Avian diets in a saline ecosystem: Great Salt Lake, Utah, USA

ANTHONY J. ROBERTS, Department of Wildland Resources, Utah State University, Logan, UT 84322, USA  tony.roberts@aggiemail.usu.edu

Abstract: Saline lakes provide a prey-rich, predator-free environment for birds to utilize during migration and stopover periods. The Great Salt Lake (GSL), Utah is the largest salt lake in North America and is utilized by millions of migratory birds. It also is host to multiple commercial endeavors. Proposed expansion of commercial use of the GSL would result in increased impounded area and water extraction for mineral production, which may increase the GSL’s salinity and negatively impact invertebrate abundance. I review previous literature and synthesize diets of avian species utilizing the GSL to determine the importance of each invertebrate species, including brine shrimp (Artemia franciscana) and brine flies (Ephydra spp.), and clarify the anthropogenic impacts on food sources and avian populations. Species considered are eared grebes (Podiceps nigricollis), northern shovelers (Anas clypeata), green-winged teals (Anas crecca), common goldeneyes (Bucephala clangula), American avocets (Recurvirostra americana), black-necked stilts (Himantopus mexicanus), Wilson’s phalaropes (Phalaropus tricolor), red-necked phalaropes (Phalaropus lobatus), and California gulls (Larus californicus). Brine shrimp and brine fly adults are consumed by all species considered. Alterations in prey abundance due to increased salinity may alter the ability of the GSL to support large avian populations.

Key words: American avocet, brine shrimp, California gull, commercial harvest, eared grebe, human–wildlife conflicts, mineral extraction, waterfowl, Wilson’s phalarope

Anthropogenic impacts on aquatic ecosystems are widespread and include draining, nutrient enrichment, and reduced water quality. Saline lakes may experience larger effects of anthropogenic disturbance due to lower species richness and specialization of resident organisms (Jellison et al. 2008). Changes to mineral balance or water levels within saline lakes may greatly reduce productivity of organisms within the lake and impact population levels of organisms that depend on saline lake food sources. The Great Salt Lake (GSL) is a large, saline lake in the Great Basin of the western United States. Each year, millions of waterbirds use the GSL to forage on brine flies (Ephydra hains and E. cinerea) and brine shrimp (Artemia franciscana; Aldrich and Paul 2002). The low gradient bottom of the GSL, along with highly variable water levels, result in expansive mudflats and sandbars that create highly productive habitats where avian species forage. High salinities exclude many invertebrate food sources, thus, creating a simple food web that may be highly impacted by changes in species composition (Wollheim and Lovvorn 1995).

Avian species utilizing the GSL compete with multiple industrial uses of the lake and may be affected by associated impacts on the ecosystem. For example, harvest of brine shrimp cysts removes an average of 3.5 million kg of these animals annually from the GSL to provide food for aquaculture facilities around the world (Stephens and Birdsey 2002). Additionally, long-term mineral extraction has reduced the surface area of the GSL by impounding previously open water areas and concentrating salinity within impoundments to exclusionary levels for brine shrimp and brine fly production. Proposed impoundments and diversions of water that would otherwise enter the GSL exceed the yearly inflow to the lake (Great Salt Lake Planning Team 2000).

The mineral extraction industry on the GSL is large and growing; for example, a recent proposal would increase the area impounded for solar evaporation and increase the amount of water diverted for evaporation and other industry uses. Principle minerals extracted from the GSL are sodium chloride (salt), magnesium chloride, and sulfate of potassium (potash). Current total impounded evaporation ponds are >80,000 ha of GSL’s surface area. The salt extraction industry has an annual removal of >1.8 million metric tons of minerals, and the magnesium industry removes >50,000 metric tons annually (Gwynn 2002). Proposed expansion would increase impounded area in Gunnison and Bear River bays, expand potash
evaporation ponds by 14,000 ha, and increase yearly water diversion by >185 million cubic meters of water. If the full expansion is carried out, evaporation ponds for potash would cover about 7.4% of the GSL water surface when at the long-term water elevation of 1,280 m above sea level. Additional evaporation area may reduce GSL levels, resulting in increased salinity. Higher salinity decreases phytoplankton abundance, which, in turn, decreases brine shrimp abundance (Belovsky et al. 2011).

