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Migratory Waterbird Ecology at a Critical Staging Area, Great Salt Lake, Utah

Maureen G. Frank

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MIGRATORY WATERBIRD ECOLOGY AT A CRITICAL STAGING AREA,
GREAT SALT LAKE, UTAH

by
Maureen G. Frank

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

of
DOCTOR OF PHILOSOPHY

in
Wildlife Biology

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UTAH STATE UNIVERSITY
Logan, Utah

2016
ABSTRACT

Migratory Waterbird Ecology at a Critical Staging Area, Great Salt Lake, Utah

by

Maureen G. Frank, Doctor of Philosophy

Utah State University, 2016

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

Despite the hemispheric importance of Great Salt Lake (GSL) as a staging area for migratory birds, little is known about the resources that GSL provides to these birds, or how changes to the GSL ecosystem might impact the avian community. Three species of migratory waterbirds that stage at GSL are Wilson’s phalaropes (Phalaropus tricolor), red-necked phalaropes (Phalaropus lobatus), and eared grebes (Podiceps nigricollis). My objective for this research was to study the impacts of prey availability on the staging ecology of these species. In Chapter 2, I examined the use of GSL habitats by both species of phalaropes. In the high-salinity bays of GSL, phalaropes were most strongly associated with shallow water. In the low-salinity bay, there were no strong associations between phalarope presence and particular habitat characteristics. In Chapter 3, I analyzed the behaviors of phalaropes relative to prey densities. Phalaropes commonly foraged in Carrington Bay, which had the highest densities of brine fly (Ephydridae) adults, and in Farmington Bay, which had high densities of benthic macroinvertebrates. Foraging behavior differed between Wilson’s and red-necked phalaropes, with Wilson’s phalaropes spinning more often than red-necked phalaropes.
In Chapter 4, I examined interannual and nightly variations in eared grebe fall migration departures in relation to prey availability and environmental conditions. Eared grebes began migration relatively early when lake temperatures were relatively warm, densities of brine shrimp (*Artemia franciscana*) adults were high, and densities of brine shrimp cysts were low. The likelihood that eared grebes would depart on a given night was positively associated with the average barometric pressure 12 hours prior to sunset.

The resources provided by GSL support substantial proportions of the staging populations of phalaropes and eared grebes. Management efforts should seek to maintain the habitats and resources needed by phalaropes and eared grebes at GSL. Future large-scale diversions of freshwater may threaten GSL’s suitability as a staging area for these birds.
Migratory Waterbird Ecology at a Critical Staging Area, Great Salt Lake, Utah

Maureen G. Frank

Millions of birds use Great Salt Lake, Utah, during their migrations every year. While many of the birds use the shorelines and wetlands around Great Salt Lake, there are three migratory species that use the open waters of Great Salt Lake: Wilson’s phalaropes (*Phalaropus tricolor*), red-necked phalaropes (*Phalaropus lobatus*), and eared grebes (*Podiceps nigricollis*). Eared grebes feed primarily on brine shrimp (*Artemia franciscana*), while phalaropes are thought to consume brine flies (Ephydridae) and brackish-water aquatic invertebrates. Despite the reliance of phalaropes and eared grebes on the invertebrate prey of Great Salt Lake, little is known about how prey availability affects the ecology of these birds at Great Salt Lake, or about how changes to the Great Salt Lake ecosystem might impact migratory birds. I studied the relationship of prey availability with phalarope habitat use, phalarope foraging behavior, and eared grebe fall migration departure.

Phalaropes used different resources in different bays of Great Salt Lake, and for different purposes. In high-salinity bays, phalarope flocks were most common in shallow water. In a low-salinity bay, phalaropes were not strongly associated with any particular habitat characteristic. Phalaropes were most likely to feed and search for prey in two particular bays, Carrington and Farmington. Farmington Bay had the high densities of aquatic invertebrates, while Carrington Bay had the most brine fly adults.

Eared grebes migrated from Great Salt Lake earlier in years when the lake
temperature was high, densities of brine shrimp adults were high, and densities of brine shrimp cysts were low. On any given night, eared grebes were more likely to migrate if the average barometric pressure was high for 12 hours before typical departure time.

Phalaropes and eared grebes require reliable food resources so they can gain mass before migration each year. A substantial proportion of these species’ populations rely on Great Salt Lake to provide those resources. Management efforts should maintain the habitats and resources that support phalarope and eared grebes at Great Salt Lake. Future large-scale diversions of freshwater may threaten these birds, because insufficient freshwater inflow can lead to decreased foraging habitat and decreased prey availability.
This work is dedicated to my family:

To Daddy, for teaching me to be curious and to be brave, and for fishing, hiking, camping, hunting, crawdad-catching, exploring, and everything adventurous.

To Mama, for teaching me to be patient and to listen, and for sunshine, wildflowers, birds, stars, mountains, front-porch talks, and everything beautiful.

To Emily, and in memory of Madisen, for understanding me better than anyone, and for building forts, catching frogs, laughing until we cry, and everything wonderful.

And to my husband, Philip, for joining me on this journey, for staying by my side through many trials, and for faith, trust, hope, family, sacrifice, perseverance, and everything life.
ACKNOWLEDGMENTS

I had no idea what I was getting myself into when I started this project, and I owe thanks to many people who have joined me on this adventure:

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I never had a bad day on the lake, and all of my thanks for that go to the GSLEP team, who were the nuts and bolts of this whole operation. For their expertise, patience, and friendship, I thank John Luft, Kyle Stone, Jim Van Leeuwen, John Neill, Ashley Kijowski, and Phil Brown, along with Kyle, Andrew, Tony, Kirsten, Joe, and Chalese.

Flying in small planes is not my favorite thing, but the DWR pilots carried us safely across the lake (and back across… and back again…) every time. Thanks to Clair Schaffer, Wayne Grant, and Bill Larsen; special thanks to Craig Hunt for being awesome.

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My amazing family has given me their unending love and support. Thank you to my parents, sisters, grandparents, cousins, aunts, uncles, in-laws, and more – you form the best support system anyone could ask for. Philip, my wonderful husband, has been by my side through this whole adventure. Thank you for your unfailing love, for making me laugh when I needed it most, and for caring for me through good and bad. Thank you for believing in me.

Above all, I give all glory, honor, and praise to my Lord and Savior Jesus Christ. None of my work would have mattered without the work of the Creator, who is my Rock. I am so thankful to be a steward of this amazing world He made. *Soli Deo Gloria.*

Maureen G. Frank
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INTRODUCTION

Great Salt Lake (GSL) and its surrounding wetlands, located at the northeastern edge of the arid Great Basin, host millions of migratory birds every year. The GSL ecosystem provides abundant, dependable food resources for birds that are preparing for the high energetic costs of migration, and is therefore considered a migratory staging area (Warnock 2010). The importance of the GSL ecosystem as a staging area is reflected in the presence of many species in numbers that represent a substantial proportion of their total populations. Gunnison Island, in the north arm of Great Salt Lake, hosts one of the largest breeding colonies of American white pelicans (*Pelecanus erythrorhynchos*) in the U.S. (Aldrich and Paul 2002). Population surveys of ducks (Anatidae) that are present on and around GSL in the fall conservatively estimate over 600,000 ducks at a given time (Aldrich and Paul 2002). Dozens of shorebird species breed and stage in the GSL ecosystem, including American avocets (*Recurvirostra americana*), black-necked stilts (*Himantopus mexicanus*), and snowy plovers (*Charadrius alexandrinus*), all of which are globally important species (Evans and Martinson 2008). While many of the birds using the GSL ecosystem spend most of their time in fresh or brackish wetland habitats adjacent to GSL, three important migratory species primarily use the high-salinity open-water habitats of GSL itself. Wilson’s phalaropes (*Phalaropus tricolor*) and red-necked phalaropes (*Phalaropus lobatus*) stage at GSL during the summer, while eared grebe populations (*Podiceps nigricollis*) peak at GSL in the fall.

The Western Hemisphere Shorebird Reserve Network (WHSRN) designates sites
that provide important resources to migratory shorebirds in an effort to conserve these habitats. The highest classification given to a site by WHSRN, Sites of Hemispheric Importance, is given to areas that host at least 500,000 shorebirds each year or at least 30% of the biogeographic population of a given species (Western Hemisphere Shorebird Reserve Network 2009). Great Salt Lake has been designated a Hemispheric Site in the WHSRN and met both qualifications for this status based on the staging population of Wilson’s phalaropes alone.

Wilson’s phalaropes arrive at GSL in late June after breeding relatively near to GSL in the Prairie Pothole Region and the Intermountain West. Red-necked phalaropes arrive at GSL later (typically mid-July) after traveling from their breeding grounds in the subarctic. While the two species breed in different areas, they converge on GSL during the staging period to take advantage of the lake’s abundant prey. In early to mid-August, Wilson’s phalaropes depart from the GSL to winter at saline lakes in South America. Red-necked phalaropes have a shorter trip to their pelagic wintering areas in the Pacific Ocean off the coast of southern California, USA, and Baja California, Mexico, and often remain at GSL into October. Specific resources that are important to these species during their time at GSL, and the habitats that correspond with those resources, have not been thoroughly studied.

Eared grebes use GSL for a considerable span of time each year. Eared grebes breed throughout the Intermountain West, including in the brackish areas adjacent to GSL. Nesting begins in late April or early May. Staging eared grebes begin to arrive in August and use the open waters of GSL for foraging. The number of eared grebes increases through late summer and fall, typically peaking between October and December
and representing over half of the continental population of eared grebes (Roberts et al. 2013). During most of the staging period, eared grebes are flightless due to the atrophy of their flight muscles (Jehl 1988). Eared grebes must redevelop their flight muscles before departing for fall migration. Departure from GSL typically begins in November or December; eared grebes winter in the Salton Sea and Gulf of California.

Despite GSL’s hemispheric importance to migrating birds, many aspects of the GSL ecosystem have not been studied. Staging birds are drawn to GSL by high abundances of invertebrate prey, including brine shrimp (*Artemia franciscana*) and brine flies (Ephydridae), but many questions remain regarding the ecology of these invertebrates. In particular, few studies have been conducted on brine fly ecology, and brine flies are an important prey resource for phalaropes. Non-prey resources that may be important to phalaropes at GSL, such as fresh water, loafing sites, and roosting sites, are likewise poorly understood. Phalarope ecology has been studied at other areas such as Mono Lake, California (Jehl 1986, 1988) and Lake Abert, Oregon (Boula 1985), but most of the knowledge about phalaropes at GSL is anecdotal. Along with phalaropes, eared grebes are the most common migratory birds found in the open-water ecosystems of GSL. While the ecology of eared grebes at GSL has been more thoroughly studied than that of phalaropes, many questions remain. One important question regarding eared grebe use of GSL as a staging area is what triggers the departure of eared grebes in the fall. Eared grebes may depart from GSL due to changes in habitat quality such as the decline of invertebrate prey or the decrease of lake temperatures.

Understanding the resources used by migratory birds at GSL is crucial because anthropogenic activities in and around the lake have already reduced habitat and may
continue to threaten the suitability of the GSL ecosystem for use by birds. In 1959, a rock-fill causeway was constructed to replace a trestle-wood railroad causeway that provided passage across GSL for the Southern Pacific Railroad. The new causeway separated Gunnison Bay to the north from Gilbert Bay to the south and restricted water flow between the north and south “arms” of GSL. Due to the lack of freshwater inflow to the north arm, the salinity of Gunnison Bay increased (Gwynn 2002a). While brine shrimp, brine flies, and birds used the north arm of GSL prior to the construction of the rock-fill causeway, the salinity of Gunnison Bay eventually became too high for aquatic invertebrates to survive. In the absence of prey, most birds ceased to use Gunnison Bay as well. The construction of solar evaporation ponds for mineral extraction have been another cause of habitat loss at GSL, as these ponds cover over 300 km² of habitat (Gwynn 2002b). The high salinities of solar evaporation ponds, like the high salinity of Gunnison Bay, have precluded the use of these areas by aquatic invertebrates and therefore reduced the amount of habitat that is available to phalaropes and other wading birds. A third major anthropogenic impact on GSL habitat availability is water diversion. While GSL experiences natural interannual variations in water level, water diversions have significantly reduced the average lake level, and future planned diversions threaten to further reduce available habitat (Wurtsbaugh et al. 2016).

Another major commercial activity on GSL is the harvest of brine shrimp eggs (or “cysts”) during the fall and winter. Cyst harvest can affect avian use of GSL by decreasing the densities of invertebrate prey. Brine shrimp adults and cysts are the primary prey of eared grebes at GSL before their fall migration (Roberts and Conover 2013), and are also an important resource for wintering waterfowl at GSL (Vest and
To maintain sustainable harvest of cysts, previous research calculated the energy needs of eared grebes so that management regulations for cyst harvest could be determined (Conover and Caudell 2009). These regulations, as well as limitations that restrict areas of cyst harvest on GSL, minimize impacts of cyst harvest on eared grebes (Roberts and Conover 2013).

Great Salt Lake

Great Salt Lake is located in northern Utah, USA and is the largest terminal lake in the Western Hemisphere, covering approximately 4,400 km² at a historic average lake elevation of 1,280 m above sea level. When the surrounding habitats of GSL are included, the GSL ecosystem covers approximately 7,800 km² (Aldrich and Paul 2002). Great Salt Lake is shallow, with an average depth of less than 4 m. Most of the freshwater inflow to GSL is provided by three rivers: the Bear River, which flows into GSL from the northeast; the Weber River, which flow into GSL from the east; and the Jordan River, which enters GSL from the southeast (Fig. 1-1). Solar evaporation ponds for mineral extraction border GSL to the southwest, northwest, and northeast. The surface area of GSL varies considerably with changes in lake elevation (Fig. 1-2).

The uneven distribution of freshwater inflow to GSL, combined with manmade causeways that restrict water exchange within the lake and spatial variations in nutrient input, results in different physical characteristics among the bays of GSL. On average, GSL is much saltier than seawater, which has a salinity of about 3.5%. The north and south basins of GSL are separated by the Southern Pacific Railroad Causeway (SPRC), which crosses GSL from Promontory Point to the northern edge of the Lakeside
Mountains. Gunnison Bay, north of the SPRC, does not receive much freshwater input and therefore has salinities as high as 28%, which is saturation. Bear River Bay is also north of the SPRC, but receives fresh water from Bear River and is therefore the freshest bay of GSL. Farmington Bay is separated from the rest of GSL by the Antelope Island Causeway (AIC) and has the most drastic and variable salinity gradient of the bays. The water in Farmington Bay is freshest in the southeast near the Jordan River inflow, often as low as < 1%, and saltiest near the AIC, usually around 5%. However, depending on the inflow from Gilbert and Ogden Bays, Farmington Bay salinities may reach > 10% near the AIC. Farmington Bay also receives high levels of nutrient input and is hypereutrophic (Wurtsbaugh et al. 2012). The salinity of Ogden Bay is lower along its eastern shoreline than in the western extent of Ogden Bay, which adjoins Gilbert Bay. Gilbert and Carrington Bays have similar salinities, ranging from 14 to 16% during this study.

