 0.001 \)) and Se (\( r^2 = 0.52, F_{4,119} = 30.64, p < 0.001 \)) concentrations during winter on the GSL (Fig. 5-2). For adult male COGO, Hg concentrations increased between late November and early February but then declined by late March. However, juvenile male COGO Hg concentrations increased between late November and mid-March. Adult male COGO Se concentrations increased from late November to late
March. Mean juvenile male COGO Se concentrations were generally lower than adults in early winter and increased between late November and late March (Fig. 5-2).

Northern Shoveler

Several NSHO trace element concentrations differed by winter collection period (MANOVA: Wilks’ λ = 0.294, $F_{16,144} = 7.61, p < 0.001$) and sex class (Wilks’ λ = 0.734, $F_{8,72} = 3.27, p = 0.003$). Mean concentrations of As, B, and Hg increased between November and February collection periods ($T-K p \leq 0.018$). Mean concentrations of Cu and Se declined between November and December collection periods ($T-K p \leq 0.004$) but then increased between December and February collection periods ($T-K p \leq 0.001$). Similarly, mean concentrations of Pb increased between December and February collection periods ($T-K p \leq 0.048$). Mean concentrations of Cd and Zn displayed no among winter period variation in NSHO (Table 5-2). Female NSHO concentrations ($n = 41$, $\bar{x} \ [95\% \ CI]$) of Cd (0.26 [0.21–0.32]) and Zn (41.0 [39.3–42.9]) were lower ($T-K p \leq 0.011$) than male NSHO ($n = 47$, Cd = 0.40 [0.32–0.51], Zn = 46.8 [44.3–49.5]).

Green-winged Teal

Temporal variation in GWT trace element concentrations was not assessed because GWT were collected over a short temporal interval in December 2004. Concentrations of all eight trace elements of concern did not vary ($0.10 \leq F_{2,17} \leq 2.45$, $0.116 \leq p \leq 0.905$) with respect to sex or age classes with the exception of Pb (Table 5-3). Average Pb concentrations in juvenile GWT ($n = 9$, $\bar{x} = 0.061 \ [0.046–0.078]$) were lower ($F_{2,17} = 4.73, p = 0.023$) than adult GWT ($n = 11$, $\bar{x} = 0.100 \ [0.078–0.127]$).
Discussion

Trace Elements

Concentrations of Cu, Pb, and Zn were generally detected within or below background concentrations and thus of little biological concern (Custer and Custer 2000; Di Giulio and Scanlon 1984; Pain 1996; Scheuhammer 1987). Mean As concentrations were elevated (> 0.5 µg/g dry weight [dw]; Goede 1985) in 97% and 96% of female and male COGO, respectively, but none exceeded a potentially harmful threshold of 2.0 µg/g ww (Goede 1985). Mean COGO As concentrations did not vary through winter suggesting As did not accumulate in COGO during winter on the GSL. However, mean concentrations of As in NSHO increased during winter and 100% of NSHO samples were elevated and 12% were at potentially harmful levels. Similarly, 100% and 5% of GWT samples were elevated and at potentially harmful levels, respectively. Variation in trends and concentrations of As between NSHO, GWT, and COGO could be related to variation in spatial and temporal use of the GSL and foraging behavior. Diets of NSHO and GWT consisted of high proportions of brine shrimp and brine shrimp cysts whereas brine fly larvae (Ephydra spp.) dominated the dietary composition of COGO during winter on the GSL (J. Vest unpublished data). However, observed variation in As concentrations between these species may also reflect differences in collection locations. Most NSHO and GWT were collected near the Lee Creek and Goggin Drain inflows into the GSL whereas COGO were collected at broader spatial and temporal scales within the GSL during winter.

Mean concentrations of B increased during winter in NSHO and 10% and 30% of NSHO and GWT samples, respectively, exceeded a median liver concentration of 15.5
µg/g, dw (range = 7–24) that may influence subsequent reproductive performance in waterfowl (Eisler 1990; Setmire et al. 1993). Boron is commonly associated with agricultural and sewage wastewater drainage (Setmire et al. 1993; Vengosh et al. 1994) and most NSHO and GWT were collected at or near GSL inflows (e.g., Lee Creek and Goggin Drain) which serve as drainage canals for portions of the Salt Lake Valley. Effects of B concentrations on health, survival, or reproduction in free-ranging populations of waterfowl are still unclear and recommended threshold concentrations are lacking. However, B is known to interact with other trace elements such as Se and can impair reproductive performance in waterfowl (Hamilton and Hoffman 2003).

Greater mean Cd concentrations in adult compared to juvenile male COGO are consistent with studies of other waterfowl (Takekawa et al. 2002; Fedynich et al. 2007) and bird species (Furness 1996). Although Cd concentrations were elevated (> 10 µg/g ww, Furness 1996) in 10%, 5%, and 36% of NSHO, female COGO, and male COGO, respectively, Cd concentrations in all species were much lower than the suggested toxic threshold of 40 µg/g ww (Furness 1996). Thus, Cd concentrations in GSL waterfowl may be of limited biological concern.