The impacts of increased salinity on the GSL can be seen in the current ecology of the separated Gunnison Bay of the GSL (Figure 1). The Southern Pacific Railroad Causeway (SPRC) is a rock-filled levee that was completed in 1959 across the GSL, cutting Gunnison Bay off from the rest of the GSL, except for 1 breach and 2 culverts. Gunnison Bay soon became supersaturated with salt due to small amounts of freshwater inflows (Loving et al. 2002); as a result, the phytoplankton community shifted to halophytic species. Brine fly and brine shrimp populations in Gunnison Bay collapsed due to low food levels and salinity near the saturation point of 30%. Before construction of the SPRC, Gunnison Bay was likely similar to the pelagic areas of Gilbert Bay, which supports abundant populations of eared grebes (Podiceps nigricollis; Figure 2), phalaropes (Phalaropus spp.), and waterfowl. Aerial surveys from 2006 to 2008 found low avian abundance throughout Gunnison Bay (Vest 2009), likely a consequence of both reduced food and salinity above the osmoregulatory capacity of most avian species.

In this paper, I review and synthesize published and unpublished reports on the diets of avian species utilizing the GSL. I am particularly interested in determining the importance of brine shrimp and brine flies to birds foraging within the GSL and the potential impact of a reduction in these food sources due to increased GSL salinity. A review of avian diets on the GSL will clarify the effect on avian populations of management decisions regarding the recreational use, commercial harvest, and mineral extraction uses of the GSL.

**Study area**

The GSL ecosystem covers nearly 780,000 ha when at a lake elevation of 1,280 m and consists of saline open water and freshwater wetlands. Brackish and freshwater marshes border the GSL, especially on the east shore at freshwater inflow sites of the Bear, Weber, Ogden, and Jordan rivers. Salinity across the GSL is variable, due to concentrated areas of freshwater inflow and anthropogenic alterations of water exchange, most notably the SPRC and the Antelope Island Causeway (AIC; Rich 2002). Bear River Bay and Farmington Bay are the least saline due to large freshwater inflow and low water exchange with the main body of the lake caused by the SPRC and AIC, respectively (Gwynn 2002).

High salinity in the pelagic areas of the GSL support populations of only 2 invertebrates (3 species), brine shrimp (1 species), and brine flies (2 species). Densities of brine shrimp and their cysts vary across the GSL; their numbers are lowest in areas with less saline water, such as Farmington and Bear River bays (Stephens and Birdsey 2002), though salinity beyond
15% is detrimental to these species. Brine fly larvae are found primarily along the substrates of the GSL that are above the anoxic water layer; larvae densities are 10 times higher on bioherms and mud substrates than on sand substrates (Collins 1980). In fresh and brackish water marshes that border the GSL, a variety of aquatic invertebrates are present (Cavitt 2006). During wet years and in freshwater influenced areas, such as Farmington and Ogden bays, common invertebrates available to foraging birds include corixids (Corixidae) and chironomids (Chironomidae).

Methods

I used on-line search engines and article databases, particularly Academic Search Premier, Web of Science, and Google Scholar, to search for articles relating to the GSL. All articles found concerning avian diets of the relevant species on the GSL are included in this manuscript. Key words used were: Great Basin, Great Salt Lake, grebes, Mono Lake, saline lakes, salt lakes, Utah, waterfowl, and all species names listed below. Unpublished data and reports were obtained from the Utah Division of Wildlife Resources or report authors.

Early dietary studies often were combined with examination of food items found throughout the birds’ digestive tract. Material collected from the proventriculus and ventriculus may represent a biased sample toward hard, difficult-to-digest food items. Recent studies recognize this bias and use only the esophagus when examining food habits. Where the distinction is made in the original publication, I state which part of the dietary tract food items were sampled.