Another important difference among the bays of GSL is the types of substrate that are predominant in each bay. Mud and sand substrates are found in all bays of GSL, but the high-salinity bays of GSL – Carrington, Gilbert, and Ogden – also have bioherms, which are calcareous, reef-like structures in the shallow waters of these bays (Eardley 1938). Gunnison Bay previously supported bioherms, but the increased salinity in that bay now prevents their growth. Bioherms are an important part of the GSL ecosystem because they are the preferred substrate of brine fly (Ephydridae) larvae and pupae (Collins 1980). Although brine shrimp feed on phytoplankton rather than periphyton, they may also use areas of the lake with bioherms more than areas without bioherms (Roberts and Conover 2014).

Brine shrimp and brine flies are the only macroinvertebrates that can survive in
the high-salinity bays of GSL, but each of these are superabundant during the summer months. A 13-year study documented average June-to-August brine shrimp densities of 1.8 adult shrimp/L (Belovsky et al. 2011). Given a June-to-August lake elevation of 1,278.5 m (the average during my study), a similar density of brine shrimp adults equates to over 14.5 trillion brine shrimp across GSL, representing almost 7 billion g dry mass. Brine shrimp feed on phytoplankton and can reproduce through ovoviviparity or oviparity, depending on environmental conditions (Stephens and Birdsey 2002). Cysts produced during oviparous reproduction can survive through harsh conditions such as cold temperatures and desiccation. Brine fly densities at GSL are not well-documented as brine shrimp, but daily biomass of brine fly larvae in GSL has been estimated at >56 million g dry mass on average throughout the year, with the highest densities in September and October (Wurtsbaugh et al. 2011). Brine fly adults lay eggs that hatch into aquatic larvae. Brine fly larvae feed on periphyton and have clawed prolegs to grip onto the substrate (Herbst 1990). When brine flies pupate, they remain attached to the substrate with the use of their prolegs. Additional types of aquatic macroinvertebrates can be found in the low-salinity bays of GSL, although there is little documentation as to their densities and distributions. Three brackish-water aquatic macroinvertebrates that may be important to staging waterbirds are corixids (Corixidae), chironomid larvae (Chironomidae), and daphnia (*Daphnia magna*), which can be found in Farmington and Bear River Bays.

**LITERATURE REVIEW**

The availability of invertebrate prey underlies the main objectives of this research.
Of the invertebrates present in GSL, brine shrimp have been most thoroughly studied. The population of brine shrimp at GSL typically peaks in late May to early June (Belovsky et al. 2011). Brine shrimp graze down the phytoplankton in GSL as their population increases; cysts are produced more frequently than ovoviviparous eggs during July when brine shrimp are food-stressed (Wurtsbaugh and Gliwicz 2001). Cyst production also increases each fall, as primary production and lake temperatures decrease. Brine shrimp can tolerate a wide range of salinities, from water that is nearly fresh to a salinity of over 19% (Barnes and Wurtsbaugh 2015). At low salinities, brine shrimp populations are limited by predation. Corixids in Farmington and Bear River bays are formidable predators that exclude brine shrimp from these areas. Although brine shrimp can survive high salinities, their growth and reproduction are reduced (Barnes and Wurtsbaugh 2015). Brine shrimp raised in a salinity of 19% had an average length 30% less than those raised in a salinity of 3%, for a corresponding threefold reduction in mass. The optimum salinity for brine shrimp is affected by temperature and other variables, and therefore is not known (Stephens and Birdsey 2002).

Brine shrimp are an important food source for eared grebes. Brine shrimp provide a good energy source for eared grebes because their energy content is similar to other aquatic invertebrates and grebes can digest them efficiently (Caudell and Conover 2006a). Eared grebe diets on GSL may be comprised of up to 87% brine shrimp adults during the grebes’ staging period (Roberts and Conover 2013). As the density of adult brine shrimp decreases in December, eared grebes increase their consumption of cysts so that cysts comprise up to 44% of their diet. Consumption of cysts by eared grebes removes a considerable amount of cysts from GSL each year. In an analysis comparing
eared grebe cyst consumption with commercial cyst harvest, eared grebes accounted for 8–12% of total cyst removal (Roberts and Conover 2013). Unlike brine shrimp adults, cysts are not easily digested by grebes and may remain viable after passing through an eared grebe’s digestive system (Caudell and Conover 2006a).

An estimated nine species of brine flies can be found at GSL, the most common of which is *Ephydra gracilis* (J. Clark, Weber State University, personal communication). Adult brine flies lay eggs on the surface of GSL, which hatch after a few days (Collins 1980). Brine fly larvae prefer to spend time on bioherms rather than sand or mud substrate; densities of brine fly larvae on bioherms may be 17 times higher than on sand, and twice as dense on sand compared to mud (Wurtsbaugh 2009). Emergence rates of adult flies are also higher over bioherms (Collins 1980). The salinity tolerance of brine fly larvae exceeds that of brine shrimp, as the larvae can survive in salinities of at least 21% (Barnes and Wurtsbaugh 2015), and may possibly survive up to saturation (W. Wurtsbaugh, Utah State University, personal communication). Like brine shrimp, brine fly larvae are not typically found in the fresher bays of GSL, possibly due to predation.

No extensive studies have been done examining chironomid and corixid ecology in the brackish waters of GSL. One study that collected benthic macroinvertebrates from Farmington Bay on a single day in October documented spatial variation in densities of chironomids and corixids across a string of sampling stations oriented from south to north (Wurtsbaugh et al. 2015). Total density of benthic macroinvertebrates was highest in the southern portions of Farmington Bay, and chironomid larvae were the most common macroinvertebrate. Biomass of chironomid larvae was decreased as sampling moved north. Corixids were most commonly found at the northernmost site.
Eared grebes prey upon brine fly larvae to a lesser degree than on brine shrimp. Brine fly larvae comprise about 10% of the biomass of eared grebe diets during the grebes’ staging period, based on esophagus contents (Roberts and Conover 2013; note that the sample size was small and stomach contents of a larger sample of birds indicated that eared grebe consumption of brine fly larvae may be slightly higher). Brine fly larvae can survive cold winter water temperatures and are a valuable prey resource for ducks that winter on GSL. Over 70% of the dry mass of prey consumed by common goldeneye (Bucephala clangula) in early and mid-winter is comprised of brine fly larvae (Vest and Conover 2011). Small samples of phalaropes collected from GSL indicate that both species feed primarily on all stages of brine flies (Roberts 2013). A study on captive red-necked phalaropes from Mono Lake, California indicated that brine fly larvae are the preferred prey of red-necked phalaropes and that red-necked phalaropes cannot survive on a diet of brine shrimp (Rubega and Inouye 1994). Wilson’s phalaropes at Mono Lake, on the other hand, consume both brine shrimp and brine flies (Jehl 1988).

Population estimates of Wilson’s phalaropes at GSL have documented over 600,000 individuals at a time (Aldrich and Paul 2002), with an average of 126,000 birds daily from July to August (Paul and Manning 2002). However, the surveys by Paul and Manning (2002) did not include the open water areas of Carrington or Gilbert bay and therefore likely underestimated the number of phalaropes present at GSL at any given time. Wilson’s phalaropes in a five-year study were most common on the open waters of Ogden Bay, along the northern half of the eastern shore of Ogden Bay, and in two lakeside ponds southwest of Carrington Island (Paul and Manning 2002). The open waters of Farmington and Bear River bays, along with the Bear River Migratory Bird
Refuge (BRMBR), were also highly used by Wilson’s phalaropes. At Mono Lake, Wilson’s phalaropes forage while swimming or wading offshore, or forage on mudflats, and roost along the shoreline at midday (Jehl 1988). Specific habitat use of phalaropes at GSL has not been studied.

Red-necked phalaropes at GSL are less numerous than Wilson’s phalaropes at GSL. Red-necked phalaropes spend most of their time in open water habitats, including up to nine months of the year spent at sea (Rubega et al. 2000). Paul and Manning (2002) estimated over 22,000 red-necked phalaropes in the areas they surveyed. In a five-year survey, red-necked phalaropes were most common in Farmington Bay Waterfowl Management Area (WMA), along the northern half of the eastern shore of Ogden Bay, and in two lakeside ponds southwest of Carrington Island (Paul and Manning 2002). The open waters of Ogden and Farmington Bays, along with Ogden WMA, were also highly used by red-necked phalaropes. Although red-necked phalaropes are present at GSL through October (Aldrich and Paul 2002; J. Neill, Division of Wildlife Resources, personal communication), population estimates have not been conducted in late summer/early fall, so estimates of red-necked phalarope numbers at GSL are likely low.

Phalaropes engage in a suite of different foraging behaviors. Wilson’s phalaropes most commonly pick prey from at or below the surface of the water, but will also chase prey from shore or snatch prey from the air (Johns 1969, Jehl 1988). Both species of phalaropes engage in spinning behavior, in which the body is turned in a circle by kicking with the feet. Spinning creates a vortex that upwells water from depths up to 0.5 m (Obst et al. 1996). Phalaropes pick upwelled prey from the water during or after spinning (Johns 1969, Jehl 1986). Red-necked phalaropes often pick prey from at or below the
surface of the water as Wilson’s phalaropes do, but red-necked phalaropes nearly always forage while swimming (Mercier and Gaskin 1985, Jehl 1986). Red-necked phalaropes have occasionally been observed to tip forward like a dabbling duck to reach prey (Brown and Gaskin 1988).

While many aspects of eared grebe ecology at GSL have been studied, conditions related to the fall departure of eared grebes from GSL have been debated. One hypothesis is that eared grebe departure coincides with decreasing brine shrimp densities and is triggered by a threshold density of shrimp (Jehl 1988). Caudell and Conover (2006b) did not find a correlation between early departure and low brine shrimp densities at GSL, but stated that eared grebes responded to low shrimp densities by increasing their foraging time rather than departing earlier for migration. Jehl (2007) argued that the GSL data did indicate an earlier migration in years with lower shrimp densities.

Eared grebe migration departures, like the migration departures of many birds, occur nocturnally. Nocturnal migrations can be difficult to observe directly, but radar data can provide a way to indirectly visualize nocturnal migration events (Gauthreaux and Belser 1998, 2003). Radar data have many limitations for tracking migrating birds and must be interpreted carefully (Beason et al. 2013, Gurbuz et al. 2015), especially when used quantitatively (Schmaljohann et al. 2008). However, radar data can provide an important window into large-scale events that could not otherwise be measured (Chilson et al. 2012). Radar data are free, archived, and easily obtained from a network of weather radar stations in the U.S., Canada, and Europe (Gauthreaux and Belser 1998, Bridge et al. 2011, Gagnon et al. 2011).

Previous studies using data from weather radar systems have investigated a wide
range of questions, including determining the characteristics of migratory stopover locations (Bonter et al. 2009, Buler and Diehl 2009, Buler and Dawson 2014), documenting habitat use (Buler et al. 2012, Sieges et al. 2014), estimating migration flight altitudes (Dokter et al. 2011), mapping migration routes (Diehl et al. 2003), and understanding bird navigation (O’Neal et al. 2015). Radar data are also important for practical applications such as evaluating the collision risk of migrating birds with wind turbines (Hüppop et al. 2006) and mitigating bird collision with aircraft (Buurma 1995). For local studies and when a project has substantial funding, marine or X-band radar can provide more precise data about migration or even allow the tracking of daily movements (Cooper et al. 2001, Bridge et al. 2011). Portable radars can also be used to ground-truth migrations observed on national weather radar networks (O’Neal et al. 2010). Numerous studies have evaluated the effects of weather on migration events (Richardson 1990, Åkesson and Hedenström 2000, Liechti 2006), including studies that have monitored migration events with radar (Van Belle et al. 2007, Gagnon et al. 2011, La Sorte et al. 2015) and automated radio telemetry (Mitchell et al. 2015, Sjöberg et al. 2015). Studies that have investigated the effects of prey availability on migration have been less common (Schneider and Harrington 1981, Studds and Marra 2011).

**RESEARCH OBJECTIVES**

I outlined three research objectives to assess migratory waterbird use of invertebrate prey at GSL. 1) Determine which GSL habitats are primarily used by phalaropes and evaluate the factors associated with phalarope use of those habitats. 2) Investigate phalarope foraging behavior in relation to prey availability. 3) Examine the
factors related to the interannual and nightly variations in eared grebe departure from
GSL, and determine whether migration departure is triggered by decreasing prey
availability.

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FIG. 1-1. Great Salt Lake at an elevation of 1,278.6 m, with major bays and tributaries, and important surrounding features. Cross-hatched areas indicate solar evaporation ponds and areas with the wetlands stippling symbol indicate important diked wetland areas.
FIG. 1-2. Surface area of Great Salt Lake (GSL) at two different lake elevations. The light blue outline shows the area of GSL at its long-term average elevation, 1,280 m. The dark blue outline indicates the area of GSL when the lake elevation is 1,278.6 m. The average lake elevation during this study was 1,278.5 m.
CHAPTER 2
PHALAROPE ASSOCIATION WITH WATER DEPTH AND AQUATIC INVERTEBRATE DENSITIES AT A MAJOR STAGING AREA, GREAT SALT LAKE

ABSTRACT Great Salt Lake (GSL) is a large, hypersaline lake in northern Utah that hosts millions of migratory birds every year. One of the main features of GSL that draws migratory birds is high densities of food, such as brine shrimp (*Artemia franciscana*) and brine flies (Ephydridae). Wilson’s phalaropes (*Phalaropus tricolor*) and red-necked phalaropes (*Phalaropus lobatus*) are two of the species that stage at GSL for an extended time while feeding upon invertebrates and gaining enough mass to successfully migrate. Documentation of phalarope use of the open waters of GSL, particularly in the western portion of the lake, was mostly anecdotal prior to this study. In addition, little was known about the specific resources sought by phalaropes during their staging periods at GSL. Invertebrate densities, water depth, water salinity, and other features that may be key components of phalarope habitat vary considerably across GSL. I collected data from sites across GSL with and without phalaropes from 2013 to 2015 to determine locations where large, dense flocks of phalaropes congregated. At each site, I measured the densities of invertebrates that are preyed upon by phalaropes, including all stages of brine flies, chironomid larvae (Chironomidae), and corixid adults (Corixidae). Abiotic characteristics measured included water depth, water salinity, water temperature, wind speed, and benthic substrate. I evaluated the importance of prey densities and abiotic characteristics to phalarope presence using mixed-effect logistic regression models.
Large, dense flocks of phalaropes were most commonly found in 2 of the 4 southern GSL bays, Carrington and Farmington. Flocks in a third bay, Gilbert, were typically small or dispersed, while phalaropes were present in large numbers in Ogden Bay only during 2013. In the high-salinity bays of GSL, likelihood of phalarope presence was higher at shallow sites and at sites with higher densities of brine fly adults. None of the variables that I measured in the low-salinity bay were strongly related to phalarope presence, but small differences in the means of environmental variables between sites with and without phalaropes suggested that future studies should further examine differences in prey densities and salinity. My results indicate that physical features and prey availability are both important in determining phalarope habitat use at GSL. Management of phalarope habitat at GSL should therefore manage both invertebrates and physical habitat to provide suitable conditions at GSL for successful phalarope staging.