Mercury and Selenium

Total Hg concentrations in COGO from the GSL increased during winter and were among the highest reported for waterfowl in North America (Braune and Malone 2006; Fimreite 1974; Gerstenberger 2004; Scheuhammer et al. 1998). Indeed, Hg concentrations in late winter female and male COGO were elevated (≥ 1.0 µg/g ww; Thompson 1996) in 100% and 93% of samples, respectively, and at potentially harmful concentrations (≥ 30 µg/g ww; Thompson 1996) in 5% and 30% of samples, respectively.
Concentrations of methylmercury (MeHg) in waterfowl liver tissues were not ascertained in this study but Naftz et al. (2008a) reported excessive MeHg concentration in GSL water samples. Determination of the MeHg:Hg ratios in GSL avifauna would improve toxicity implications for waterbirds that use the GSL during portions of their annual cycle. Sheuhammer et al. (1998) reported a negative relationship between total Hg and MeHg in common loon (Gavia immer) and common merganser (Mergus merganser) liver and kidney tissues suggesting demethylation of MeHg may occur in some waterbird species. Therefore, toxicological assessment based on total Hg concentrations may be imperfect (Sheuhammer et al. 1998).

The nonlinear relationship between Hg concentrations and collection day observed in female and adult male COGO was primarily driven by several birds collected in March and April with Hg concentrations < 3.0 µg/g ww. Several potential explanations for lower Hg concentrations in late winter COGO exist. Reduced Hg concentrations may have resulted from normal physiological pathways such as elimination by feces, urine, or into new feather growth (Monteiro and Furness 2001; Weiner et al. 2003). Common goldeneye undergo a prealternate molt during winter (Eadie et al. 1995) and molt intensity increased through winter in GSL female COGO but not in males (J. Vest, unpublished data). Declines in Hg concentrations may also reflect a shift in habitat or food use. Interestingly, salt gland mass and total GSL COGO population estimates exhibited a curvilinear association with annual day, similar to that observed for Hg (J. Vest unpublished data). Aerial winter surveys of the GSL suggest COGO abundance and use was positively related to the amount and distribution of ice on the GSL and nearby freshwater bodies (J. Vest unpublished data). Thus, given the half-
life of Hg for some marine birds ranges from 33–65 days (Bearhop et al. 2000; Monteiro and Furness 2001; Wayland et al. 2007), lower Hg concentrations in some birds collected during late winter may reflect reduced exposure to Hg sources in the GSL as use of freshwater habitats increased after mid-winter. Indeed, a higher proportion of freshwater food sources was observed in COGO during late winter compared to other time periods (J. Vest, unpublished data). However, duration of GSL use by individual COGO was not ascertained and lower Hg concentrations in some late winter birds may simply reflect new migrants with little residence time in the GSL system. Regardless, it is clear that a significant portion of late winter COGO contained high Hg concentrations and is therefore of concern, particularly for females. If Hg concentrations remain high into the early breeding period, females may be at risk of depositing excess Hg into eggs during clutch formation (Heinz and Hoffman 2004). Assuming an average Hg half-life of 49 days for other marine birds (Bearhop et al. 2000; Monteiro and Furness 2001; Wayland et al. 2007), 79% of late winter GSL females may still harbor elevated Hg concentrations, with an average of 7.6 µg Hg/g ww (range = 0.4–19.3), by the median nest initiation date of May 4th for western breeding COGO (Eadie et al. 1995). Increased Hg concentrations during this critical time period could impair reproductive success via reduced clutch size, egg viability and hatchability, as well as embryo and chick survival (Heinz and Hoffman 2003; Thompson 1996).

Mean concentration of total Hg in GWT from the GSL exceeded concentrations reported throughout North America for this species (Braune and Malone 2006; Gerstenberger 2004) but only 15% of GWT samples from the GSL were elevated. However, concentrations of total Hg in NSHO were elevated in 97% of samples and
among the highest reported for NSHO in published literature (Gerstenberger 2004). Additionally, mean Hg concentrations in NSHO more than doubled between November and February collection periods when all NSHO samples were elevated. NSHO collected during November were primarily collected from Farmington and Ogden Bays where salinity concentrations are generally lower than other areas of the GSL due to larger freshwater inputs on the eastern side of the GSL. NSHO use freshwater wetlands adjacent to Ogden and Farmington Bays during fall and early winter (Aldrich and Paul 2002). However, December and February collections of NSHO occurred primarily at the southeast shore of the GSL near the Goggin Drain and Lee Creek inflows during cold weather events when many adjacent freshwater habitats were iced over. Thus, increases in Hg concentrations may have resulted from shifts in available resource use from more freshwater to saline habitats, differences in collection locations, or a combination of these factors. However, NSHO and other waterbirds are highly mobile and able to move easily between habitats within the GSL system. Consequently, relative use of habitat types within the GSL by NSHO is largely unknown. Hence, the migratory nature of waterfowl create significant challenges for ascertaining factors influencing contaminant dynamics and ecotoxicology.

Uncertainty remains regarding sources of Hg to the GSL. However, atmospheric deposition is a major source of Hg to many aquatic environments (Krabbenhoft and Rickert 1995). The GSL is located downwind from regionally large sources of atmospheric Hg and may be especially susceptible to accumulation of local and regional deposits of atmospheric Hg because of the GSL’s large surface area and terminal nature (Naftz et al. 2008a). Additionally, the GSL is adjacent to the Salt Lake City metropolitan
area and the GSL receives industrial, mining, agricultural, and urban discharge from its watershed (Brix et al. 2004; Naftz et al. 2008a). Regardless of Hg sources, the geophysical, chemical, and biotic properties of the GSL, including low dissolved oxygen, high sulfate reduction rates, and acetate-utilizing bacteria, provide ideal conditions for Hg methylation (Naftz et al. 2008a). Indeed, concentrations of methyl Hg in GSL water samples were among the highest measured in surface water by the USGS Mercury Research Laboratory (Naftz et al. 2008a).