The most abundant species utilizing the GSL and its food resources are eared grebes, northern shovelers (Anas clypeata), green-winged teal (Anas crecca), common goldeneyes (Bucephala clangula), American avocets (Recurvirostra americana; Figure 3), black-necked stilts (Himantopus mexicanus), Wilson’s phalaropes (Phalaropus tricolor), red-necked phalaropes (Phalaropus lobatus), and California gulls (Larus californicus). I focused the review on these species.

Results

Eared grebes

Eared grebes nest in the marshes surrounding the GSL, and they also use pelagic regions as staging areas during spring and fall migration. The largest concentrations of eared grebes on the GSL exist during fall migration, when 1.5 million individuals, or approximately half of the North American population, stage at the GSL. While staging, eared grebes’ flight muscles atrophy, body weight increases, and digestive organs increase in size, resulting in flightlessness (Jehl 1997). Fall staging is also the time when adult birds molt. Prior to leaving the GSL in the fall, eared grebes build up fat reserves, and organ trends reverse. With an increase in flight muscles, flight capacity is regained (Jehl 1997).

Food habit studies of eared grebes on the GSL have been conducted during migration and staging and have reported that adult brine shrimp were an important part of eared grebe diets (Table 1). During the early fall, eared grebes consumed both brine shrimp and brine fly adults (Paul 1996, Conover and Vest 2009); by late November, they ate brine...
Table 1. Avian species diet studies done on the Great Salt Lake, Utah, including presence in avian diets of principle macro-invertebrates common to the Great Salt Lake.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Year(s)</th>
<th>Month(s)</th>
<th>N</th>
<th>Brine shrimp adults (%)</th>
<th>Brine fly adults (%)</th>
<th>Brine shrimp cysts (%)</th>
<th>Brine fly larvae (%)</th>
<th>Method of diet measurement</th>
<th>Digestive organ used</th>
<th>Area of Great Salt Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eared grebe</td>
<td>Cullen et al. 1999</td>
<td>1966</td>
<td>Jul–Nov</td>
<td>63</td>
<td>93</td>
<td>5</td>
<td>NA&lt;sup&gt;b&lt;/sup&gt;</td>
<td>NA&lt;sup&gt;#&lt;/sup&gt;</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Paul 1996</td>
<td>1996</td>
<td>Aug–Nov</td>
<td>45</td>
<td>90</td>
<td>5</td>
<td>Trace</td>
<td>AV</td>
<td>Stomach</td>
<td>Near Antelope Island Cause-way</td>
<td></td>
</tr>
<tr>
<td>Conover and Vest 2009</td>
<td>2006</td>
<td>Sept</td>
<td>17</td>
<td>88</td>
<td>70</td>
<td>FO</td>
<td>Esophagus</td>
<td>Antelope and Stansbury Islands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conover and Vest 2009</td>
<td>2006</td>
<td>Nov</td>
<td>16</td>
<td>100</td>
<td>FO</td>
<td>Esophagus</td>
<td>Antelope and Stansbury Islands</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gaffney 2009</td>
<td>2006</td>
<td>April</td>
<td>16</td>
<td>40</td>
<td>45</td>
<td>RP</td>
<td>Stomach</td>
<td>Farmington and Gilbert bays</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gaffney 2009</td>
<td>2007</td>
<td>April</td>
<td>27</td>
<td>8</td>
<td>85</td>
<td>RP</td>
<td>Stomach</td>
<td>Farmington Bay</td>
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<tr>
<td>Cullen et al. 1999</td>
<td>2004–2006</td>
<td>Nov–March</td>
<td>355</td>
<td>0.2</td>
<td>3.7</td>
<td>67.6</td>
<td>AP</td>
<td>Esophagus</td>
<td>Pelagic areas</td>
<td></td>
</tr>
<tr>
<td>Common goldeneye</td>
<td>Vest and Conover 2011</td>
<td>2004–2006</td>
<td>Nov–March</td>
<td>241</td>
<td>20.2</td>
<td>0.1</td>
<td>51.8</td>
<td>7.8</td>
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<td>2004–2006</td>
<td>Nov–March</td>
<td>137</td>
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<td>Trace</td>
<td>79.5</td>
<td>10.8</td>
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<td>1925</td>
<td>March–Oct</td>
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<td>10</td>
<td>2</td>
<td>Count</td>
<td>Stomach</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Wilson 1973</td>
<td>1972</td>
<td>NA</td>
<td>17</td>
<td>17</td>
<td>FO</td>
<td>Esophagus</td>
<td>BRMBR</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mahoney and Jehl 1985</td>
<td>1984</td>
<td>NA</td>
<td>3</td>
<td>100</td>
<td>FO</td>
<td>Stomach</td>
<td>Mud flat</td>
<td></td>
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<tr>
<td>Osmundson 1990</td>
<td>1989</td>
<td>May–Aug</td>
<td>95</td>
<td></td>
<td></td>
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</table>