**INTRODUCTION**

Great Salt Lake (GSL) is an important staging area for migratory birds in the arid Great Basin region. The GSL ecosystem spans a diverse range of habitats, from fresh and brackish wetlands to hypersaline open-water bays. These habitats provide consistent food resources that draw a variety of birds to the ecosystem throughout the year. The high-salinity, open-water areas of GSL support large populations of brine shrimp (*Artemia franciscana*) and brine flies (Ephydridae), which are the only 2 macroinvertebrates that can survive in GSL’s high-salinity bays. Brine shrimp densities from June to August average 1.8 adult shrimp/L (Belovsky et al. 2011). At a lake elevation of 1,278.5 (the average elevation during the summers of this study), there may be over 14.5 trillion brine
shrimp lake-wide, totaling almost 7 billion g dry mass. Much less is known about brine flies compared to brine shrimp, but average daily biomass of brine fly larvae in GSL has been estimated at over 56 million g dry mass, with densities peaking in September or October (Wurtsbaugh et al. 2011). The southeastern bay of GSL, Farmington Bay, has lower average salinities than the rest of GSL and therefore supports additional types of aquatic macroinvertebrates that are suited for brackish-water habitats. Two macroinvertebrates in Farmington Bay that are important for foraging birds are chironomids (Chironomidae) and corixids (Corixidae). Chironomids are more common in the southern portion of Farmington Bay, while corixid densities are higher in the saltier waters of the northern portion of Farmington Bay (Wurtsbaugh et al. 2015).

The abundant resources at GSL support millions of migratory birds every year (Aldrich and Paul 2002). In addition to hosting numerous species of waterfowl and waterbirds, GSL has been designated by the Western Hemisphere Shorebird Reserve Network (WHSRN) as a site of hemispheric importance because the lake and its surrounding wetlands are a critical staging area for several species of shorebirds (Charadriiformes). The GSL ecosystem hosts over one-third of the world’s population of Wilson’s phalaropes (Phalaropus tricolor) each summer, which alone qualified the site for WHSRN status (Aldrich and Paul 2002). At the peak of the staging period, nearly 200,000 Wilson’s phalaropes may be present on GSL on one day (Paul and Manning 2002). Red-necked phalaropes (Phalaropus lobatus) also stage at GSL. Counts of red-necked phalaropes at GSL have not been conducted during the peak of their migration, but early-season counts estimate over 22,000 birds at a time (Paul and Manning 2002). Great Salt Lake also hosts globally important species such as snowy plovers (Charadrius
alexandrinus), American avocets (Recurvirostra americana), and marbled godwits (Limosa fedoa). From April to September each year, GSL supports an estimated 87 million waterbird bird-use days (Manning and Paul 2003).

Both species of phalaropes take advantage of the abundant prey at GSL before their long southerly migrations. Red-necked phalaropes winter in the Pacific Ocean off the coast of southern California and the Baja Peninsula of Mexico, while Wilson’s phalaropes have an even longer journey to saline lakes in Bolivia and Argentina (Colwell and Jehl 1994, Rubega et al. 2000). Great Salt Lake is an important staging location for these species that can tolerate high-salinity environments: not only is invertebrate prey abundant in the lake, but interspecific competition for this prey may be lower in the high-salinity bays because many of the migrating birds that use GSL prefer to forage in brackish areas. The ecology of brine shrimp at GSL has been well-studied, and long-term data are available regarding their abundance in the lake (Belovsky et al. 2011). Small studies of Wilson’s phalaropes at GSL indicate that they consume both brine flies and brine shrimp (Mahoney and Jehl 1985, Colwell and Jehl 1994). However, red-necked phalaropes prefer to eat brine flies and may not consume brine shrimp at all (Rubega and Inouye 1994). Information about brine fly ecology at GSL has been documented in only a few studies. Phalaropes also consume chironomid larvae and corixids in Farmington Bay (M. Frank, Utah State University, unpublished data), and hardly any literature exists on the ecology of these invertebrates.

Prey densities may not be the only factor affecting phalarope habitat use. Little is known about the particular resources sought by phalaropes at GSL and how abiotic factors may interact with prey densities, thereby affecting prey availability and phalarope
habitat use. Studies of other shorebirds (Scolopacidae) have indicated that the ability of shorebirds to access prey can be affected by sediment size or sediment resistance to shorebirds’ probing bills (Quammen 1982, Finn et al. 2008, VanDusen et al. 2012). Phalaropes do not typically probe in the sediment to catch prey, but substrate may still affect phalarope foraging by affecting densities of prey that area available in an area. For example, densities of brine fly larvae are an order of magnitude higher on bioherms – calcareous, reef-like structures in GSL – than on mud or sand substrates (Collins 1980). Water depth and water salinity are also important characteristics related to shorebird habitat use. Salinity can be closely related to the biomass and species richness of prey present in an area (Andrei et al. 2008), while water depth can partition shorebird use according to species’ ability to access different depths (Colwell and Oring 1988, Cole et al. 2002). Both species of phalaropes can swim while foraging, allowing them to access deeper water than other shorebirds can reach, and sometimes employ a unique spinning behavior to upwell prey from deeper water (Obst et al. 1996). Another consideration regarding habitat is scale. Even when prey densities explain a large proportion of variation in foraging shorebird densities, the perceived relationship between shorebirds and prey may vary depending on the scale at which the study was conducted (Colwell and Landrum 1993).

The first objective of my study was to document sites across GSL with large, dense flocks of phalaropes. I marked the GPS locations of phalarope flocks during bi-monthly aerial surveys and documented changes within and among years. The second objective was to determine which biotic and abiotic factors were most strongly correlated with the likelihood that large, dense flocks of phalaropes would be present at a particular
site. I predicted that phalaropes would occur more frequently in areas with high prey densities regardless of bay salinity, but that phalarope presence in relation to abiotic habitat characteristics would be different between high-salinity and low-salinity bays.

**STUDY AREA**

Great Salt Lake is a shallow, hypersaline lake. The surface area of GSL fluctuates considerably depending on the lake elevation; at GSL’s long-term mean lake elevation of 1,280 m the lake covers approximately 4,400 km² and has an average water depth of 4.9 m. The mean lake elevation during this study was 1,278.5 m, which corresponds with an approximate surface area of 2,700 km² (Baskin 2005, Wurtsbaugh et al. 2016). Water enters GSL via three main tributaries: the Bear, Weber, and Jordan rivers. The concentration of the rivers along the north and east sides of the lake, combined with manmade causeways that restrict water flow, results in a wide range of salinities across GSL. This study took place in the southern portion of GSL, which included Carrington, Gilbert, Ogden, and Farmington Bays. Of these areas, Carrington and Gilbert had the highest salinity (study average 15%, both bays). The salinities of Ogden (8–16%) were lower along the north and east sides of the bay (near freshwater inflow), and higher to the west. The lowest salinities in GSL occurred in Farmington (study range 0.2–12%). The bays of GSL also differed in average depth. Gilbert and Carrington were the deepest bays (up to 8 m during the study), while Ogden and Farmington were much shallower (study averages 0.4 and 0.3 m, respectively). Beginning in early July 2014 and continuing through the study, low lake levels precluded sampling in Ogden Bay, so sites in Ogden were only included in 2013 data.
METHODS

I located phalarope flocks during aerial surveys conducted approximately every other week from late June to early September for 3 years, 2013–2015. Each survey began between 07:00 and 07:30 and typically lasted 2–2.5 hr. Surveys were flown in a fixed-wing aircraft (Cessna 185) at ~150 km/hr and ~150 m above the lake surface (Pearse et al. 2008). I built each flight plan based on the selection of north-south transects running across GSL. Transects were divided into strata based on different areas of habitat (Fig. 2-1). I randomly chose transects from each stratum, but sampling effort was higher in strata that I knew a priori to be preferred by phalaropes (Paul and Manning 2002; J. Neill, Utah Division of Wildlife Resources, personal communication). I typically allotted ~25% of the flight time for transects along GSL shoreline; ~15% for stratum 7; ~12% for strata 1, 2, and 5; ~10% for stratum 4; and ~7% for strata 3 and 6. Additionally, I flew 1 random east-west transect in stratum 8 and 1 fixed north-south transect in Bear River Bay on each flight. The number and length of transects varied (25 transects on average; minimum length = 2.4 km, maximum length = 16.5 km), but at least 1 transect was flown in each stratum on each survey. The total length surveyed was ~120 km for each flight.

I recorded the GPS coordinates of sites with phalarope flocks and sites without any phalaropes (“phalarope” and “non-phalarope” sites, respectively). For logistic purposes, I chose 2 sets of sites, “east” and “west,” according to accessibility by boat: east sites were located in Farmington or Ogden Bays and were accessible by airboat, while west sites were located in water >1 m deep in Carrington or Gilbert Bays and required the use of a larger boat to access. During each biweekly aerial survey, I chose at least 2 phalarope sites and an equal number of non-phalarope sites in each of the 2 lake
sections (east and west). In 2013, I chose 3 phalarope sites and 1 non-phalarope site in each section of the lake, and therefore modeled these data separately.

The size and density of phalarope flocks varied. The smallest groups of phalaropes that I observed had <10 phalaropes, while the largest flocks I observed had >30,000 phalaropes. I recorded locations with >10 phalaropes for the purpose of observing inter- and intra-annual variations in flock locations, but only included flocks with >500 phalaropes in my model analyses. Phalarope flocks also varied in how close together phalaropes within a flock were located. I only recorded the locations of dense flocks, where phalaropes were sitting on the water within <1 m of each other as the plane approached (flocks typically flushed as the plane flew over). I therefore excluded “disperse flocks” where thousands of phalaropes were present but were spread over a large area. On each survey, I chose the largest dense flocks that I saw as phalarope sites.

Non-phalarope sites had no phalaropes. I chose non-phalarope sites ≥1 km from the nearest flock of phalaropes, in habitat that was as similar as possible to the phalarope sites based on my knowledge of water depth in a given area.

The goal of using transects to construct flight plans was not to estimate lake-wide population size but rather to ensure that the lake was thoroughly and randomly surveyed, so if I observed a large, dense flock of phalaropes in between transects, that location could be chosen as a phalarope site. Species could not be identified from the plane and flocks were frequently mixed when both species were present, so I did not examine differences between species.
Biotic and Abiotic Measurements

After I identified phalarope and non-phalarope sites, 2 boat teams measured prey densities and environmental variables at those sites. The time difference between when I marked the locations and when the habitat variables were measured averaged ~3 hours. Upon arrival in the boat, the presence or absence of phalaropes was noted. At sites where the status had changed (i.e., a phalarope site that did not have phalaropes or a non-phalarope site that did have phalaropes), prey and physical variables were measured, but I excluded those sites from analysis. At each site, I collected 2 invertebrate prey samples. For sites <0.3 m deep, I used a stovepipe sampler to measure invertebrates that would be accessible to phalaropes (invertebrates in the water column and in the top 0.02 m of soft substrate). Stovepipe samplers consisted of a 19-liter plastic bucket with the bottom removed; the bucket had a top diameter of 29 cm and a bottom diameter of 24.6 cm. Stovepipe sampling followed the procedures of DiFranco (2006), with agitation of the top 0.02 m of sediment and filtration of water through a 500-μm sieve. For sites ≥0.5 m deep, I sampled invertebrates in the water column using a vertical tow net with a diameter of 50 cm and mesh size 153 μm (Research Nets Inc., Bothell, WA). For sites deeper than 0.5 m, I only sampled to a depth of 0.5 m, which is the estimated maximum depth from which spinning phalaropes can upwell prey (Obst et al. 1996). Invertebrate samples from the water column were placed on ice for transport and then preserved in ethanol.

I used floating sticky traps to determine the relative abundance of adult brine flies at each location in 2014 and 2015. Floating sticky traps consisted of a length of commercial fly paper (Black Flag®, Chemsico, St. Louis, MO) attached to a blue foam board with an area of ~722 cm² (Sharkfin® Kiefer, Zion, IL). The fly paper was 4 cm
wide and was cut to a length of approximately 6 cm. Adult brine flies are attracted to any surface on which they can land, so to standardize sampling at each site, I tethered the kickboards with rope and floated the traps 5 m away from the anchored boat. The fly paper was exposed for 10 minutes (Boula 1985), then covered with wax paper to prevent additional captures. All adult flies were placed on ice for transport and euthanized by freezing. In 2013, I attempted to measure density of brine fly adults using photographs of the water surface (because brine fly adults sit on the surface of the water), but this was not successful so data on densities of brine fly adults were not available for this year.

In the laboratory, aquatic invertebrates were sorted by type and counted. Invertebrate types included brine fly larva, brine fly pupa, brine shrimp adult, chironomid larva (Chironomidae), and corixid adult (Corixidae). All other invertebrates were classified as “other.” Each aquatic invertebrate from 2013 and 2014 was digitally photographed and the length of the invertebrate was measured using ImageJ (Rasband 1997). From these data I calculated average lengths of each invertebrate type for the bays in which it was found, and for each month of the study. I used these average values to estimate the lengths of the 2015 samples, which were counted but not photographed. I converted the lengths of invertebrates to dry mass using published length-weight regression equations. Species-specific equations were only available for brine shrimp and for brine fly larvae (Wurtsbaugh 1992, Wurtsbaugh et al. 2011). For the other types of invertebrates, I used the most taxonomically-similar equations available (Wurtsbaugh 1992, Benke et al. 1999, Sabo et al. 2002). Biomass estimates for each site were calculated based on the area sampled (mg/m²). I averaged the biomass of each invertebrate type from the 2 samples collected at each site to create the biomass variables.
From the high-salinity bay data, I summed the biomasses of brine fly larvae and pupae to create a single variable. From the low-salinity bay data, I summed the biomasses of chironomid larvae and corixids to create a “benthic macroinvertebrates” variable. Corixids move throughout the water column but spend much of their time on the surface of the benthos, hence their classification with chironomid larvae as benthic macroinvertebrates.

To estimate the densities of adult brine flies, I counted the adult brine flies captured on each sticky paper. For each site, I averaged the number of adult flies from the 2 samples and converted this estimate to number of adult brine flies/m² based on the area of the fly paper. Because fly paper lengths varied, I measured the length of each to calculate the sample area for each site. Dry biomass estimates for adult brine flies followed the same procedure as for aquatic invertebrates, and I used a length-weight regression equation for Diptera of the suborder Brachycera (Sabo et al. 2002). The method used to capture adult brine flies did not yield a true biomass estimate, as the floating sticky traps accumulated flies over time. I therefore referred to abundance of adult brine flies as “accumulation,” which was expressed as mass per area per time, mg/m²/10min.

I measured local environmental conditions that may have directly or indirectly affected the presence of phalaropes and/or prey biomass at each site. These included water temperature (°C), wind speed (m/s), water depth (m), water salinity (%), and benthic substrate. Water temperature was measured at approximately 3 cm below the surface of the water at east sites, and 20 cm below the surface of the water at west sites (due to differences in sampling equipment). Salinity was measured from the top 3 cm of
the water at all sites using a refractometer. Wind speed was measured from ~2 m above the surface of the water at east sites and ~3 m above the surface of the water at west sites, using a weather meter (Kestrel 3000 Wind Meter ® Nielsen-Kellerman, Boothwyn, PA).