Concentrations of Se in both male and female COGO on the GSL also increased progressively between early and late winter and COGO likely acquire Se from GSL resources. Naftz et al. (2008b) reported recent (2006–2007) Se loading into the GSL from some inflow sites (i.e., Lee Creek and Goggin Drain) were greater than historic (1972–1984) estimates. A net increase in Se concentrations in GSL water was also observed over a 15 month (May 2006–July 2007) monitoring period and total daily Se loads from major freshwater inflow sites (e.g., Bear River Bay and Farmington Bay) generally increased between mid-winter and spring (Naftz et al. 2008b). Additionally, Brix et al. (2004) reported a strong positive relationship ($r^2 = 0.92$) in total Se concentrations between GSL water and brine shrimp. Thus, waterbirds may acquire Se from various GSL resources.

By late winter, 88% of female COGO contained Se concentrations that exceeded thresholds (> 3.0 µg/g ww) associated with reproductive impairment and 14% possessed concentrations (> 10 µg/g ww) associated with health-related problems for laboratory mallards (Heinz et al. 1989; Heinz 1996). However, marine systems generally have higher Se concentrations than freshwater environments (Ohlendorf 2003) and there is
increasing evidence that marine birds may have evolved to tolerate higher Se concentrations (DeVink et al. 2008a; Skorupa 1998). High Se concentrations in female white-winged scoters (*Melanitta fusca*) from the boreal forest did not appear detrimental to female body condition or breeding propensity (DeVink et al. 2008a). Average liver Se concentrations in late winter female COGO from the GSL were approximately 45% lower than those reported for breeding scoters (\( \bar{X} = 32.6 \mu g/g \) dw) by DeVink et al. (2008a). Similarly, Heard et al. (2008) reported Barrow’s goldeneye (*Bucephala islandica*) and harlequin ducks (*Histrionicus histrionicus*) from Alaska were in good condition despite high blood Se concentrations. Furthermore, studies of several marine vertebrates indicate Hg and Se may interact to form biologically inert complexes such as mercuric selenide (HgSe) (Ikemoto et al. 2004; Ohlendorf 2003) so that absorption of Se may provide birds some protection from Hg toxicity (Ohlendorf 2003; Wiener et al. 2003). Thus, an interaction between Hg and Se may have caused enhanced accumulation and retention of both elements in COGO (Furness and Rainbow 1990; Henny et al. 2002; Scheuhammer et al. 1998; Spalding et al. 2000). Excess Se can also be quickly eliminated from birds following a reduction in dietary Se concentrations (Heinz et al. 1990; Ohlendorf 2003). Dietary Se concentrations for ducks in northern breeding areas such as the boreal forest, a major breeding region for COGO (Eadie et al. 1995), are likely lower than those of the GSL (DeVink et al. 2008a). Therefore, given the half-life of Se reported for laboratory mallards of 18.7 days (Heinz et al. 1990) and 19 days for lesser scaup (*Aythya affinis*; DeVink et al. 2008b; range 16–22 days), Se concentrations in many GSL COGO could decrease substantially by the average nest initiation date of May 4th for western breeding COGO (Eadie et al. 1995).
Concentrations of Se were elevated (> 3.0 µg/g ww) in 57% of NSHO collected from the GSL. However, 10% of NSHO samples exceeded 5 µg/g ww for which evidence of reduced immune system function was found for laboratory mallards (Hoffman 2002). Mean Se concentrations declined in NSHO between November and December and then increased again by the February collection period. Temporal variation observed in NSHO Se concentrations could also reflect differences in collection locations. Most NSHO collected in November were obtained from Farmington and Ogden Bays whereas most NSHO collected in December and February were obtained from near the Lee Creek and Goggin Drain inflows into the GSL. Additionally, Naftz et al. (2008b) reported both temporal and spatial variability of total Se loads from major freshwater inflows into the GSL. However, the lower Se concentrations observed in December could potentially reflect new migrants into the GSL system with lower Se concentrations. Regardless, 79% and 21% of NSHO Se concentrations in February were above thresholds associated with reproductive impairment and immune system function in laboratory mallards. Although Se depuration rates are relatively rapid, reproductive output could be jeopardized if NSHO continue to maintain high Se concentrations through winter and spring. Indeed, total Se loads into the GSL from freshwater inflows peaked during spring runoff (Naftz et al. 2008b).