<sup>a</sup> Method of diet measurement: FO = fraction of organs, RP = relative percent, AP = absolute percent<br><sup>b</sup> Digestive organ used: Stomach (Stomach), Esophagus (Esophagus), Count (Count), BRMBR (BRMBR).
<table>
<thead>
<tr>
<th>Reference</th>
<th>Year(s)</th>
<th>Month(s)</th>
<th>N</th>
<th>Brine shrimp adults (%)</th>
<th>Brine fly adults (%)</th>
<th>Brine shrimp cysts (%)</th>
<th>Brine fly larvae (%)</th>
<th>Method of diet measurement</th>
<th>Digestive organ used</th>
<th>Area of Great Salt Lake</th>
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<td>24</td>
<td>9</td>
<td>4</td>
<td>53.7</td>
<td></td>
<td>AV</td>
<td>Esophagus</td>
<td>BRMBR</td>
</tr>
<tr>
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<td>Wetmore 1925</td>
<td>1925</td>
<td>March–Aug</td>
<td>NA</td>
<td>4</td>
<td>16</td>
<td>7</td>
<td>Count</td>
<td>Stomach</td>
<td>NA</td>
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<tr>
<td>Mahoney and Jehl 1985</td>
<td>1984</td>
<td>NA</td>
<td>3</td>
<td>100</td>
<td>FO</td>
<td>Stomach</td>
<td>Mud flat</td>
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<tr>
<td>Colwell and Jehl 1994</td>
<td>NA</td>
<td>NA</td>
<td>23</td>
<td>21.1</td>
<td>69.6–100</td>
<td>AV</td>
<td>NA</td>
<td>NA</td>
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<td>Wetmore 1925</td>
<td>1925</td>
<td>May–Oct</td>
<td>NA</td>
<td>8</td>
<td>19</td>
<td>19</td>
<td>Count</td>
<td>Stomach</td>
<td>NA</td>
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<tr>
<td>California gull</td>
<td>Cottam and Williams 1939</td>
<td>1938</td>
<td>July</td>
<td>6</td>
<td>Trace</td>
<td>46.5</td>
<td>AV</td>
<td>Stomach</td>
<td>Gunnison Island, various</td>
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<td>1940–1946</td>
<td>March–Aug</td>
<td>529</td>
<td>Trace</td>
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<td>AV</td>
<td>Stomach</td>
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<td></td>
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<tr>
<td>Conover et al. 2009</td>
<td>2006</td>
<td>May</td>
<td>30</td>
<td>72</td>
<td>10</td>
<td>AP</td>
<td>Esophagus</td>
<td>Antelope and land Hat islands, mineral facility</td>
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<td></td>
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<tr>
<td>Conover et al. 2009</td>
<td>2007</td>
<td>May</td>
<td>32</td>
<td>50</td>
<td></td>
<td>AP</td>
<td>Esophagus</td>
<td>Hat Island, mineral facility</td>
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</table>

*AP = aggregate percentage; AV = aggregate volume; Count = number observed; FO = frequency of occurrence; NA = no information available; RP = relative percentage.

b NA = the information was not specified.
shrimp exclusively (Conover and Vest 2009). Only 1 study to date has recorded brine shrimp cysts within eared grebes’ diets. Paul (1996) found trace amounts of cysts in the stomachs of a few birds collected in the fall. Eared grebes collected in Farmington Bay consumed corixids when that prey source was abundant, though eared grebe abundances were lower within this bay (Paul 1996). However, Farmington Bay is less saline than the more open waters of Gilbert Bay, allowing corixids to occur where they cannot in other areas, especially during wet years.