Statistical Analysis

I used an information-theoretic approach in analyzing models containing parameterizations of the data described above (Burnham and Anderson 2002). My study was a retrospective case-control study in which I focused on evaluating the importance of the explanatory variables rather than on predicting the probability that phalaropes would occur at a site. All statistical analyses were conducted in R (R Core Team 2016). I coded the presence or absence of phalaropes at each site as a binary variable, with 0 representing the absence of phalaropes from the site and 1 representing the presence of a large, dense flock of phalaropes at the site. Before beginning analysis, I examined the distribution of the data across months, years, and substrates to ensure that a similar number of phalarope and non-phalarope sites had been chosen in each category (Table 2-1). All continuous variables were z-standardized before analysis so that coefficient estimates would be comparable.

Invertebrate species differed across bays of GSL according to salinity, so I split the data into 2 datasets: 1 for the high-salinity bays and 1 for the low-salinity bay. Due to differences in sampling methodology of brine fly adults, I only analyzed high-salinity bay data from 2014 and 2015. In the low-salinity bay, the number of phalarope sites relative to non-phalarope sites was different between 2013 and 2014–2015. I therefore analyzed the low-salinity bay data 2 ways: using data from 2013–2015, and using just data from

I evaluated habitat characteristics related to the likelihood of phalarope presence at a site using generalized linear models. My data were overdispersed, so I included a random term for sample occasion in all models. I tested an a priori set of models for each dataset, based on the variables that were relevant to that area of GSL (Table 2-2). Variables included in the models were prey variables, abiotic variables, and combinations of prey and abiotic variables. In the low-salinity bay, 2 different methods were used to sample aquatic invertebrate densities, depending on depth; I compared aquatic invertebrate densities between these methods with a Welch’s t-test to examine whether I could combine the data. Models were built using glmer in package lme4 (Bates et al. 2016), and compared using Akaike’s Information Criterion (AICc) in package MuMIn (Bartoń 2015). I created plots to present data visually using the packages Rmisc (Hope 2013) and ggplot2 (Wickham and Chang 2016). Where appropriate throughout the results, means are given with standard errors.

RESULTS

Of all the sites documented in the study (n = 135), I only considered those that did not change status from the time I marked the location to the time at which prey and physical samples were taken (n = 107; 63 phalarope sites and 44 non-phalarope sites). There were uneven numbers of phalarope sites versus non-phalarope sites, due to choosing an uneven number of sites in 2013, sites changing status, and habitat reduction in Farmington Bay. Habitat availability in Farmington Bay decreased over the 3 years of the study as the lake elevation decreased. As a result, phalarope flocks were found closer
together, so I was occasionally unable to define an equal number of non-phalarope sites in similar habitat that were >1 km from phalarope sites.

Out of all the sites I marked as phalarope sites, 83% were located in either Carrington Bay or Farmington Bay. However, phalaropes occurred in different locations throughout the staging period (Fig. 2-2). From the beginning of the staging period until about mid-July, large flocks were common in Carrington Bay, especially just north of Hat Island. As the season progressed, large flocks became increasingly common in Farmington Bay. By mid-August, the largest phalarope flocks were nearly always found in Farmington Bay. On weeks when aerial surveys were not flown, I observed Carrington and Gilbert Bays from a boat, and did not find large, dense flocks of phalaropes there after late August. In 2013, phalaropes used Ogden Bay during the early portion of the staging period.

**High-salinity Bays (Carrington and Gilbert)**

The final list of sites for modeling phalarope presence in the high-salinity bays included 13 phalarope sites and 21 non-phalarope sites. Phalarope presence did not differ by month ($\chi^2_1 = 0.06, P = 0.81$) or year ($\chi^2_1 = 0.50, P = 0.48$) in the high-salinity bays, so I did not include these time variables in the models. The top model indicated that phalaropes were more likely to be present at relatively shallow sites ($\beta_{\text{depth}} = -0.68 \pm 0.38, P = 0.07$), and this model performed better than a null model ($\chi^2_1 = 3.43, P = 0.06$). The average depth at phalarope sites was 3.8 ± 0.8 m, while the average depth at non-phalarope sites was 5.6 ± 0.6 m (Fig. 2-3). The second-ranked model was competitive ($\Delta\text{AIC}_c < 2$) with the top model and indicated that large, dense flocks of phalaropes were
more likely to be present at sites with higher accumulations of brine fly adults ($\beta_{BFA} = 0.71 \pm 0.57, P = 0.20$; Table 2-3). The average accumulation of brine fly adults was $1023 \pm 444 \text{ mg/m}^2/10 \text{ min}$ at phalarope sites and $376 \pm 148 \text{ mg/m}^2/10 \text{ min}$ at non-phalarope sites (Fig. 2-3). For a full set of comparisons between phalarope and non-phalarope sites for all continuous variables in the high-salinity bays, see Table A-1.

**Low-salinity Bay**

There were 20 phalarope sites and 12 non-phalarope sites in Farmington Bay. I did not include accumulation of brine fly adults as a predictor variable in the models for Farmington Bay because brine fly adults occurred in Farmington Bay only rarely, resulting in data that were highly zero-skewed. The mean accumulation of brine fly adults in the high-salinity bays was $554 \text{ mg/m}^2/10 \text{ min}$, while the mean accumulation of brine fly adults in the Farmington Bay was just $162 \text{ mg/m}^2/10 \text{ min}$. For a full set of comparisons between phalarope and non-phalarope sites for all continuous variables in the low-salinity bay, see Table A-2.

Models built with 2013–2015 data had similar results to the models built with 2014–2015 data. Results for 2014–2015 are given here and corresponding results can be found in Table A-3. Phalarope presence did not differ by month ($\chi^2_1 = 1.31, P = 0.25$) or year ($\chi^2_1 = 0.02, P = 0.90$) in the low-salinity bay, so I did not include time variables in the models. Biomass of benthic macroinvertebrates did differ by sampling type ($t_{24} = 5.55, P < 0.001$); I therefore only analyzed data from sites where a stovepipe sampler was used, which included 15 phalarope sites and 8 non-phalarope sites. The top 3 models of phalarope presence in Farmington Bay were very closely ranked (Table 2-4). Large,
dense flocks of phalaropes were weakly related to sites with low salinity ($\beta_{\text{salinity}} = -0.59 \pm 0.63, P = 0.35$), high biomass of benthic macroinvertebrates ($\beta_{\text{BnIn}} = 0.50 \pm 0.52, P = 0.33$), and shallow water ($\beta_{\text{depth}} = -0.45 \pm 0.49, P = 0.36$). However, there was not a significant difference in the means of these variables between phalarope and non-phalarope sites (Fig. 2-4), and the top-ranked model did not perform better than a null model ($\chi^2 = 1.46, P = 0.23$).

**DISCUSSION**

**Limitations of this Study**

Several logistic constraints on the methods of this study should be noted, as they limit conclusions that can be drawn from the results. One important limitation was the depth of water that could be accessed by the large boat used in the deeper bays. Large flocks of phalaropes in Carrington Bay, for instance, often spanned from the shoreline into deeper water. I marked the center of each flock as the sampling location during the aerial surveys, but in some instances the exact coordinates were too shallow to reach and the deeper edge of the flock was sampled. Whenever possible, a canoe was taken along with the big boat to allow sampling at the exact coordinates. Whether or not sampling was conducted at the center of the flock, my analyses assumed that the conditions I measured were homogenous throughout the area covered by the flock. This assumption is probably true for wind, water temperature, salinity, substrate, and densities of aquatic invertebrates, but may not have been true for density of brine fly adults and certainly was not true for water depth. However, the depth measured at the center of the flock should
have been approximately equal to the average depth experienced by the whole flock.

I focused my selection of phalarope sites on large, dense flocks to compare with non-phalarope sites that were completely absent of phalaropes. Sampling from the area of large, dense flocks minimized the variation of prey and environmental variables within a site, but did not provide information on small flocks or disperse flocks. This study should not therefore be considered a thorough documentation of all locations at GSL used by phalaropes, but rather of the sites and characteristics that support large, dense flocks.

To ensure timely measurement of prey and environmental variables, I flew aerial surveys early each morning, so that boat sampling could begin by mid-morning and finish by early afternoon. All of the phalarope locations documented, then, are locations used by phalaropes during the first part of the day. However, personal observations suggest that phalaropes use similar locations throughout the day. Little is known about where phalaropes may roost in the evenings, although I have often observed them flying from west to east in the late afternoon, presumably to roost in fresher waters east of GSL.

**Phalarope Locations**

This study documented inter- and intra-annual changes in phalarope use of GSL. Ogden Bay was used by phalaropes in 2013 and the first week or two of the staging period in 2014, but phalaropes were not observed in Ogden Bay after mid-July 2014. Two of the locations that had flocks of phalaropes in 2013 lacked water in 2014 (Fig. 2-2); all 4 locations were dry in 2015. Falling lake levels also led to changes in flock locations in Farmington Bay. As the swath of water in Farmington Bay narrowed from the beginning to the end of the study, phalarope flocks followed the water, so that all the
flocks observed in 2015 occurred in a narrow strip corresponding to the remaining water. Intra-annual changes were consistent from year to year, with phalaropes using Carrington Bay more frequently at the beginning of the staging period, and then shifting use to primarily Farmington Bay later in the staging period.

This study provided a comparison with the data collected for a five-year survey of waterbirds at GSL (Paul and Manning 2002). Paul and Manning (2002) documented Ogden Bay as an important location for large numbers of both Wilson’s and red-necked phalaropes, supporting my suggestion that the absence of phalaropes from Ogden Bay during 2014 and 2015 was unusual. Another site where both species were documented in very high numbers during the five-year survey was a strip of water southwest of Carrington Island that bordered solar evaporation ponds. I never observed phalaropes at that site because it was dry during my entire study. Even though my study focused on the southern bays of GSL (bays south of the South Pacific Railroad Causeway), I flew 1 transect through Bear River Bay during each survey (Fig. A-1). I chose to monitor Bear River Bay for phalarope use based on the importance of the bay to Wilson’s phalaropes documented in the five-year study; Bear River Bay was mostly or totally dry throughout my study and I did not observe any phalaropes there. Additionally, I flew 1 transect across Gunnison Bay during each survey, even though previous studies had not document phalaropes in that bay. I did not observe any phalaropes in Gunnison Bay during my study.

Models

There was not a convincing “best model” for either dataset, in part due to the
small sample size that resulted after removing from analysis sites that had changed status and flocks that were too small. However, some patterns across the models suggest characteristics that are likely to be important components of phalarope habitat. Depth was the top predictor of phalarope likelihood for the high-salinity bays and was among the competitive models for the low-salinity bay. The mean depth of phalarope sites in the high-salinity bays (3.8 m) was deep relative to the mean depth of sites in the low-salinity bay, but may still indicate a trend toward selection of shallower sites. One reason phalaropes may choose shallower sites is that prey may be more readily available at shallow sites. For instance, brine fly larvae and pupae typically remain attached to bioherms and therefore out-of-reach of phalaropes in deeper areas. Although brine fly adults were present in open-water areas, their densities were highest along shorelines. My sampling methods did not adequately represent the shallowest areas of the high-salinity bays and therefore more precise associations between phalarope habitat use and depth cannot be deduced from my data. Previous studies have noted that Wilson’s phalaropes prefer shallow areas (Jehl 1988, Lesterhuis and Clay 2010), so shallow areas at GSL may therefore be especially important for Wilson’s phalaropes. I did not attempt to split flocks by species, so whether the association with shallow depths holds for both species at GSL is unknown. Red-necked phalaropes are often found in deeper, pelagic habitats (Mercier and Gaskin 1985).

In the low-salinity bay, the best model of phalarope presence contained only a term for water salinity, and this slightly outranked the model for water depth. Farmington Bay is relatively shallow throughout in comparison to Carrington and Gilbert Bays, so the depths preferred by phalaropes may be available in greater abundance relative to the total
habitat and low salinities may have a greater impact on drawing phalaropes to a particular site. The salinities measured in Farmington Bay during the study ranged from 0.2–12%. Because phalaropes can tolerate salinities much higher than those of Farmington Bay, the negative relationship between salinity and likelihood of phalarope presence is probably not due to a direct response of phalaropes to salinity. Rather, the relationship may be due to the variation in types and densities of brackish-water invertebrates throughout the bay (Wurtsbaugh et al. 2015). However, the proximity of Farmington Bay to fresh water for drinking and bathing may also be important to phalaropes, and phalaropes may seek lower-salinity areas for reasons other than prey availability.

Prey density variables were important in both model sets, even though the types of prey differed between high- and low-salinity bays. In the high-salinity bays, the best model of phalarope presence included accumulation of brine fly adults, which are important prey for both species of phalaropes at GSL (M. Frank, unpublished data). Aquatic invertebrate prey in the high-salinity bays also included brine fly larvae and pupae. Phalaropes may seek both flying and aquatic prey in the high-salinity bays, but these two types of prey do not necessarily overlap. High densities of brine fly larvae and pupae were not correlated with high accumulations of brine fly adults ($r = 0.07, P = 0.69$). The association between phalarope presence and prey was weak in the low-salinity bay. Phalaropes using the low-salinity bay may select sites based primarily on non-prey characteristics; for instance, if densities of prey are high throughout Farmington Bay, phalaropes may select for other resources such as distance to fresh water.
Conclusions and Future Research

Phalaropes staging at GSL use a range of habitat types. This study documented the importance of phalarope use of Farmington Bay, which contains a substantial amount of shallow-water habitat. Additionally, although the sampling of this study focused on deeper habitat in Carrington and Gilbert Bays, many large flocks of phalaropes were observed in shallow areas of these high-salinity bays. Shallow habitats at GSL have already been lost due to the construction of causeways that restrict water flow throughout the lake, evaporation ponds built for mineral extraction, and low lake elevations caused by recent droughts and water diversion. In 1959, shallow habitats in GSL began to decrease dramatically after the construction of a semi-porous railroad causeway that separated the north and south arms of GSL, causing the salinity of the north arm to increase above the tolerance level of aquatic invertebrates (White et al. 2015). Mineral extraction ponds, which are likewise too salty for use by aquatic invertebrates and birds, have taken an additional 800 km² of habitat (Roberts 2013). Low lake elevations due to recent persistent drought and anthropogenic water diversions have caused further habitat loss. Maintaining an adequate amount of shallow-water habitats for phalaropes at GSL should be a goal of management. Phalaropes were also associated with high densities of brine fly larvae, brine fly pupae, chironomid larvae, and corixids, and adequate densities of these invertebrates should be maintained. Little is known about the ecology of non-brine shrimp aquatic invertebrates in GSL, so further study is needed to properly manage this resource.