Conclusion

Several trace elements were accumulated by waterfowl utilizing the GSL during winter but many appear to be within reported normal ranges. However, a large proportion of COGO from the GSL contained disturbing amounts of Hg and Se during winter. Additionally, concentrations of Hg in COGO, NSHO, and GWT were among or
exceeded the highest reported values in these species. However, the effect of Hg and Se on bird fitness is speculative as little information exists regarding behavioral or physiological responses to increased Hg and Se levels for these species while in the GSL system or after they depart for breeding habitats. Therefore information regarding behavior, body condition, foraging, habitat use, and survival of these birds is needed. Information regarding trace elements, including MeHg, in sediments, water, and other biota from the GSL and adjacent freshwater habitats is also needed to better understand the transfer and ecotoxicology of trace elements to waterbirds in the GSL system. Although COGO, NSHO, and GWT do not commonly breed in the GSL system, the high concentrations of Hg and Se found in these species warrants evaluation of reproductive performance of other waterbirds within the GSL system.

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specific water quality standard for selenium in the Great Salt Lake, Utah, USA.
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Table 5-1 Geometric mean concentrations (μg/g wet weight), 95% CI, and ranges of trace elements in liver tissues of female and male common goldeneye collected from the Great Salt Lake, Utah during winters 2004-05 and 2005-06. Values were combined across years and age classes within gender classes and winter collection periods. Winter periods: Early = November 20–December 31; Mid = January 1–February 27; Late = February 28–April 5. Means with different uppercase letters (within a trace element and gender class) differed significantly ($p < 0.05$).

<table>
<thead>
<tr>
<th>Element</th>
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<th>n</th>
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<th></th>
<th>Male</th>
<th></th>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\bar{x}$</td>
<td>95% CI</td>
<td>Range</td>
</tr>
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<td>As</td>
<td>0.001</td>
<td>Early</td>
<td>40</td>
<td>0.38</td>
<td>(0.33–0.43)</td>
<td>(0.10–1.34)</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mid</td>
<td>37</td>
<td>0.40</td>
<td>(0.35–0.45)</td>
<td>(0.10–1.00)</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Late</td>
<td>43</td>
<td>0.38</td>
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<td>(0.12–0.89)</td>
<td>0.41</td>
</tr>
<tr>
<td>B</td>
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<td>Early</td>
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<td>1.23A</td>
<td>(1.06–1.43)</td>
<td>(0.34–2.21)</td>
<td>1.13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mid</td>
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<td>1.20AB</td>
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<tr>
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<td></td>
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<td>(6.4–42.7)</td>
<td>11.2</td>
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<td>(0.4–38.4)</td>
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<td></td>
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<tr>
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<td>(2.26–11.1)</td>
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<tr>
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<td></td>
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<td>(29.8–55.5)</td>
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<td>(22.6–64.9)</td>
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<td>(38.1–41.9)</td>
<td>(26.3–56.1)</td>
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Table 5-2  Geometric mean concentrations (µg/g wet weight), 95% CI, and ranges of trace elements in northern shoveler liver tissues collected from the Great Salt Lake in Utah during winters 2004-05 and 2005-06. Values were combined across years and sex classes within winter collection periods. Winter periods: Nov = October 27–November 31; Dec = December 1–31; Feb = February 1–28. Means with different uppercase letters (within a trace element) differed significantly (p < 0.05).

<table>
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<th>Element</th>
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<th>( \bar{x} )</th>
<th>95% CI</th>
<th>Range</th>
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<td>(0.18–1.73)</td>
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<td></td>
<td></td>
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<td>42</td>
<td>1.34B</td>
<td>(1.14–1.57)</td>
<td>(0.39–3.09)</td>
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<tr>
<td></td>
<td></td>
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<td>(0.30–0.53)</td>
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<td>Cu</td>
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<td>(6.0–68.2)</td>
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<tr>
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<td></td>
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<td>(5.0–58.3)</td>
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<tr>
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<td></td>
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<td>(0.08–0.64)</td>
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<td>(0.05–0.59)</td>
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<tr>
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<td></td>
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<td>(0.24–0.37)</td>
<td>(0.12–1.60)</td>
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<td>3.74A</td>
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<td>(2.61–8.60)</td>
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<td>(42.1–46.6)</td>
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<td>42.9</td>
<td>(40.3–45.7)</td>
<td>(29.0–63.6)</td>
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</tbody>
</table>
Table 5-3. Geometric mean concentrations (µg/g wet weight), 95% CI, and ranges of trace elements in liver tissues of American green-winged teal collected from the Great Salt Lake, Utah during December 2004. *N* = 20. Values were combined across age and sex classes.

<table>
<thead>
<tr>
<th>Element</th>
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<th>Range</th>
</tr>
</thead>
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<td>(0.01–0.02)</td>
<td>(0.01–0.03)</td>
</tr>
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<td>0.18</td>
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*a ND = detectable residues measured in < 60% of birds.

*b Number before nd indicates nondetection values.

*c See results for age related differences.
Table 5-4. Geometric mean concentrations (µg/g wet weight), 95% CI, and ranges of trace elements in liver tissues of female and male common goldeneye collected from the Great Salt Lake, Utah during winters 2004-05 and 2005-06. Values were combined across years and age classes within gender classes and winter collection periods. Winter periods: Early = November 20–December 31; Mid = January 1–February 27; Late = February 28–April 5.

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a Number before nd indicates nondetection values.

b ND = detectable residues measured in < 60% of bird livers.
Table 5-5. Geometric mean concentrations (µg/g wet weight), 95% CI, and ranges of trace elements in northern shoveler liver tissues collected from the Great Salt Lake, Utah during winters 2004-05 and 2005-06. Values were combined across years and gender classes within winter collection periods. Winter periods: Nov = October 27–November 31; Dec = December 1–31; Feb = February 1–28.