Eared grebes collected during spring of 2006 in Gilbert Bay had diets composed of equal parts brine shrimp and brine fly adults, while birds from Farmington Bay during the same time period contained mostly Hemipterans (Gaffney 2009). During the spring of 2007, eared grebes collected from Farmington Bay were consuming up to 92% brine fly adults, with the remaining diet composed of brine shrimp and Hemipterans (Gaffney 2009). Brine shrimp densities are lower during spring migration, so this food source is not readily available to eared grebes (Belovsky et al. 2011).

**Waterfowl**

Waterfowl population numbers are highest during fall migration, particularly on impounded wetlands and brackish marshes. When considering open, saline waters of the GSL, populations during winter months (December to February) often are around 300,000 ducks (A. Roberts, unpublished data). Primary species are northern shoveler, green-winged teal, and common goldeneye. Waterfowl diet studies within saline areas of the GSL are restricted to a single investigation. Vest and Conover (2011) examined diets of northern shovelers, green-winged teal, and common goldeneye over 2 consecutive winters from 2004 to 2006. All dietary samples were from the esophagus exclusively. Common goldeneye utilized brine fly larvae for ≤77% of their diet throughout the winter, with brine shrimp cysts, freshwater invertebrates, and seeds providing the remainder of the diet (Table 1). Wetland plant seeds, particularly widgeon grass (*Ruppia maritima*) and alkali bulrush (*Scirpus maritimus*), were consumed more when ice-cover retreated from freshwater marshes. Brine shrimp cysts comprised 80% of the aggregate percentage biomass of green-winged teal, and 52% of northern shoveler diets from October through March (Table 1). Brine fly larvae also were a dietary component for these species (Vest and Conover 2011). During fall migration in fresh and brackish marshes, waterfowl relied on wetland plant seeds, such as alkali bulrush and widgeon grass, and freshwater invertebrates for their nutritional needs (Wetmore 1921, Vest and Conover 2011). Northern shovelers and green-winged teal need daily access to freshwater. This restricts their range within the GSL ecosystem to freshwater inflow sites, particularly near the southern end of Gilbert Bay. Freshwater inflow sites likely have higher populations of freshwater invertebrates compared to much of the GSL, increasing the overall percentage of freshwater invertebrates and plant seeds in the diet, even when most freshwater sources have frozen over (Vest and Conover 2011).

**American avocets and black-necked stilts**

American avocets and black-necked stilts are two of the most common shorebirds that utilize the GSL during migration. They are most abundant during fall migration, particularly August through October, when adult brine flies are extremely abundant throughout GSL marshes and open waters (Stephens 1977). Diets of American avocets and black-necked stilts on the GSL are usually dominated by fresh or salt water macro-invertebrates, such as adult brine flies (Table 1).

Wetmore (1925) examined the stomachs of American avocets from across the western United States and Canada. Though collection sites were not clearly presented, common GSL foods found were brine fly larvae and adults, along with many corixids. Seeds of many wetland plants also were observed, including sago pondweed (*Potamogeton pectinatus*), widgeon grass, and bulrush species (*Scirpus* spp.). Wilson (1973) collected staging American avocets from the mud flats of BRMBR (Figure 1) to compare diets of healthy and botulism-infected birds. I restricted this summary to healthy American avocets and black-necked stilts to represent typical diets. Larval stages of brine flies were consumed more than adults, with >72% of adult American avocets’ diet composed of brine fly larvae. Breeding American avocet diets were examined in 2
studies, conducted mostly on areas of brackish or fresh water (Osmundson 1990, Cavitt 2006). Though results are not typical of open, saline waters, they represent the available food to birds on the GSL margins. Corixids and chironomids comprised most of the diet of breeding American avocets; in particular, chironomid larvae accounted for nearly 80% of the diet. Seeds and sprouts also were present in the diet of breeding American avocets and were represented by numerous taxa, including Typha, Scirpus, and Graminaceae (Osmundson 1990).