The importance of water depth and salinity should both be considered across GSL. Although the salinities in Carrington and Gilbert Bays are currently suitable for
brine shrimp and brine flies, salinity has increased over the past few years with the
decrease in lake elevation. The effects of increased salinity can be seen in Gunnison Bay,
where the construction of the railroad causeway led to increased salinity beyond the
tolerance levels of brine shrimp and brine flies, and bird use of the bay ceased. Even
though brine shrimp and brine flies can tolerate salinities even higher than current lake
measurements, their size and population growth decrease with increasing salinity (Barnes
and Wurtsbaugh 2015). Maintaining adequate water in GSL not only directly provides
phalarope habitat, but also keeps water salinity within a range that can support robust
populations of prey. Future studies regarding the salinity tolerances of brackish-water
prey such as chironomid larvae and corixids would be helpful in managing the low-
salinity bays of GSL.

The results of this study do not fully explain phalarope use of particular areas. For
example, while most of the dense phalarope flocks ≥10,000 birds were found in shallow
areas, three very large, dense flocks were located in areas with water ≥8 m deep, even
though the prey biomass at these sites was low. One explanation for large numbers of
phalaropes in deeper areas of GSL is that the flocks are using these areas for non-
foraging activity. Phalaropes in deep areas of Carrington and Gilbert frequently preen,
loaf, or rest (Ch. 3). While GSL’s prey resources are critical for migratory birds, these
birds may also seek areas of the lake that are farther from predators or provide other non-
prey resources. Behavior studies of individual birds within a flock could provide clearer
answers to questions about areas of phalarope use relative to resource availability.
MANAGEMENT IMPLICATIONS

The shallow nature of GSL means that habitat is lost rapidly with decreases in elevation; a decrease in GSL elevation from 1280 m to 1279 m corresponds with a 243 km$^2$ decrease in lake surface area, or a 12% loss of surface area (Baskin 2005). Combined with other causes of habitat loss that have already occurred at GSL, drought and anthropogenic use of inflowing freshwater will continue to pose a threat to GSL habitat that are critical for migratory birds. The remaining shallow-water habitat at GSL needs to be maintained to support phalarope use. I frequently observed large numbers of other wading birds in the vicinity of phalarope sites, so managing shallow habitats at GSL will likely also benefit many other wading birds. Maintaining a variety of water depths in all the bays of GSL will allow a greater number of birds to use those areas. In addition to habitat loss, a decrease in shallow habitat increases crowding and disease transmission in birds, making maintenance of adequate habitat at GSL even more critical. Managers should seek to maximize the water that reaches GSL in periods of drought and ensure that additional water is not diverted from the lake.

LITERATURE CITED


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Table 2-1. Percentage of sites observed on a whole-lake scale that were phalarope sites for each of the categorical variables of the study, and the $P$-value from a Fisher’s exact test of each group.

<table>
<thead>
<tr>
<th>Factor</th>
<th>n</th>
<th>Phalarope sites</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>All sites</td>
<td>92</td>
<td>54%</td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td></td>
<td></td>
<td>0.53</td>
</tr>
<tr>
<td>June</td>
<td>14</td>
<td>36%</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>27</td>
<td>56%</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>34</td>
<td>59%</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>17</td>
<td>59%</td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td></td>
<td></td>
<td>0.40</td>
</tr>
<tr>
<td>2013</td>
<td>26</td>
<td>65%</td>
<td></td>
</tr>
<tr>
<td>2014</td>
<td>28</td>
<td>46%</td>
<td></td>
</tr>
<tr>
<td>2015</td>
<td>38</td>
<td>53%</td>
<td></td>
</tr>
<tr>
<td>Bay</td>
<td></td>
<td></td>
<td>0.14</td>
</tr>
<tr>
<td>Carrington</td>
<td>31</td>
<td>52%</td>
<td></td>
</tr>
<tr>
<td>Gilbert</td>
<td>13</td>
<td>31%</td>
<td></td>
</tr>
<tr>
<td>Ogden</td>
<td>5</td>
<td>40%</td>
<td></td>
</tr>
<tr>
<td>Farmington</td>
<td>43</td>
<td>65%</td>
<td></td>
</tr>
<tr>
<td>Substrate</td>
<td></td>
<td></td>
<td>0.44</td>
</tr>
<tr>
<td>Bioherm</td>
<td>11</td>
<td>64%</td>
<td></td>
</tr>
<tr>
<td>Sand</td>
<td>30</td>
<td>63%</td>
<td></td>
</tr>
<tr>
<td>Mud/sand</td>
<td>7</td>
<td>57%</td>
<td></td>
</tr>
<tr>
<td>Mud</td>
<td>44</td>
<td>45%</td>
<td></td>
</tr>
</tbody>
</table>
Table 2-2. Variables that were measured from boats at phalarope and no-phalarope sites.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Units</th>
<th>Measured&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Modeled&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Prey</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BFL/P</td>
<td>Sum of the dry biomasses of the aquatic life stages of brine flies (larvae and nunae) captured in a water column sample</td>
<td>mg/m(^2)</td>
<td>All</td>
<td>All</td>
</tr>
<tr>
<td>BFA</td>
<td>Dry biomass of brine fly adults accumulated on a sticky trap over a 10-min period of time</td>
<td>mg/m(^2/10) min</td>
<td>All</td>
<td>High</td>
</tr>
<tr>
<td>BnInv</td>
<td>Sum of the dry biomasses of chironomid larvae and corixids captured in a water column sample</td>
<td>mg/m(^2)</td>
<td>Low</td>
<td>Low</td>
</tr>
<tr>
<td><strong>Physical</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subs</td>
<td>Primary composition of benthic substrate: bioherm, mud, mud/sand, or sand</td>
<td>Categorical</td>
<td>All</td>
<td>All</td>
</tr>
<tr>
<td>Depth</td>
<td>Distance from surface of water to benthic surface</td>
<td>m</td>
<td>All</td>
<td>All</td>
</tr>
<tr>
<td>Salinity</td>
<td>Percentage of all salts dissolved in water, as measured by refractometer from ~3 cm below the surface of the water</td>
<td>%</td>
<td>All</td>
<td>Low</td>
</tr>
<tr>
<td>Water</td>
<td>Temperature of water, measured ~3 cm below the surface of the water in Farmington Bay, and ~20 cm elsewhere</td>
<td>°C</td>
<td>All</td>
<td>Low</td>
</tr>
<tr>
<td>Wind</td>
<td>Speed of wind, measured ~2 m above the surface of the water in Farmington Bay, and ~3 m elsewhere</td>
<td>m/s</td>
<td>All</td>
<td>High</td>
</tr>
<tr>
<td><strong>Time</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>Calendar month of the survey</td>
<td></td>
<td>All</td>
<td>All</td>
</tr>
<tr>
<td>Year</td>
<td>Calendar year of the survey</td>
<td></td>
<td>All</td>
<td>All</td>
</tr>
</tbody>
</table>

<sup>a</sup>All = All bays, High = high-salinity bays (Carrington and Gilbert), Low = low-salinity bay (Farmington)
Table 2-3. Mixed-effect logistic regression models of phalarope presence in the high-salinity bays of Great Salt Lake over 2 years, 2014–2015. Total number of phalarope and non-phalarope sites was 34. Variables included water depth (Depth; m), accumulation of brine fly adults (BFA; mg/m²/10 min), biomass of brine fly larvae and pupae (BFL/P; mg/m²), and wind speed (Wind; m/s). All models included a random term for sampling occasion. The sign noted in parentheses before each variable indicates whether the coefficient was positive or negative for that parameter. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights (weight) to determine which variable(s) were most related to the likelihood of phalarope presence at a site.

<table>
<thead>
<tr>
<th>Model parameters</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>Δ AICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>(-) Depth</td>
<td>4</td>
<td>-20.9</td>
<td>48.6</td>
<td>0.00</td>
<td>0.338</td>
</tr>
<tr>
<td>(+) BFA</td>
<td>4</td>
<td>-21.2</td>
<td>49.2</td>
<td>0.63</td>
<td>0.247</td>
</tr>
<tr>
<td>(+) BFL/P</td>
<td>4</td>
<td>-21.9</td>
<td>50.6</td>
<td>2.00</td>
<td>0.124</td>
</tr>
<tr>
<td>(+) BFL/P (+) BFA</td>
<td>5</td>
<td>-20.6</td>
<td>50.7</td>
<td>2.06</td>
<td>0.121</td>
</tr>
<tr>
<td>(+) BFA (-) Wind</td>
<td>5</td>
<td>-21.1</td>
<td>51.5</td>
<td>2.92</td>
<td>0.078</td>
</tr>
<tr>
<td>(-) Wind</td>
<td>4</td>
<td>-22.5</td>
<td>51.8</td>
<td>3.18</td>
<td>0.069</td>
</tr>
<tr>
<td>(+) BFA (-) Wind (+) BFA*Wind</td>
<td>6</td>
<td>-21.0</td>
<td>54.0</td>
<td>5.43</td>
<td>0.022</td>
</tr>
</tbody>
</table>
Table 2-4. Mixed-effect logistic regression models of phalarope presence in a low-salinity bay of Great Salt Lake over 2 years, 2014–2015. All sites were sampled using a stovepipe sampler (n = 23). Variables included: water salinity (Salinity; %), biomass of benthic macroinvertebrates (BnInv; mg/m²), water depth (Depth; m), and water temperature (Water; °C). All models included a random term for sampling occasion. The sign noted in parentheses before each variable indicates whether the coefficient was positive or negative for that parameter. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights (weight) to determine which variable(s) were most related to the likelihood of phalarope presence at a site.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>Δ AICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>(-) Salinity</td>
<td>4</td>
<td>-14.1</td>
<td>35.5</td>
<td>0.00</td>
<td>0.275</td>
</tr>
<tr>
<td>(+) BnInv</td>
<td>4</td>
<td>-14.3</td>
<td>35.8</td>
<td>0.30</td>
<td>0.237</td>
</tr>
<tr>
<td>(-) Depth</td>
<td>4</td>
<td>-14.4</td>
<td>36.0</td>
<td>0.47</td>
<td>0.217</td>
</tr>
<tr>
<td>(+) BnInv (-) Depth</td>
<td>5</td>
<td>-13.7</td>
<td>37.7</td>
<td>2.18</td>
<td>0.092</td>
</tr>
<tr>
<td>(+) BnInv (-) Salinity</td>
<td>5</td>
<td>-13.9</td>
<td>38.0</td>
<td>2.45</td>
<td>0.081</td>
</tr>
<tr>
<td>(+) BnInv (-) Water</td>
<td>5</td>
<td>-13.9</td>
<td>38.0</td>
<td>2.45</td>
<td>0.081</td>
</tr>
<tr>
<td>(+) BnInv (+) Depth (+) BnInv*Depth</td>
<td>6</td>
<td>-13.7</td>
<td>41.0</td>
<td>5.45</td>
<td>0.018</td>
</tr>
</tbody>
</table>
Figure 2-1. Map of Great Salt Lake showing strata and example transects for an aerial survey of phalarope presence during the staging period, 2013–2015. Light blue fill indicates average lake level during the study (1,278.6 m), while the dashed dark blue line indicates the sampling strata, which was based on a lake elevation of 1,280 m. Strata 1 and 2 covered Carrington Bay; strata 3, 4, and 6 covered Gilbert Bay; stratum 5 covered Ogden Bay; and stratum 7 covered Farmington Bay. Strata 1, 2, 5, 6, and 7 were known a priori to be common areas used by phalaropes.
Figure 2-2. Locations of dense phalarope flocks recorded during bimonthly aerial surveys at Great Salt Lake during a) early staging, 15 June – 10 July; b) mid staging, 15 July – 10 August; and c) late staging, 15 August – 10 September. Surveys were conducted during the staging periods of Wilson’s and red-necked phalaropes from 2013–2015. Blue circles indicate 2013 locations, gray triangles indicate 2014 locations, and green squares indicate
2015 locations. Shape size is relative to estimated flock size, with larger shapes indicating larger flocks. Surveys were not flown randomly and survey effort was higher in areas of the lake that were known a priori to be used by phalaropes; consequently, locations mapped should not be taken as a lake-wide documentation of phalarope abundance. The lake outline indicates a lake elevation of 1,278.6 m.
Figure 2-3. Comparison of mean a) water depth and b) accumulation of brine fly adults between sites with and without phalaropes in the high-salinity bays of Great Salt Lake from 2014–2015 (n = 34), with standard error intervals. Mean water depth at sites without phalaropes was 5.6 m, while the mean depth at sites with phalaropes was 3.8 m ($t_{23} = 1.83$, $P = 0.08$). Mean accumulation of brine fly adults was 375.9 mg/m$^2$/10 min at non-phalarope sites and 1,022.7 mg/m$^2$/10 min at phalarope sites ($t_{15} = 1.38$, $P = 0.19$).
Figure 2-4. Comparison of mean a) water salinity, b) biomass of benthic macroinvertebrates, and c) water depth between sites with and without phalaropes in a low-salinity bay of Great Salt Lake from 2013–2015 (n = 23). Error bars represent standard error intervals.
CHAPTER 3
PHALAROPE FORAGING IN RELATION TO PREY ABUNDANCE
AT GREAT SALT LAKE

ABSTRACT Great Salt Lake (GSL) is a critical staging area for 2 species of phalaropes, Wilson’s (*Phalaropus tricolor*) and red-necked (*Phalaropus lobatus*). Phalaropes use a diverse range of habitats at GSL, from shallow (< 0.1 m) to deep (8 m), and from low-salinity (0.2%) to high salinity (16%). The GSL ecosystem currently faces a suite of potential threats that may decrease its suitability as phalarope habitat, including water diversions, mineral extraction, harvest of brine shrimp cysts, and climate change. However, little is known about phalarope ecology at GSL or about how these threats may impact phalarope use of GSL. I observed phalarope behavior in different habitats to investigate which areas of GSL were used by phalaropes for foraging, which specific foraging behaviors were most common, and whether the proportion of phalaropes foraging at a site was related to prey availability. During 2014 and 2015, I quantified phalarope behavior, measured biomass of invertebrates that were potential phalarope prey, and measured environmental variables that may have affected the availability of invertebrate prey. I analyzed the high-salinity bays of GSL (Carrington, Gilbert) separately from the low-salinity bay (Farmington), because the types of invertebrates present throughout GSL varied with salinity. On average, 75% of phalaropes observed in Farmington Bay were foraging, while just 41% foraged in Gilbert Bay. Foraging via surface picking was more common in red-necked phalaropes than Wilson’s phalaropes; 60% of red-necked phalaropes that were foraging used surface picking, compared to 32%
of Wilson’s phalaropes. Spinning behavior to upwell prey was more common in Wilson’s (19%) than red-necked (3%) phalaropes. In all bays, high numbers of foraging phalaropes were positively associated with biomass of invertebrate prey. This study indicates the importance to phalaropes of invertebrate availability throughout GSL, and highlights specific areas of GSL that phalaropes used for foraging. The habitats and resources that are used by phalaropes need to be maintained so that the GSL ecosystem will continue to be a valuable staging area.