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<td>(211–407)</td>
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### Table 5-5 continued.

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<td>(0.003–0.03)</td>
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<td>(0.010–0.016)</td>
<td>(0.002–0.070)</td>
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<td>(0.002–0.004)</td>
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<td>V</td>
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<td>(0.03–0.04)</td>
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<td>28</td>
<td>0.07</td>
<td>(0.06–0.08)</td>
<td>(0.02–0.26)</td>
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</tbody>
</table>

a Number before nd indicates nondetection values.

b ND = detectable residues measured in < 60% of birds.
Fig. 5-1  Geographic distribution of locations in the Great Salt Lake, Utah where common goldeneye, northern shoveler, and green-winged teal were collected winters 2004-05 and 2005-06. Triangles (▲) represent location of major freshwater inflow sites to the Great Salt Lake.
Fig. 5-2  Temporal dynamics of total Hg (A) and Se (B) concentrations (µg/g, wet weight) in liver tissues of female (circles) and male (triangles) common goldeneye collected from the Great Salt Lake, Utah winters 2004–05 and 2005–06. Adult males = filled triangles and solid line; juvenile males = open triangles and dashed line. The horizontal dashed lines in A at 1.0 and 30 µg/g represent the thresholds above which Hg concentrations may be considered elevated and potentially harmful, respectively, for other waterbirds. The horizontal dashed lines in B at 3.0 and 10 µg/g represents the Se concentration thresholds above which laboratory mallards may experience reproductive impairment and health-related problems, respectively. Day 0 on X axis = November 19.
CHAPTER 6

CONCLUSIONS

The GSL has long been recognized for its significance to aquatic birds in North America during migratory and breeding periods of the annual cycle. My research has further elucidated the significance of the GSL as an important wintering area for several duck species including common goldeneye (*Bucephala clangula*), northern shoveler (*Anas clypeata*), green-winged teal (*A. crecca*), northern pintail (*A. acuta*), and gadwall (*A. strepera*). Additionally, hypersaline areas and the associated halophile resources of GSL are important to wintering ducks particularly for common goldeneye, northern shoveler, and green-winged teal.

Waterfowl distribution and abundance in winter generally responds positively to increases in wetland availability and foraging habitats at multiple spatial scales (Nichols et al. 1983, Heitmeyer and Vohs 1984, Cox and Afton 2000, Fleskes et al. 2002, Pearse et al. 2012). Persistent drought conditions between 1999–2004 throughout much of the Intermountain West, including the GSL watershed, resulted in diminished wetland and aquatic resources both regionally and locally in the GSL system. In Chapter 2, I identified total duck abundance was lower with 33% fewer duck use-days in winter 2004-05, which was associated with drought impacts, compared to the subsequent winter of 2005-06 when precipitation and hydrologic conditions improved regionally and locally within the GSL watershed. These differences in duck abundance and use-days between winters were primarily due to annual variation in early- and late- winter time periods, when adjacent marshes are generally not frozen. Total duck abundance was generally similar between years in mid-winter when temperatures are generally coldest. Thus, I
conclude that lower total duck abundance and use of the GSL system in 2004-05 was directly influenced by either the lower availability or quality of wetland and aquatic habitats due to cumulative impacts of regional and local drought conditions. I also identified in Chapter 2 total duck use of hypersaline areas of GSL was higher in 2004-05 when freshwater wetland and aquatic habitats were diminished in the GSL system. I suggest ducks likely rely on hypersaline areas to a greater extent as either foraging or secure loafing sites because of lower availability of such resources in adjacent freshwater habitats. Climate conditions in winter also played an important role in relative duck abundance and use of the GSL system, especially for those species using abundant halophile invertebrates (i.e., brine shrimp \textit{[Artemia franciscana]} and their cysts, and brine fly [Ephydridae] larvae) as food resources. Higher duck use of hypersaline areas was observed during mid-winter when temperatures were coldest (Chapter 2) and freshwater habitats are typically frozen limiting their availability as foraging habitat for ducks. Thus, hypersaline resources are likely more important to ducks when access to freshwater wetland and other aquatic resources is low due to environmental conditions such as drought or extensive ice conditions.

The use of GSL halophile invertebrates by wintering ducks as a food resource has been previously suggested (Aldrich and Paul 2002). In Chapter 3, I corroborate this speculation and identified that brine fly larvae were an important food source (68% overall dietary composition) of common goldeneye whereas brine shrimp cysts were important foods (≥ 52% overall dietary composition) of northern shoveler and green-winged teal during winter. Therefore, common goldeneye, northern shoveler, and green-winged teal do not use the GSL hypersaline areas only as refugia from disturbance or
predation but also to meet energetic and nutritional needs during winter. To date, management of GSL hypersaline invertebrate populations have been primarily concerned with potential effects on the large population of eared grebes (*Podiceps nigricollis*) that migrate through annually (Conover and Caudell 2009, Belovsky et al. 2011). My results indicate the foraging needs of wintering ducks should also be considered in management decisions of GSL resources.