Black-necked stilts consume both larval and adult brine flies on the GSL. An unknown number of black-necked stilts collected from the Great Basin, including the GSL, contained both adult and larval stages of brine fly (Wetmore 1925). Black-necked stilts, particularly juveniles, collected from the mud flats on BRMBR fed principally (54% biomass) on brine fly larvae (Wilson 1973). In the marshes on the eastern shore of the GSL, invertebrates, such as corixids, chironomids, Ephemeroptera, and Tendipedidae were the primary food source (Cavitt 2006). Differences in the 2 studies are likely due to varying salinities. Cavitt (2006) collected a variety of birds from breeding areas near freshwater marshes. Wilson’s (1973) work occurred on mudflats of the BRMBR, an area whose salinities change drastically from year to year as water levels fluctuate; salinity during the study are not enumerated.

**Phalaropes**

Wilson’s phalaropes and red-necked phalaropes both use the GSL extensively during fall migration, particularly from July through October. Phalarope species are the only shorebirds that regularly occur in pelagic areas of the GSL, and the GSL hosts >50% of North America’s Wilson’s phalaropes each fall. Throughout their range, Wilson’s phalaropes forage on brine shrimp, as well as brine fly larvae, pupae, and adults (Table 1). Three birds collected from shallow water mud flats of the GSL in 1984 had consumed solely adult brine flies (Mahoney and Jehl 1985a). Colwell and Jehl (1994) found age difference in foraging exists among Wilson’s phalaropes, with adults consuming a mix of brine shrimp, brine fly adults, and other aquatic invertebrates, while juveniles collected in this study (n = 7) fed exclusively on adult brine flies, although the authors state that the age difference may be due to a bias in of their collection habitat (near shore) or small sample size (Colwell and Jehl 1994).

Red-necked phalaropes utilize more pelagic areas than do Wilson’s phalaropes (Aldrich and Paul 2002) both on the GSL and the Pacific Ocean, where much of the North American population winters (Rubega et al. 2000). Early diet studies found brine shrimp and brine fly larvae and adults present in red-necked phalarope intestines (Wetmore 1925). Adult brine flies accounted for 95 to 100% of red-necked phalaropes’ diet on the GSL in early August 1992 (n = 3), but, by late August (n = 9), brine fly larvae accounted for 60 to 100% of their diet (Aldrich and Paul 2002). In October, their diet consisted entirely of brine fly larvae and pupae.

**California gulls**

California gulls have an omnivorous diet and are opportunists in both their food choice and feeding styles (Behle 1958; Figure 4). Foods obtained directly from the GSL include brine shrimp, brine fly adults, and brine fly larvae (Table 1). Cottam and Williams (1939) found that brine fly adults, larvae, and pupae made up 46% of the diet of 6 individuals collected in early July from the GSL vicinity. Carrion and various plant matter made up 17% of the diet of those 6 individuals (Cottam and Williams 1939). A sample of 529 birds collected across 4 years from Antelope Island and surrounding marshes, including the BRMBR, contained a
variety of food items (Greenhalgh 1952). Brine fly adults and other Diptera made up 5% of the diet in this sample. Brine shrimp were also recovered from California gull stomachs but made up ≤1% of their diet (Greenhalgh 1952). Greenhalgh (1952) found that Orthoptera made up 53% of California gulls’ diet around the GSL. During the breeding seasons of 2006 and 2007, Conover et al. (2009) collected 54 California gulls with food in their crops from around the GSL near Antelope Island (n = 10), Hat Island (n = 24), and at a commercial mineral facility along Bear River Bay (n = 20). Most (77%) California gulls had eaten brine shrimp, and two had fed on brine fly larvae. Garbage, carrion, larval and adult midges, and corixids made up the remainder of their diets (Conover et al. 2009). Brine shrimp cysts have not been found in any samples reported, though California gulls are often seen in pelagic areas of the GSL near concentrations of cysts.