INTRODUCTION

Great Salt Lake (GSL) hosts over one-third of the world’s population of Wilson’s phalaropes (*Phalaropus tricolor*) each summer (Aldrich and Paul 2002). The reliance of Wilson’s phalaropes, red-necked phalaropes (*Phalaropus lobatus*), and other species of shorebirds (Charadriiformes) on the GSL ecosystem was an important factor in GSL’s designation as a hemispheric site in the Western Hemisphere Shorebird Reserve Network (Aldrich and Paul 2002). Despite the importance of GSL as a staging area for phalaropes, little is known about the ecology of these birds at GSL. Areas of use and phalarope densities at many different sites across GSL have been documented (Paul and Manning 2002), but the activities of phalaropes at these locations are unknown. Furthermore, little is known about which aquatic invertebrates are consumed by phalaropes, or about the ecology of these invertebrates.

Research on phalaropes has shown that their foraging behaviors can vary greatly among locations. Phalaropes are best known for their unique foraging behavior in which they spin in a circle by kicking the water below them, thereby upwelling prey (Obst et al.
1996). At Mono Lake, however, Jehl (1988) rarely observed spinning behavior by foraging Wilson’s phalaropes. Instead, phalaropes on Mono Lake typically swam and picked at the surface of the water or walked along shore to catch brine fly adults (Ephydridae). Haney and Stone (1988) recorded a much more diverse suite of pelagic foraging behaviors by red phalaropes (*Phalaropus fulicaria*) in Kongkok Bay in the Bearing Sea, Alaska, including surface picking, spinning, head dunking, and vertical bobbing (Haney and Stone 1988). On the other hand, Mercier and Gaskin (1985) only observed surface picking among pelagic-foraging red-necked phalaropes in the Quoddy region of the Bay of Fundy, New Brunswick. Whether the behavioral differences in these studies are due to species differences, prey availability differences, or other factors is unknown. In each of the studies listed, only one species was present in the area so interspecies comparisons in a given region could not be made.

The high-salinity bays of GSL support only 2 types of macroinvertebrates: brine shrimp (*Artemia franciscana*) and brine flies. Brine fly larvae are aquatic, spending most of their time feeding on periphyton and then attaching themselves to the substrate when they pupate (Herbst 1990). Brine fly larvae prefer to spend their time on bioherms (calcareous, reef-like structures in GSL) and typically only swim to find better habitat, but strong waves or currents can suspend larvae and pupae in the water column (Collins 1980), where they are more easily accessible to phalaropes and other birds. Brine fly larvae that remain attached to bioherms can only be obtained by birds foraging in shallow water or by birds that forage while diving (phalaropes do not dive). A low-salinity bay of GSL, Farmington, supports a higher diversity of aquatic invertebrates relative to the rest of GSL. Macroinvertebrates found in Farmington Bay include chironomids (i.e., midges,
Chironomidae), corixids (Corixidae), and daphnia (*Daphnia magna*). Brine shrimp and brine flies are less common in Farmington, but may occur there occasionally.

I had 3 main objectives for this study. First, I sought to determine which areas of GSL were most frequently used by phalaropes for foraging. Both Wilson’s and red-necked phalaropes at GSL used areas that varied in prey availability, salinity, depth, substrate, and other characteristics. I hypothesized that phalarope behavior would differ across sites, with some areas used predominately for foraging and other areas used for loafing, preening, and other activities. Second, I examined specific foraging behaviors to determine which types of behavior were most common at GSL and whether frequency of the types of behavior differed by bay or by species. Finally, I compared the proportion of phalaropes foraging at a site to prey densities and environmental variables, using logistic regression. I expected to find a higher proportion of birds foraging at sites with higher densities of invertebrates. The main goal of modeling was to evaluate which specific resources were most strongly associated with a high number of foraging phalaropes so that those resources can be considered in management decisions at GSL.

**STUDY AREA**

Great Salt Lake is a large (4,400 km² at average surface elevation), terminal lake in northern Utah, USA. Freshwater inflow to GSL is primarily from the Bear, Weber, and Jordan rivers, which flow into the northeast, east, and southeast of the lake, respectively (Fig. 3-1). The uneven dispersion of freshwater inflow, combined with causeways that restrict water flow within the lake, results in different salinities in the different bays of the lake. This research took place in 3 bays of GSL, Carrington, Gilbert, and Farmington.
Over the study, the salinity of Carrington ranged from 14–16% and the salinity of Gilbert ranged from 13–16%, with higher salinities typically occurring in 2015. The salinity of Farmington Bay ranged from 0.2–12%, with salinities varying both temporally and spatially. For comparison, the salinity of seawater is ~3.5%. The 3 bays of the study also differed in average depths, with Gilbert having the deepest areas, up to 10 m, and Farmington having the shallowest habitat, often just a skim of water over mud during my study. The bays of GSL differed from one another in the types of substrate predominantly present in each bay. Mud and sand substrates were found in all bays of GSL, but Carrington and Gilbert also had bioherms, which are calcareous, reef-like structures in the shallow waters of these bays (Eardley 1938). I originally planned to include Ogden Bay in this study, but low lake levels during this study prevented boat access to the bay and aerial surveys revealed that phalaropes rarely used Ogden Bay during the period of low lake elevation. Only limited data were therefore obtained from Ogden Bay; the sample size from Ogden Bay was too small to effectively analyze.

METHODS

Phalaropes forage on shore, while wading, and while swimming, but I only included foraging sites with water (phalaropes wading or swimming) in this study. Phalarope behavior was surveyed from a boat once a week from June until September in 2014 and 2015. Surveys were typically done after 10:00 and before 13:00, and 89% of the surveys were done before 14:00. I divided the lake into “east” and “west” sites according to accessibility by boat: east sites were located in Farmington Bay and were accessed by airboat, while west sites were located in Carrington or Gilbert Bays and were
accessed with a larger boat. Some sampling methods varied between east and west sites due to equipment differences, and all west-site samples were >1 m deep. Each bay was therefore analyzed separately. From June until August, phalaropes were found all across GSL, so I chose 1 east site and 1 west site each week with ≥200 individuals of either species of phalaropes. In September, phalarope use of west sites decreased, so I surveyed smaller flocks or only chose an east site. Phalarope locations across GSL were documented at least once per week by various methods. I chose observation sites based on knowing the locations of these large flocks of phalaropes. Flock locations varied each week so that observations occurred over a range of habitats. I surveyed phalarope behavior through binoculars and recorded the observations using an audio recorder (Altmann 1974). After completing these behavior surveys, I sampled invertebrate availability at each observation site and took physical habitat measurements.

**Phalarope Behavior**

The boats were slowed upon approach to each site to minimize disturbance to phalaropes at the site. Some phalaropes flushed when the boats approached, but they typically resettled and often swam closer to the boats as the survey progressed; therefore, I assumed that the impact of the observers’ presence on phalarope behavior was negligible. Each survey began with an instantaneous scan during which I surveyed the behaviors of all birds ≤50 m from the boat. I watched each phalarope for 1 sec to determine its current behavior. After the instantaneous scan, 5-min focal surveys (n ≥ 5) were conducted for another study, wherein I observed the behavior of a single bird for the entire time period. In most instances, I conducted a second instantaneous scan after the
focal surveys and averaged the number of foraging phalaropes from the 2 scans. I did not
determine the species of each individual bird recorded in the instantaneous scans because
I had to record observations quickly to avoid double-counting fast-moving phalaropes.
Instead, while I did the instantaneous scan, another observer estimated the number of
birds present in the flock and estimated either the number or ratio of each of the 2
species. Most (86%) of the flocks I observed were not mixed. All of the mixed flocks
except 1 were composed >90% of one species or another and were thus treated as a
homogenous flock.

I classified behavior into 6 categories: movement, preening, alert, inactive,
interaction, or foraging. Movement included swimming, flying, walking, and other
motions that caused the phalarope to change location but did not occur while the
phalarope was foraging. Preening was defined as the use of the bill to straighten or oil
feathers. Alert was defined as a phalarope remaining in one spot, not foraging, but
looking around. Inactive was defined as resting, either remaining in one spot and not
looking around, or having eyes closed. Interaction was defined as an activity that
involved another bird, whether conspecific or another species.

Foraging behavior included any attempted or successful capture of prey that was
observed during the 1-sec scan. I subdivided foraging behaviors into 5 categories: air
picking, surface picking, spinning, dunking, and vertical bobbing. In air picking, the
phalarope lunged, picked, or otherwise attempted to catch a flying invertebrate, and no
part of the phalarope’s head or bill contacted the water. In surface picking, only the bill
contacted the water; head dunking consisted of the head and/or neck entering the water
while the body remained horizontal; and vertical bobbing was recorded when a phalarope
tipped its entire body upward like a dabbling duck, completely submerging its head and neck (Haney and Stone 1988). Spinning occurred when the phalarope rotated at least 180° before surface picking, or spun simultaneously with surface picking. I also included “interaction spins” in the spinning classification. Interaction spins were defined as two or more phalaropes spinning <2 body lengths away from one another, so that prey upwelled by one phalarope could be picked at by another phalarope.

**Invertebrate Densities**

To assess invertebrate densities at each site, I took 2 samples and averaged their contents. At sites <0.3 m deep, I used a stovepipe sampler to assess densities of pelagic and benthic invertebrates that would be accessible to phalaropes (invertebrates in the water column and in the top 0.02 m of soft substrate). Stovepipe samplers consisted of a 19-L bucket with the bottom removed; the bucket had a top diameter of 29 cm and a bottom diameter of 24.6 cm. Stovepipe sampling followed the procedures of DiFranco (2006), with agitation of the top 2 cm of sediment and filtration of water through a 500 μm sieve. At sites ≥ 0.3 m deep, I sampled pelagic invertebrates using a vertical tow net with a diameter of 50 cm and mesh size 153 μm (Research Nets Inc., Bothell, WA). For sites deeper than 0.5 m, I only sampled to a depth of 0.5 m, which is the estimated maximum depth from which spinning phalaropes can upwell prey (Obst et al. 1996). Invertebrate samples from the water column were placed on ice for transport and then preserved in ethanol.

I used floating sticky traps to measure adult brine flies at each observation site. Floating sticky traps consisted of a length of commercial fly paper strip (Black Flag®
Chemsico, St. Louis, MO) attached to a blue foam board with an area of ~722 cm$^2$
(Sharkfin® Kiefer, Zion, IL). The fly paper was 4 cm wide and was cut to a length of
approximately 6 cm. Adult brine flies are attracted to any surface on which they can land.
To standardize attraction at each site I tethered each kickboard with a rope and floated the
traps 5 m away from our anchored boat. I exposed the sticky surfaces for 10 min (Boula
1985), then covered the sticky paper with wax paper to prevent additional captures. All
adult flies were placed on ice for transport and euthanized by freezing.

In the laboratory, I sorted invertebrates by type. Types of aquatic invertebrates
identified from benthic and pelagic samples included brine fly larva, brine fly pupa, brine
shrimp adult, chironomid larva, and corixid adult. All other invertebrates were classified
as “other.” For each invertebrate type, I counted the number of individuals and averaged
the numbers from the 2 samples collected at each site. In 2014, I took a digital image of
each invertebrate and used ImageJ to measure its length (Rasband 1997). From these data
and images from Ch. 2, I calculated average lengths for each type of invertebrate for the
bays in which it was found, for each month of the study. These average values were used
to estimate the lengths of the 2015 samples, which were counted but not photographed. I
converted the lengths using published length-weight regression equations. Species-
specific equations were only available for brine shrimp and for brine fly larvae
(Wurtsbaugh 1992, Wurtsbaugh et al. 2011). For the other types of invertebrates, I used
the most taxonomically-similar equations available (Wurtsbaugh 1992, Benke et al. 1999,
Sabo et al. 2002). I created biomass variables based on the area of water sampled
(mg/m$^2$).

To estimate the abundance of adult brine flies, I counted the adult brine flies
captured on each sticky paper. For each site, I averaged the number of adult flies from the 2 samples and converted this estimate to number of adult brine flies/m² based on the area of the fly paper. Because fly paper lengths varied, I measured the length of each to calculate the sample area for each site. Dry biomass estimates for adult brine flies followed the same procedure as for aquatic invertebrates, and I used a length-weight regression equation for Dipterans of the suborder Brachycera (Sabo et al. 2002). The method used to capture adult brine flies did not yield a true biomass estimate, as the floating sticky traps accumulated flies over time. I therefore referred to abundance of adult brine flies as “accumulation,” which was expressed as mass per area per time, mg/m²/10min.

Environmental Conditions

I measured local environmental variables that may have indirectly affected the behavior of phalaropes by affecting presence, activity, or accessibility of invertebrate prey. Conditions that may have affected aquatic invertebrates included water temperature (°C), water depth (m), and water salinity (%). Brine fly activity is affected by microclimate (Willmer 1982), so at each site I also measured air temperature (°C), wind speed (m/s), and solar radiation (W/m²; Willmer 1983). Water temperature was measured at approximately 3 cm below the surface of the water at east sites, and 20 cm below the surface of the water at west sites, due to differences in sampling equipment. Salinity was measured from the top 3 cm of the water at all sites with a refractometer. Air temperature, wind speed, relative humidity, and solar radiation were measured from ~2 m above the surface of the water at east sites and ~3 m above the surface of the water at west sites.
Temperature and wind speed were measured with a weather meter (Kestrel 3000 Wind Meter ® Nielsen-Kellerman, Boothwyn, PA); solar radiation was measured with a solar power meter (SP-216 Ambient LLC, Chandler, AZ). I noted the composition of the benthic substrate at all sites based on the classifications of Eardley (1938).

**Statistical Analyses**

From the instantaneous scans, I calculated the proportion of individuals within a flock engaged in each behavior. Of the phalaropes that were classified as “movement,” I created 2 categories: “true movement” and “searching,” which accounted for birds that were moving as part of their foraging. From the focal surveys, I knew that in a foraging flock, a bird might be moving from one foraging spot to another, but during the instantaneous scan, this behavior would be recorded as "movement." To account for the fact that movement between foraging spots should be classified as foraging, I assumed that the proportion of birds I saw foraging relative to other, non-movement, non-foraging activities also held for moving birds. For example, if out of 20 phalaropes, I recorded 5 surface picking, 5 alert, and 10 swimming, I assumed that half of the swimming individuals were actually foraging and labeled these birds “searching,” which was counted as a foraging behavior. Phalaropes engaged in non-searching foraging behaviors (i.e., surface picking, spinning, air picking, dunking, or bobbing) were termed “actively foraging.”

I conducted all statistical analyses in R (R Core Team 2016). For all objectives, I used generalized linear models to account for unobserved variation in each observation occasion (Warton and Hui 2011). Models were built using package lme4 (Bates et al.
I compared the proportions of flocks that were foraging across different factors using mixed-effects logistic regression. In my first objective, I examined differences in foraging by bays and by species. For my second objective, I examined differences in the most common types of active foraging behaviors across bays and between species. I also evaluated whether searching behavior differed across bays and years. For my third objective, I used an a priori set of models to compare prey and abiotic factors with the proportion of a flock foraging for bay/species combinations, although data were sparse for some such combinations (Table 3-1). Invertebrate types at GSL varied with salinity, so for each bay/species model set, I only considered invertebrates and related abiotic variables that were appropriate for that bay (Table 3-2).