Environmental and climatic conditions influenced diets of wintering ducks and relative use of hypersaline resources. In Chapter 3, I presented results indicating that higher proportions of freshwater invertebrates were detected in diets of goldeneye in early winter 2005-06 relative to 2004-05 likely because availability of freshwater wetland resources had increased compared to the drought impacted winter of 2004-05. More goldeneye remained in the GSL (Chapter 2) and consumed more brine fly larvae in late winter 2005-06 when conditions were colder relative to late winter 2004-05. Additionally, the proportion of hypersaline invertebrates in northern shoveler diets increased from early to mid-winter as average temperatures declined and ice conditions became more prevalent in freshwater wetlands. These dietary patterns lead me to conclude that halophile invertebrate food resources are likely more important to ducks when access to freshwater wetland and other aquatic resources is low because of environmental conditions such as drought, cold temperatures, or extensive ice conditions.

Habitat and climatic conditions also influenced lipid dynamics of common goldeneye during winter. In Chapter 4, I identified that goldeneye lipid reserves were, overall, 17% lower in winter 2004-05 when regional and local wetland and aquatic habitat conditions were diminished because of drought and indices of brine fly larvae in
GSL were low compared to winter 2005-06. On average, lipid reserves declined 34% through winter, apparently influenced, at least partially, by an endogenous mechanism common to other wintering ducks at northern and mid-latitudes in North America (Baldassarre and Bolen 2006). However, lipid dynamics were also strongly influenced by local environmental conditions during winter at GSL. Reduced availability of foraging habitats from ice conditions can be an important factor influencing habitat selection and lipid dynamics of waterfowl in winter and ice extent in aquatic environments is positively correlated with the cumulative number of days < 0° C ambient temperature (Lovvorn 1989, Schummer et al. 2012). Similarly, female goldeneye at GSL exhibited a declining trend in lipids as freezing conditions persisted in the GSL system whereas males generally maintained high lipid reserves even at lowest temperatures. Because of their smaller size, female goldeneye have higher metabolic rates, store fewer lipids per unit mass, are less efficient at insulating themselves, and have a higher heat conductance per unit body mass than larger males (Calder 1974, Goudie and Ankney 1986). Consequently, higher energy demands and thermoregulatory costs in females may explain the higher proportion in female diets of freshwater invertebrates, primarily corixids (Corixidae), which have a higher energy density than halophile invertebrates at GSL (Caudell and Conover 2006). However, during extended periods of low ambient temperatures, goldeneye likely rely more on hypersaline food resources because of reduced access to freshwater foods resulting from ice conditions (see Chapter 3). As females respond to cues from declining temperatures, they may also seek to lower body mass through lipid catabolism to make foraging in hypersaline conditions more energetically profitable by reducing buoyancy and energetic demands. Thus, I posit that
lipid declines in females are more likely a lipid optimization strategy than a direct impact from thermal stress because food resources (i.e., brine fly larvae) were likely not limiting. However, temporal and spatial dynamics of benthic brine fly larvae densities are not well understood at GSL, and further elucidation of these patterns will be important to devising conservation strategies for wintering ducks and other aquatic birds.

The process of acclimating to varying salinities and maintaining osmotic homeostasis by developing and maintaining active salt glands and other osmoregulatory mechanisms is energetically costly (Nelhs 1996, Peaker and Linzell 1975, Guitérrez et al. 2011). Although goldeneye likely experienced energetic costs during acclimation to hypersaline resources, my data suggest that those adaptations did not impose a significant barrier to maintenance of lipid reserves through winter. Regional environmental conditions in conjunction with local habitat conditions at GSL (e.g., Ephydridae productivity, freshwater and wetland availability, climate) likely play a more prominent role in lipid reserve dynamics for goldeneye than osmotic stress. For example, goldeneye at GSL were able to maintain lipid reserves similar to levels reported in freshwater systems with abundant macroinvertebrate food resources (c.f. Schummer 2005, Schummer et al. 2012). Persistence of the abundant and available halophile food resource through winter at GSL likely played an important role in maintaining energy reserves during inclement winter weather and energetic stress.

In Chapter 5, I identified several trace elements that were accumulated by ducks using the GSL during winter. Many elements appear to be within reported normal ranges. However, a large proportion of common goldeneye from the GSL contained unusually high amounts of Hg and Se. Concentrations of Hg in common goldeneye,
northern shoveler, and green-winged teal were among or exceeded the highest reported values in these species. More than 30% of goldeneye samples contained potentially harmful concentrations of Hg and Se based on biological thresholds identified for waterfowl. Lipid reserves of common goldeneye during winter were similar to those reported for this species at other wintering sites (Chapter 4) suggesting these trace elements may not have interfered with maintenance of lipid reserves (a key index of fitness), at least at the population scale. However, the effect of Hg and Se on bird fitness is speculative as little information exists regarding behavioral or direct physiological responses to increased Hg and Se levels for these species while in the GSL system or after they depart for breeding habitats. Also, impacts of excessive Hg and Se accumulation could be manifested for these species outside of winter through deposition into eggs during the breeding season. Therefore, further information regarding behavior, physiological condition, foraging, habitat use, and survival of these birds is needed to elucidate impacts. Information regarding trace elements, including methylmercury (CH$_3$Hg$^+$), in sediments, water, and other biota from the GSL and adjacent freshwater habitats is also needed to better understand the transfer and ecotoxicology of trace elements to waterbirds in the GSL system. Additionally, further information regarding dynamics of mercury and selenium interactions in GSL biota is needed to fully evaluate ecotoxicological impacts of these trace elements.