**Discussion**

For many avian species, the GSL offers a predator-free, prey-rich environment during critical times of the year. All species considered here except American avocets and black-necked stilts, have been shown to consume both brine shrimp and brine flies. Brine flies are present in the diet of all species discussed, but brine fly abundance, distribution, and population fluctuations within the GSL are not well-understood (Belovsky et al. 2011).

Current GSL salinity is near 9%, but decreased water levels due to increased evaporation or water diversion may quickly increase salinity to >14%, which would be detrimental to long-term populations of both brine shrimp and brine flies. Brine shrimp adults can survive in salinity up to saturation level, but cannot reproduce. Newly hatched brine shrimp cannot survive in salinity >14% (Stephens and Birdsey 2002), so, brine shrimp production is effectively limited at that salinity. There is no information on the salt tolerance of brine flies on the GSL, but it is likely that osmoregulation in salinity near saturation is prohibitive to brine fly production. Corixids and other more freshwater-tolerant aquatic invertebrates are abundant near freshwater inflows and low-salinity bays of the GSL. During unusually wet years, the resulting decrease in salinity in pelagic areas, from >10% to around 5%, can support populations of more invertebrate species (Wurtsbaugh 1991). Predatory invertebrates, such as corixids, reduced brine shrimp populations by an order of magnitude by consuming brine shrimp nauplii (Wurtsbaugh 1991). There is no information on the ability of avian species to switch from brine shrimp to corixids during these times. Increased salinity due to diversion of fresh water from the GSL would reduce the primary food of avian species utilizing the GSL and result in the reduction of avian use, as we have seen occur in Gunnison Bay in recent years.

The importance of food availability in regulating avian populations changes with salinity levels. In saline lakes in the western United States, the effect of salinity on invertebrates' food appears to be less important to top avian predators than osmoregulation (Wollheim and Lovvorn 1995). Wilson's phalaropes, eared grebes, American avocets, and California gulls all exhibit physiological or behavioral adaptations to counteract increased ingestion of salt (Mahoney and Jehl 1985a, b, c). Waterfowl distributions on the GSL are likely determined by access to fresh water. Northern shovelers and green-winged teal do not have well-developed salt glands and need to drink fresh water to aid in osmoregulation. When salinity impacts brine shrimp and brine fly populations, avian population levels are impacted by food availability, rather than by osmoregulatory capacity.

Estimates of food abundance needed for continued avian use of the GSL have been demonstrated for 1 species, eared grebes. Conover and Caudell (2008) estimated that eared grebes needed a minimum adult brine shrimp density of 0.38 shrimp/L to maintain body mass. A decrease in densities of brine shrimp below these densities would have large consequences on the survival of eared grebes. Belovsky et al. (2011) hypothesized that a higher density of adult brine shrimp (5.80 adult brine shrimp/L) was needed to maintain and increase eared grebe body mass for migration from the GSL. They illustrated a relationship between per capita eared grebe abundance on the GSL and density of brine shrimp during the previous year. This implies that these birds have reduced survival after staging in years of low brine shrimp abundance or that they
change migration route the next year, staging at Mono Lake rather than the GSL. Both estimates of brine shrimp abundance needed for eared grebes are above the long-term average in the GSL, but Gunnison Bay does not support those densities, and eared grebes are not seen there.

Avian diets on Mono Lake, California, are similar to avian diets on the GSL and may help fill information gaps regarding age- and sex-specific dietary differences on the GSL. Diets of eared grebes and other birds on Mono Lake have been studied more extensively than those at the GSL. Investigation of eared grebes’ diets found that they ate mostly brine shrimp during the fall (Jehl 1988), and that this may account for 80% of fall adult brine shrimp depletion through predation (Cooper et al. 1984). Four years of data (1981 to 1984) from Mono Lake show that eared grebes fed primarily on the most abundant prey items. Brine fly larvae and pupae dominated diets from mid-winter through May; when brine shrimp became abundant in June, eared grebes switched to this resource (Jehl 1988). Large waterfowl concentrations are not found on Mono Lake, although gadwalls (Anas strepera) breed there in small numbers that consume adult brine flies, though survival when eating this food is low (Jehl 2005).