Before building models, I used logistic regression to compare foraging across 2 categorical variables, year and substrate, to assess whether these needed to be included in the models. My sampling covered all weeks of the staging period, so I used Pearson’s correlation from the package Hmisc to evaluate whether there were significant differences in the proportion of a flock foraging by week (Harrell 2014). Although most observations were conducted in the morning, some occurred later in the day, so I also examined the correlation between proportion of a flock foraging and time of day. All continuous variables were z-standardized before analysis so that coefficient estimates would be comparable. I compared models using second-order Akaike’s Information Criterion ($\text{AIC}_c$) in package MuMIn (Bartoń 2015). For all analyses, I considered $\alpha \leq 0.10$ to be significant.
RESULTS

Foraging by Bay at GSL

During the study, a total of 55 observations were conducted across GSL (Fig. 3-1). On average, 65% of phalaropes in a given flock were foraging during the study, but the proportion of a flock with phalaropes engaged in foraging behaviors varied by bay of GSL (Fig. 3-2). Flocks of phalaropes in Farmington Bay had the highest average proportion of foraging (75%), followed by Carrington Bay flocks (62%). Phalarope flocks in Gilbert Bay had the lowest proportion of foraging on average (41%), and therefore the highest proportion of non-foraging behaviors. Of the non-foraging behaviors in Gilbert Bay, alert was most common (62%; Table A-4). The proportion of a flock foraging differed significantly by bay ($\chi^2 = 10.25, P = 0.006$), but not by species ($\chi^2 = 0.19, P = 0.67$). Most (90%) of the observations were in areas deep enough for phalaropes to swim rather than wade, but the mean proportions of birds foraging were similar at sites where phalaropes swam (66%) to sites where phalaropes waded (63%).

I analyzed differences in prey biomass among the 3 bays. Accumulation of brine fly adults differed among the bays and was highest in Carrington Bay (Fig. 3-3A). The average accumulation in Carrington Bay was 3.6 g/m$^2$/10 min, while the average accumulation in Gilbert Bay was 0.6 g/m$^2$/10 min. All stages of brine flies were less common in Farmington Bay than in the other bays; the accumulation of brine fly adults in Farmington was just 0.1 g/m$^2$/10 min. While the bays did not differ in total pelagic invertebrate biomass, Farmington Bay had the highest densities of aquatic invertebrates other than brine shrimp (Fig. 3-3B). When biomass of benthic invertebrates was added to
pelagic biomass at sites that were sampled with a stovepipe sampler (Fig. 3-3C), the
average biomass of aquatic invertebrates other that brine shrimp that were accessible to
phalaropes at the sites I sampled was 2 orders of magnitude higher in Farmington Bay
(293.0 mg/m²) than in Carrington (6.1 mg/m²) or Gilbert (10.4 mg/m²).

**Specific Foraging Behaviors at GSL**

I observed at least 1 instance of all the foraging behaviors described previously
(Table A-5). Additionally, I observed 2 other types of behavior: “sallying” and “scything.”
In sallying behavior, a phalarope twisted its body from side to side while swimming
forward, often while picking at the surface of the water. I observed 3 birds sallying
during the study, all of which were in Farmington Bay in September. I only observed 1
instance of scything, in which the phalarope held its bill open at the surface of the water
and swung its head back and forth in the manner typical of American avocets
(*Recurvirostra americana*). Jehl (1988) also observed scything behavior once during a
survey of Wilson’s phalaropes. Consistent with other studies, I never observed
phalaropes dive to capture prey, as phalaropes are too buoyant to dive efficiently.

Of birds that were foraging, the most common type of foraging behavior was
surface picking (49% of all birds foraging). The proportion of surface picking among
foraging birds differed by bay ($\chi^2_1 = 14.16, P < 0.001$) and by species ($\chi^2_1 = 11.86, P <
0.001$). The interaction term between bay and species was not significant ($\chi^2_1 = 0.76, P =
0.38$). Surface picking was most common in Carrington Bay (79%) and by red-necked
phalaropes (60%; Fig. 3-4). Surface picking was observed while phalaropes were wading
and while swimming. Of the active foraging behaviors, the second-most common type
observed was spinning (10% of all birds foraging). As with surface picking, frequency of spinning differed by bay ($\chi^2 = 6.29, P = 0.01$) and by species ($\chi^2 = 8.96, P = 0.003$). The interaction term between bay and species was not significant ($\chi^2 = 0.20, P = 0.65$).

Spinning behavior was most common in Farmington Bay (16%) and by Wilson’s phalaropes (20%; Fig. 3-4). Spinning occurred both at sites where phalaropes were wading and sites at which phalaropes were swimming. At sites where phalaropes were wading, spinning consisted of rotation of the body while turning with the feet, presumably to disturb prey in soft sediments.

Searching behavior was observed in 36% of foraging phalaropes on average. In Carrington, searching increased from an average of 7% in 2014 to an average of 21% in 2015. Searching behavior also increased in Farmington, from an average of 35% in 2014 to an average of 48% in 2015. Searching rates were similar between years in Gilbert Bay (34% in 2014 and 36% in 2015). However, the differences in searching were not significant by bay ($\chi^2 = 2.46, P = 0.12$) or by year ($\chi^2 = 0.42, P = 0.52$). The interaction term was also not significant ($\chi^2 = 0.02, P = 0.88$).

**Foraging Models**

I did not build foraging models for either species in Gilbert Bay due to the low rates of foraging and small sample sizes in that bay (Table 3-1). I also did not build models for Wilson’s phalaropes in Carrington Bay (n = 3). The remaining bay/species combinations for modeling were red-necked phalaropes in Carrington Bay (n = 8), Wilson’s phalaropes in Farmington Bay (n = 13), and red-necked phalaropes in Farmington Bay (n = 18). All of these datasets were overdispersed, so I included a
random term to account for the observation number. Competitive models were defined as any model with \( \Delta AIC_c < 2 \).

**Carrington Bay, red-necked phalaropes.**—All of the Carrington Bay/red-necked phalarope (CBRN) observation sites were >0.5 m deep, so I did not account for substrate in the CBRN models. The proportion of phalaropes foraging at these sites was different between years (\( \chi^2_1 = 5.59, P = 0.02 \)), so I included year as a categorical variable in all models. The proportion of phalaropes foraging at the CBRN sites was not related to time of day (\( r = -0.09, P = 0.84 \)), and only weakly related to week of observation (\( r = -0.55, P = 0.15 \)). I therefore did not include time of day or week in any of the models. Of the models I tested, the top model indicated a positive relationship between proportion of phalaropes foraging and summed biomass of brine fly larvae and pupae (\( \beta_{BFL/P} = 1.11 \pm 0.19, P < 0.001 \)). The top model outperformed a null model (\( \chi^2_1 = 15.76, P < 0.001 \)), and no models were competitive (Table 3-3).

**Farmington Bay, Wilson’s phalaropes.**—The Farmington Bay/Wilson’s phalarope (FBWI) observation sites were the shallowest of any surveyed, with a mean water depth of just 0.24 m. However, the proportion of phalaropes foraging at these sites did not differ among substrates (\( \chi^2_1 = 0.03, P = 0.87 \)). The proportion of phalaropes foraging at FBWI sites did differ between years (\( \chi^2_1 = 3.10, P = 0.08 \)) and among weeks, (\( \chi^2_1 = 3.96, P = 0.05 \)), although the effects of year and week were similar, so I only included week in my models. The proportion of phalaropes foraging did not differ by time of day (\( \chi^2_1 = 0.04, P = 0.84 \)). Biomass of benthic macroinvertebrates was negatively correlated with depth (\( r = -0.54, P = 0.06 \)), so I did not include the variables for depth and biomass of
benthic macroinvertebrates in models together. In the top model, proportion of phalaropes foraging at FBWI sites was positively related to salinity ($\beta_{\text{salinity}} = 1.13 \pm 0.35, P = 0.001$) and week ($\beta_{\text{week}} = 0.28 \pm 0.13, P = 0.04$). Biomass of benthic macroinvertebrates was also included in the model, although it was not significantly related to proportion of a flock foraging ($\beta_{\text{BnInv}} = -0.21 \pm 0.29, P = 0.47$). The top model performed better than a null model ($\chi^2 = 9.87, P = 0.01$). One model was competitive and suggested a positive relationship between foraging and depth (Table 3-4).

*Farmington Bay, red-necked phalaropes.*—The proportion of phalaropes foraging at the Farmington Bay/red-necked phalarope (FBRN) sites did not differ among substrates ($\chi^2 = 1.42, P = 0.49$). The proportion of phalaropes foraging at FBRN sites did differ by year ($\chi^2 = 5.84, P = 0.02$), but did not differ by week ($\chi^2 = 1.14, P = 0.29$) or time of day ($\chi^2 = 1.24, P = 0.26$). I therefore did not include substrate, week, or time of day in the models, but did include year as a categorical variable. Biomass of benthic macroinvertebrates was negatively correlated with depth ($r = -0.54, P = 0.02$) and positively correlated with water temperature ($r = 0.61, P = 0.01$), so I did not include depth or water temperature in models with biomass of benthic macroinvertebrates. The top model indicated that the proportion of phalaropes foraging at FBRN sites was negatively related to depth ($\beta_{\text{depth}} = -0.29 \pm 0.20, P = 0.15$). Two models were competitive (Table 3-5), but the top model did not perform better than a null model ($\chi^2 = 2.01, P = 0.16$).
DISCUSSION

The bays of GSL included in this study varied considerably in biological and physical characteristics during the staging periods of both species of phalaropes, which spans 3 months from late June to late September. This study identified broad-scale areas of GSL where a high proportion of phalaropes were foraging during the birds’ staging period and documented locations where different types of invertebrates were most abundant. A limitation of this study was the depth of sites sampled in Carrington Bay. Only sites >1 m deep could be accessed by the large boat, so my observations did not include phalaropes that were foraging in the shallow areas of Carrington Bay, nor did my invertebrate samples evaluate the benthic invertebrates that may have been available to phalaropes in shallow water. Shallow areas were also not sampled in Gilbert Bay, but I did not typically observe any phalaropes using the shallow areas of that bay.

Phalaropes foraged most often in Farmington Bay and least often in Gilbert Bay. Frequencies of the different types of foraging behavior differed by bay and may have been related to different types of prey that were available in different bays. Surface picking was observed in all bays, but the highest rates of surface picking occurred in Carrington Bay and corresponded with high accumulations of brine fly adults, which sat on the surface of the water or on debris that was floating on the surface of the water. Spinning was likewise observed in all bays, but was more common in the shallow bays compared to the deep bays. Spinning is most effective in shallow water when prey are concentrated in a layer within 0.5 m of the surface (Obst et al. 1996). Phalaropes may spin more often in Farmington Bay because the density of brine fly adults is lower in that bay, so phalaropes need to upwell other prey types from the water column and soft
sedi ments. Furthermore, the shallower average depths of Farmington make spinning more effective. Carrington Bay had high accumulations of brine fly adults and low densities of aquatic invertebrates other than brine shrimp. Spinning is more energetically costly than surface picking, so phalaropes would theoretically be less likely to spin when prey can be readily taken with surface picking, as was observed in Carrington Bay. However, I have observed phalaropes spinning even when it is unnecessary, such as while resting, so the energetic costs of this behavior may not be an important consideration.

Foraging behavior differed by species, with Wilson’s phalaropes spinning more often than red-necked phalaropes, and red-necked phalaropes surface picking more often than Wilson’s phalaropes. Different behaviors between the species may be related to differences in each species’ preferred habitat. Of all phalarope flocks in Carrington Bay, 73% were mostly red-necked phalaropes; 56% of the flocks observed in Farmington Bay were red-necked phalaropes. However, the interaction term between bay and species for the proportion of a flock foraging was not significant. Another potential driver of behavior differences is prey preference. Red-necked phalaropes prefer to eat brine fly larvae over brine fly adults, and prefer either over brine shrimp (Rubega and Inouye 1994). Only limited studies have been done on phalarope prey at GSL, but have indicated that Wilson’s phalaropes at GSL may consume some brine shrimp (Roberts 2013). Red-necked phalaropes may prefer prey that is typically at or near the surface of the water, and therefore forage via surface picking more often than do Wilson’s phalaropes. The types of aquatic invertebrates consumed by Wilson’s phalaropes in Farmington Bay are unknown, but Wilson’s phalaropes may prefer invertebrates in Farmington that are easily upwelled by spinning. Another hypothesis for the differences in behavior between
phalarope species relates to changing prey densities throughout the summer. Wilson’s phalaropes stage at GSL from late June to early August, while red-necked phalaropes typically stage at GSL from late July to late September, so each species may overlap with high concentrations of different types of prey.

In Carrington Bay, the proportion of red-necked phalaropes foraging at a site was most strongly related to the biomass of brine fly larvae and pupae, and this model outperformed all other models. A caution in interpreting these models is that my sample size was small and data were overdispersed; however, aquatic stages of brine flies appear to be an important influence on foraging behavior of red-necked phalaropes in Carrington Bay. In Farmington Bay, the proportion of Wilson’s phalaropes foraging was not related to prey biomass. Instead, the top-ranked model of foraging Wilson’s phalaropes in Farmington Bay indicated that foraging was more likely at sites with higher salinities. High proportions of red-necked phalaropes foraging in Farmington Bay occurred at shallower sites, although this relationship was not significant. Prey densities may have been sufficiently high throughout Farmington Bay so that phalaropes could forage successfully at a variety of locations. Abundant prey throughout the bay would contribute to the weak relationships between foraging phalaropes and invertebrate biomass in Farmington Bay. Local depletion of prey could also contribute to weak relationships between proportion of flock foraging and prey biomass. Phalaropes feeding heavily on chironomid larvae and corixids could deplete biomass of these benthic macroinvertebrates at sampling locations, similar to prey depletion by other shorebirds demonstrated in exclosure experiments at stopover areas (Schneider and Harrington 1981).
MANAGEMENT IMPLICATIONS

Phalaropes rely on aquatic invertebrate prey at GSL, and aquatic invertebrates depend on sufficient water quality. Great Salt Lake is subject to natural inter- and intra-annual variations in water supply, but additional anthropogenic demands on the main rivers that flow into GSL have combined with recent droughts to drastically reduce the water level of GSL (Wurtsbaugh et al. 2016). As the lake level has decreased, areas that were formerly underwater are now exposed, so that potential phalarope foraging habitat has decreased across GSL. While the volume of Gilbert Bay has been least affected by low lake levels and is an area used by phalaropes, I found that this bay was not primarily used for foraging and does not support substantial densities of their prey. Gilbert Bay was still used by phalaropes, however, and may be an important loafing area.

In addition to impacting habitat availability, decreasing lake levels can impact prey availability, especially because salinity increases as lake elevation decreases. Although salinity was not a major factor in my models, its importance has been demonstrated by the extreme example of Gunnison Bay. When a railroad causeway bisected GSL into 2 separate arms, salinity in Gunnison Bay gradually increased to the point of saturation. Gunnison Bay no longer supports aquatic invertebrates and, consequently, is not typically used by phalaropes or other birds. Even though brine shrimp and brine flies are adapted to high salinities, the body lengths and survival of these invertebrates are reduced as salinity increases (Barnes and Wurtsbaugh 2015), and aquatic invertebrates in Farmington Bay are even more sensitive to high salinities.