Lower total duck abundance and use of the GSL system as well as lower lipid reserves of goldeneye in association with the drought impacted winter (2004-05) provides an interesting perspective of potential impacts to further planned reductions in water supply to the GSL (Bennett 2008, Downard 2010) or climatic changes (Bedford and
Douglass 2008, White 2011). My results suggest that persistent reductions in hydrologic inputs to the GSL system will result in lower duck abundance and relatively lower body condition of those using the GSL system—a continental priority area for waterfowl conservation and management in North America (NAWMP 2004, 2012). Providing sufficient wetland and hypersaline food resources will be important to provide resiliency for wintering ducks to adapt to winter conditions and maintain adequate energy reserves for survival and subsequent annual cycle events. Conservation and management strategies for water resources that 1) sustain halophile productivity at GSL and wetland function in associated wetland complexes and 2) improve resiliency to climate and anthropogenic induced modifications will be important to sustain wintering ducks and other aquatic bird populations at one of the most significant aquatic resources in the Pacific Flyway.

LITERATURE CITED


Request for Permission to Reprint Letter

Stephanie Jones <editor.waterbirds@gmail.com>  Fri, Nov 8, 2013 at 8:47 AM
To: Josh Vest <jvest1@gmail.com>
Cc: Sandra MacPherson <sandy.waterbirds@gmail.com>

Hi Joel:
Yes, you have our permission. This email should be your permission to reprint the paper as a chapter in your dissertation.
Best,
Steph

---
On Wed, Nov 6, 2013 at 7:02 PM, Josh Vest <jvest1@gmail.com> wrote:
Hello Stephanie and Ms. MacPherson,

In 2011, I was fortunate to have a manuscript published in Waterbirds:

URL: http://www.bioone.org/doi/full/10.1675/063.034.0105

This work was part of my dissertation research and degree program at Utah State University (USU). I am currently in the process of completing my degree program at USU and have included the manuscript referenced above, with only minor editorial & formatting changes, as a chapter in my current dissertation draft. Thus, I am requesting a letter from Waterbirds indicating permission to reprint the manuscript as a chapter of my dissertation at USU. Thank you for your consideration and I appreciate your assistance. Please do not hesitate to contact me directly if you have any questions or need further clarification.

Sincerely
josh

p.s. I can also be reached via my work contact:

Josh Vest
Science Coordinator
Intermountain West Joint Venture
406-552-3657
josh_vest@fws.gov

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Dear Josh,

Thank you for the note.

It should be fine to publish your article as a chapter in your dissertation provided the appropriate acknowledgement of the original source of publication is included. However, I am forwarding your email to the Springer permissions department in case they have some specific recommendations or requirements to communicate.

Best,

Lindy

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Melinda (Lindy) Paul
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Environmental Science
Senior Editor
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---
www.springer.com
Hello Ms. Paul and Dr. Doerge,

In 2009, I was fortunate to have a manuscript published along with my colleagues in Archives of Environmental Contamination and Toxicology:


This work was part of my dissertation research and degree program at Utah State University (USU). I am currently in the process of completing my degree program at USU and have included the manuscript referenced above, with only minor editorial & formatting changes, as a chapter in my current dissertation draft. Thus, I am requesting a letter from the journal and copyright holder indicating permission to reprint the manuscript as a chapter of my dissertation at USU. Thank you for your consideration and I appreciate your assistance. Please do not hesitate to contact me directly if you have any questions or need further clarification.

Sincerely

josh

________________________
Josh Vest
Science Coordinator
Intermountain West Joint Venture
406-549-0354 (o)
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CURRICULUM VITAE

JOSH L. VEST
Intermountain West Joint Venture
1001 Higgins Avenue, Suite A1
Missoula, MT 59801

EDUCATION

**Doctorate of Philosophy.** Candidate (IN PROGRESS).
Utah State University; College of Natural Resources
Major: Wildlife Biology
Dissertation: Wintering waterfowl ecology on the Great Salt Lake, Utah.

**Master of Science.** December 2002.
Mississippi State University; College of Forest Resources
Major: Wildlife & Fisheries Science
Thesis: Body mass and gastrointestinal parasites of lesser scaup in the Mississippi Flyway
GPA: 3.62

**Bachelor of Science.** May 1999.
Mississippi State University; College of Forest Resources
Major: Wildlife Science
GPA: 3.79

PROFESSIONAL EXPERIENCE

*Science Coordinator/Biologist–Intermountain West Joint Venture; U.S Fish & Wildlife Service.* September 2009 – present.

Utah State University; Department of Wildland Resources. Dissertation title: Wintering waterfowl ecology on the Great Salt Lake, Utah. Designed and implemented an aerial survey program; planned, coordinated, and implemented field and laboratory data collection. Interviewed, hired, and supervised technicians (9).
Mississippi State University; Department of Wildlife & Fisheries. Coordinated, supervised, and implemented waterfowl collections throughout the Mississippi Flyway and laboratory research procedures. Interviewed, hired, and supervised technicians (8).

Research Technician. 1999.
Delta Waterfowl and Wetlands Research Station (Canada). Conducted breeding waterfowl pair and brood surveys, nest searches, trapping, telemetry, vegetation surveys, and banding. Assisted with surgical attachment of radio transmitters to waterfowl.