Adult female and male Wilson’s phalaropes on Mono Lake fed on 66% and 38% brine shrimp and 34% and 62% brine flies by volume, respectively (Colwell and Jehl 1994). On both the GSL and Mono Lake, juveniles fed exclusively on brine fly adults (Colwell and Jehl 1994). Jehl (1986) found that brine fly adults were the only food eaten in July and August by red-necked phalaropes on Mono Lake and made up >90% of the diet during the remainder of the year. Rubega and Inouye (1994) found that red-necked phalaropes were unable to switch to diets composed principally of brine shrimp. They concluded that birds are unable to survive on brine shrimp alone and must feed on brine fly adults and larvae to survive and gain weight while on Mono Lake. The loss of brine flies on the GSL may severely impact survival of migrating red-necked phalaropes. The omnivorous nature of California gulls likely buffers their population from the loss of individual food sources. On Mono Lake, California gulls are likely eating adult brine flies (Young 1952), but they are able to utilize many anthropogenic food sources that occur on the GSL. Reduced GSL food sources may increase the instances of California gulls raiding other avian nests for eggs and young. This activity is seen on the BRMBR (Greenhalgh 1952) and has been seen in other parts of their breeding range, as well. At Mono Lake, California gulls are predators of snowy plovers’ (Charadrius alexandrines) nests (Page et al. 1985), and in Manitoba, they have been a major predator of Western grebes’ (Aechmophorus occidentalis) nests (Knapton 1988).

Conclusions
Increased salinity due to reduced water inflow or increased water evaporation would be detrimental to brine shrimp and brine flies found in the GSL. It is clear that many avian species rely on these invertebrates on the GSL as a principle food source, and reduction in their food availability would result in the loss of avian populations. Knowledge of avian diets is fundamental to management of continued avian populations, but we lack any knowledge beyond basic food habits. Most importantly, we do not know if avian species can shift their diet to another prey species if their preferred food is no longer available due to altered prey abundances and increased salinities.

Literature cited


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AEL 06-03. Weber State University, Ogden, Utah, USA.
Great Salt Lake Planning Team. 2000. Great Salt Lake comprehensive management plan and decision document. Utah Department of Natural Resources, Salt Lake City, Utah, USA.
Jehl, J. R., Jr. 1988. Biology of the eared grebe and Wilson’s phalarope in the nonbreeding season: a study of adaptations to saline lakes, Studies in Avian Biology 12, Cooper Ornithological Society, University of Oklahoma, Norman, Oklahoma, USA.
Osmundson, B. C. 1990. Feeding of American avocets (Recurvirostra americana) during the breeding season. Thesis, Utah State University, Logan, Utah, USA.
Paul, D. S. 1996. Eared grebe progress report. Utah Department of Natural Resources, Division of Wildlife Resources, Salt Lake City, Utah, USA.


Stephens, D. W. 1977. Brine shrimp ecology in the Great Salt Lake, Utah, for the period of July 1996 through June 1997, administrative report. publication #76-19, Utah Department of Natural Resources, Salt Lake City, Utah, USA.


Vest, J. L. 2009. Overwinter ecology of ducks and other waterbirds. Performance report to Utah Division of Wildlife Resources, Salt Lake City, Utah, USA.


Wilson, G. W. 1973. The foods and feeding habits of botulism intoxicated and healthy waterbirds on the Bear River Refuge, Utah, with emphasis on the American avocet and black-necked stilt. Thesis, Utah State University, Logan, Utah, USA.


Anthony J. Roberts is a Ph.D. student at Utah State University studying wintering ecology of waterfowl and waterbirds on the Great Salt Lake. He has a B.S. degree from the University of Wyoming and a M.S. degree from Texas Tech University.