Department of Wildlife & Fisheries, Mississippi State University. Supervised technician (1), collected data from wood duck boxes, banded (standard, plasticine bands, web tags) assisted with surgical attachment of radio transmitters to waterfowl, conducted radio telemetry, wood duck pair surveys, and wetland habitat classification, waterbird surveys, and predator surveys.

Department of Wildlife & Fisheries, Mississippi State University. Installed and maintained water sampling devices in agricultural fields, collected water quality data, and conducted agricultural productivity surveys.

Research Technician. 1996.
Delta Waterfowl and Wetlands Research Station (U.S, Canada). Conducted waterfowl breeding pair surveys, nest searches and monitoring, trapping, and assisted with abdominal implants of radio transmitters to waterfowl, and predator inventory surveys.

PUBLICATIONS

Manuscripts in press or review


PRESENTATIONS AT SCIENTIFIC CONFERENCES

Oral


Poster

Petrie, M. J., J. P. Fleskes, W. D. Smith, J. L. Vest, J. P. Donnelly. Conserving flood-irrigated habitats for spring migrating ducks in southern Oregon-northeast


RESEARCH/EXTENSION COMMUNICATIONS


Invited Presentations


TECHNICAL REPORTS


Joint Venture, Missoula, Montana.


TEACHING EXPERIENCE

Utah State University


Mississippi State University


Course: Waterfowl Ecology and Management; College of Forest Resources. Laboratory assistant and guest lecturer. Fall 2001.

Course: Wildlife Techniques; College of Forest Resources. Laboratory and teaching assistant. Spring 2001.

PROFESSIONAL AFFILIATIONS

The Wildlife Society
The Waterbird Society
Society of Wetland Scientists

PROFESSIONAL SERVICE

Reviewer for Journal of Fish and Wildlife Management
Reviewer for Wetlands
Reviewer for International Society of Salt Lake Research
Reviewer for Human-Wildlife Conflicts
External reviewer for USGS-Biological Resource Division
External reviewer for Illinois Natural History Survey
External research proposal reviews for Utah Division of Wildlife Resources

GRANTS


AWARDS/HONORS

Student Presentation Award (oral) – 5th North American Duck Symposium and Workshop (2009).
Stokes–Leopold Memorial Scholar, 2007–2008. Utah State University, College of
Natural Resources.
Best Oral Presentation, College of Natural Resources 2007. Utah State University 10th Annual Graduate Research Symposium.
Outstanding Undergraduate in Wildlife & Fisheries, 1998–1999. Mississippi State University, College of Forest Resources.
Senior Academic Achievement Award in Wildlife & Fisheries, 1997–1998. Mississippi State University, College of Forest Resources.
Outstanding Undergraduate in Wildlife & Fisheries, 1995–1996. Mississippi State University, College of Forest Resources.
REFERENCES

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**Dr. Michael R. Conover**
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**Dr. Richard M. Kaminski**
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**John Luft**
Manager
Great Salt Lake Ecosystem Program
Utah Division of Wildlife Resources
1594 West North Temple
Salt Lake City, UT 84114
801-537-3342
johnluft@utah.gov
November 12, 2013

Utah State University
Office of Graduate Studies

RE: Release of publication for dissertation

I am a coauthor with Josh Vest in the publication:

Josh has identified his desire to include this publication as part of his dissertation, Ecology of Wintering Waterfowl on the Great Salt Lake, Utah. I approve this request and hereby provide my consent to include the above referenced publication in his dissertation.

Sincerely

[Signature]

John Luft
Program Manager
Great Salt Lake Ecosystem Program
Utah Division of Wildlife Resources
4790 S 7500 W
Hooper, UT 84315
(801)9853700
November 15, 2013

Utah State University
Office of Research and Graduate Studies

RE: Release of publication for dissertation

To Whom It May Concern:

I am a coauthor with Josh Vest in the publication:

Josh has identified his desire to include this publication as part of his dissertation, Ecology of Wintering Waterfowl on the Great Salt Lake, Utah. I approve this request and hereby provide my consent to include the above referenced publication in his dissertation.

Sincerely

[Signature]

Jeffery O. Hall, D.V.M., Ph.D.
Professor, Animal, Dairy & Veterinary Sciences
Utah State University
Head, Diagnostic Veterinary Toxicology
Utah Veterinary Diagnostics Laboratory
950 E 1400 N
North Logan, UT 84341
435-797-2805
November 22, 2013

Utah State University
Office of Graduate Studies

RE: Release of publication for dissertation

I am a co-author with Josh Vest in the publication:


Josh has identified his desire to include this publication as part of his dissertation, *Ecology of Wintering Waterfowl on the Great Salt Lake, Utah*. I approve this request and hereby provide my consent to include the above referenced publication in his dissertation. I believe this aspect of our work is of critical importance for present management needs and documentation of existing conditions at Great Salt Lake. Inclusion in his dissertation will make this knowledge available to others far into the future.

Sincerely

W. Clay Perschon
Utah Division of Wildlife Resources, Retired
Fisheries Research and Special Projects Coordinator
Great Salt Lake Ecosystem Program Manager
5714 South Weber Drive
Riverdale, Utah 84405
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