Managers at GSL face numerous challenges that threaten GSL’s water supply. Proposed upstream impoundments and water diversion would reduce the lake elevation
by an estimated 0.2 m, for a corresponding surface area loss of nearly 80 km²
(Wurtsbaugh et al. 2016). Changes in precipitation and climate may also decrease the
amount of water that reaches GSL and increase evaporation from GSL (Gillies et al.
2012). To protect the foraging habitat of phalaropes and other migratory birds at GSL,
managers need to ensure that as much water reaches GSL each year as possible. Without
sufficient water, the aquatic prey of phalaropes cannot survive. Further studies are needed
to better understand the ecology of aquatic invertebrates at GSL, how prey availability
may change throughout the staging period, and whether phalarope foraging is already
being affected by changes in GSL habitat.

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Table 3-1. Summary of data collected on the average numbers of 2 species of phalaropes foraging in 3 bays of Great Salt Lake during their staging periods, 2014–2015. The first column lists the bays of observation for each species, the second column lists the number of observations for each bay, and the third column lists the mean and standard error of the number of phalaropes engaged in foraging behaviors, by species, in a given bay.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>$\bar{x} \pm SE$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilson’s phalarope</td>
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<td></td>
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<tr>
<td>Carrington</td>
<td>3</td>
<td>112 ± 80</td>
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<tr>
<td>Gilbert</td>
<td>5</td>
<td>48 ± 28</td>
</tr>
<tr>
<td>Farmington</td>
<td>13</td>
<td>198 ± 60</td>
</tr>
<tr>
<td>Red-necked phalarope</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrington</td>
<td>8</td>
<td>107 ± 44</td>
</tr>
<tr>
<td>Gilbert</td>
<td>6</td>
<td>11 ± 5</td>
</tr>
<tr>
<td>Farmington</td>
<td>18</td>
<td>168 ± 27</td>
</tr>
</tbody>
</table>
Table 3-2. Variables related to phalarope foraging that were measured from boats at observation sites during the staging periods of Wilson’s and red-necked phalaropes at Great Salt Lake in 2014 and 2015.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Units</th>
<th>Measured</th>
<th>Modeled</th>
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</thead>
<tbody>
<tr>
<td><strong>Prey</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>BFL/P</td>
<td>Sum of the dry biomass estimate of the aquatic life stages of brine flies (larvae and pupae) captured in a water column sample</td>
<td>mg/m²</td>
<td>All</td>
<td>Carr</td>
</tr>
<tr>
<td>BnInv</td>
<td>Sum of the dry biomasses of chironomid larvae and corixids captured in a water column sample</td>
<td>mg/m²</td>
<td>Farm</td>
<td>Farm</td>
</tr>
<tr>
<td>BFA</td>
<td>Dry biomass of brine fly adults captured on a sticky trap</td>
<td>mg/m²/10 min</td>
<td>All</td>
<td>Carr</td>
</tr>
<tr>
<td><strong>Physical</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subs</td>
<td>Primary composition of benthic substrate: bioherm, mud, mud/sand, or sand</td>
<td>Categorical</td>
<td>All</td>
<td>Farm</td>
</tr>
<tr>
<td>Depth</td>
<td>Distance from surface of water to benthic surface</td>
<td>m</td>
<td>All</td>
<td>All</td>
</tr>
<tr>
<td>Salinity</td>
<td>Percentage of all salts dissolved in water, as measured by refractometer from ~3 cm below the water surface at all sites</td>
<td>%</td>
<td>All</td>
<td>Farm</td>
</tr>
<tr>
<td>Water</td>
<td>Temperature of water, measured ~3 cm below the water surface in Farmington Bay and ~20 cm below the water surface in the high-salinity bays</td>
<td>°C</td>
<td>All</td>
<td>All</td>
</tr>
<tr>
<td>Air</td>
<td>Temperature of air, measured ~2 cm above the water surface in Farmington Bay and ~3 m above the water surface in the high-salinity bays</td>
<td>m/s</td>
<td>All</td>
<td>Carr</td>
</tr>
</tbody>
</table>
Table 3-2 continued.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Units</th>
<th>Measured</th>
<th>Modeled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wind</td>
<td>Speed of wind, measured ~2 m above the water surface in Farmington Bay and ~3 m above the water surface in the high-salinity bays</td>
<td>m/s</td>
<td>All</td>
<td>Carr</td>
</tr>
<tr>
<td>RH</td>
<td>Relative humidity, measured ~2 m above the water surface in Farmington Bay and ~3 m above the water surface in the high-salinity bays</td>
<td>%</td>
<td>All</td>
<td>Carr</td>
</tr>
<tr>
<td>SR</td>
<td>Solar radiation, measured ~2 m above the water surface in Farmington Bay and ~3 m above the water surface in the high-salinity bays</td>
<td>W/m²</td>
<td>All</td>
<td>Carr</td>
</tr>
</tbody>
</table>

**Time**

<table>
<thead>
<tr>
<th>Hour</th>
<th>Time of day when the survey was conducted, with 10:00 equaling hour 0.</th>
<th></th>
<th>All</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Week</td>
<td>Week of the phalarope staging period, starting period, starting on June 17 and ending September 29</td>
<td></td>
<td>All</td>
<td>All</td>
</tr>
<tr>
<td>Year</td>
<td>Calendar year of the survey</td>
<td></td>
<td>All</td>
<td>All</td>
</tr>
</tbody>
</table>

*aAll = all bays, Carr = Carrington Bay, Farm = Farmington Bay.*
Table 3-3. Mixed-effect logistic regression models of the proportion of red-necked phalaropes foraging in Carrington Bay, Great Salt Lake during the staging period in 2014 and 2015. Variables included: biomass of brine fly larvae/pupae (mg/m²; BFL/P), accumulation of brine fly adults (mg/m²/10 min; BFA), relative humidity (%; RH), water depth (m; Depth), solar radiation (W/m²; SR), and wind speed (m/s; Wind). Year was included as a categorical variable in all models. The sign in parentheses indicates whether the parameter estimate was negative or positive. K is the number of the parameters estimated in the model, including a random term for observation. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights (weight) to determine which variable(s) were most strongly associated with the number of phalaropes foraging at a site.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>Δ AICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>(+) BFL/P</td>
<td>5</td>
<td>-25.3</td>
<td>71.9</td>
<td>0.00</td>
<td>0.999</td>
</tr>
<tr>
<td>(+) BFA</td>
<td>5</td>
<td>-33.2</td>
<td>87.6</td>
<td>15.75</td>
<td>0.000</td>
</tr>
<tr>
<td>(+) BFL/P (+) Depth</td>
<td>6</td>
<td>-24.7</td>
<td>89.4</td>
<td>17.48</td>
<td>0.000</td>
</tr>
<tr>
<td>(+) BFL/P (-) BFA</td>
<td>6</td>
<td>-25.2</td>
<td>90.4</td>
<td>18.48</td>
<td>0.000</td>
</tr>
<tr>
<td>(+) BFA (-) SR</td>
<td>6</td>
<td>-31.3</td>
<td>102.6</td>
<td>30.75</td>
<td>0.000</td>
</tr>
<tr>
<td>(+) BFA (-) RH</td>
<td>6</td>
<td>-31.8</td>
<td>103.7</td>
<td>31.79</td>
<td>0.000</td>
</tr>
<tr>
<td>(+) BFA (+) Wind</td>
<td>6</td>
<td>-32.6</td>
<td>105.2</td>
<td>33.32</td>
<td>0.000</td>
</tr>
</tbody>
</table>
Table 3-4. Mixed-effect logistic regression models of the proportion of Wilson’s phalaropes foraging in Farmington Bay, Great Salt Lake during the staging period in 2014 and 2015. Variables included: biomass of benthic macroinvertebrates (mg/m²; BnInv), water salinity (%) (Salinity), water depth (m; Depth), and water temperature (°C; Water.temp). Week of the staging period (Week) was included in all models as a continuous variable. The sign in parentheses indicates whether the parameter estimate was negative or positive. K is the number of the parameters estimated in the model, including random term for observation. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights (weight) to determine which variable(s) were most related to the likelihood of phalarope presence at a site.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>(-) BnInv (+) Salinity (+) Week</td>
<td>6</td>
<td>-68.5</td>
<td>155.7</td>
<td>0.00</td>
<td>0.625</td>
</tr>
<tr>
<td>(+) Depth (+) Week</td>
<td>5</td>
<td>-72.3</td>
<td>157.6</td>
<td>1.88</td>
<td>0.245</td>
</tr>
<tr>
<td>(-) BnInv (+) Week</td>
<td>5</td>
<td>-73.0</td>
<td>159.1</td>
<td>3.39</td>
<td>0.115</td>
</tr>
<tr>
<td>(-) BnInv (+) Water.temp (+) Week</td>
<td>6</td>
<td>-73.1</td>
<td>163.1</td>
<td>7.47</td>
<td>0.015</td>
</tr>
<tr>
<td>(-) BnInv (+) Water.temp</td>
<td>7</td>
<td>-73.0</td>
<td>172.1</td>
<td>16.37</td>
<td>0.000</td>
</tr>
</tbody>
</table>
Table 3-5. Mixed-effect logistic regression models of the proportion of red-necked phalaropes foraging in Farmington Bay, Great Salt Lake during the staging period in 2014 and 2015. Variables included: water depth (m; Depth), water temperature (°C; Water.temp), biomass of benthic macroinvertebrates (mg/m²; COR), and water salinity (%; Salinity). Year was included in all models as a categorical variable. The sign in parentheses indicates whether the parameter estimate was negative or positive. K is the number of the parameters estimated in the model, including a random term for observation. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights (weight) to determine which variable(s) were most related to the likelihood of phalarope presence at a site.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>(-) Depth</td>
<td>5</td>
<td>-98.4</td>
<td>207.9</td>
<td>0.00</td>
<td>0.501</td>
</tr>
<tr>
<td>(+) Water.temp</td>
<td>5</td>
<td>-99.1</td>
<td>209.3</td>
<td>1.40</td>
<td>0.249</td>
</tr>
<tr>
<td>(+) BnInv</td>
<td>5</td>
<td>-99.3</td>
<td>209.7</td>
<td>1.72</td>
<td>0.212</td>
</tr>
<tr>
<td>(+) BnInv (-) Salinity</td>
<td>6</td>
<td>-99.1</td>
<td>213.1</td>
<td>5.17</td>
<td>0.038</td>
</tr>
</tbody>
</table>
Figure 3-1. Map of Great Salt Lake, Utah, showing major bays, tributaries, and phalarope behavior observation sites from studies conducted during the staging period, 2014–2015. Carrington Bay is delineated by a line running north from the northernmost point of Hat Island. Adjacent diked wetlands are outlined in green. The lake outline indicates the approximate average surface area of GSL during this study, 1,278.6 m. Yellow circles
indicate locations where Wilson’s phalaropes were observed and red triangles indicate locations where red-necked phalaropes were observed. Transparency of the symbol is relative to the proportion of the flock foraging during the survey, with lighter symbols indicating a lower proportion of birds foraging.
Figure 3-2. Mean proportions of phalaropes in a flock that were engaged in foraging behaviors in 3 bays of Great Salt Lake during 2014 and 2015. Error bars indicate standard error around the mean and sample sizes are given above each bay.
a) Graph showing average biomass (g/m²) for Carrington, Gilbert, and Farmington Bays. Bars represent different categories: BFA, BFP, CHL, BFL, BSA, COR.

b) Graph showing average biomass (g/m²) for Carrington, Gilbert, and Farmington Bays. Bars represent different categories: BSA, BFL, BFP, CHL, COR.
Figure 3-3. Mean biomass (mg/m²) of a) all invertebrates (including brine fly adults, which are mg/m²/10 min), sampled in 3 bays of Great Salt Lake, b) aquatic invertebrates sampled with a vertical tow in 3 bays of Great Salt Lake, and c) aquatic invertebrates sampled by 2 methods in Farmington Bay. All samples were taken at phalarope observation sites during the staging periods of Wilson’s and red-necked phalaropes, 2014–2015. Abbreviations in the keys indicate types of invertebrates: BFA = brine fly adult, BFP = brine fly pupae, BFL = brine fly larvae, CHL = chironomid larvae, and COR = corixid. For a) and b), Carrington n = 11, Gilbert n = 11, and Farmington n = 19. For stovepipe samples in Farmington Bay (c), n = 12. In Farmington Bay, vertical tows sampled aquatic invertebrates from the upper 0.5 m of the water column, while the stovepipe method sampled both aquatic invertebrates and, at sites with loose sediment, benthic invertebrates from the top 0.02 m of substrate.
Figure 3.4. Proportion of foraging phalaropes that were a) engaged in surface picking behavior and b) spinning, by bay and species at Great Salt Lake during 2014 and 2015. Sample sizes are listed in Table 3.1. Error bars indicate standard error around the mean.
CHAPTER 4

EFFECTS OF PREY DENSITIES AND WEATHER ON EARED GREBE FALL MIGRATION

ABSTRACT Great Salt Lake (GSL) is a critical staging area for eared grebes (*Podiceps nigricollis*), but the factors influencing the timing of eared grebe fall migrations have not previously been investigated. Fall migration is challenging and dangerous for eared grebes because they are poor fliers and are susceptible to mass downings when they encounter inclement weather. I used archived Doppler radar data to visualize the nocturnal departures of eared grebes from GSL over 16 years, from 1999–2014. I examined timing of migration on 2 scales: first, by examining how prey availability and lake temperature were related to interannual variation in the timing of departures, and second, by examining how weather conditions were related to the likelihood that eared grebes would depart on a given night. I also examined whether eared grebe departures were correlated with a threshold density of brine shrimp adults, and whether a wind speed threshold existed above which eared grebes would not depart from GSL on a given night. On average, eared grebes departed from GSL over a period of 31 days each year, with departures occurring on 17 of those days. Departures typically began earlier in the season when densities of brine shrimp adults (*Artemia franciscana*) were high, densities of brine shrimp cysts were low, and lake temperatures were warmer than average. Median departure day also occurred earlier when lake temperatures were warmer than average. I did not find any trend toward earlier median departures over the years of the study as would be expected if eared grebe fall departures were impacted by climate change. The
span of migration departures was most strongly related to the day of first departure. On a
given night during the potential migration period, the likelihood that eared grebes would
depart from GSL was greater on nights with high barometric pressure over the previous
12 hours, which was consistent with the findings of other migration studies. I did not
detect a brine shrimp threshold or a wind threshold relative to migration departures.
Improved understanding of the conditions that affect eared grebe migration timing will
contribute to the proper management of GSL as an important staging area for eared
grebes.

INTRODUCTION

Great Salt Lake (GSL) hosts millions of migratory birds every year, including
waterfowl, waterbirds, and shorebirds (Aldrich and Paul 2002). Over half of the North
American population of eared grebes (*Podiceps nigricollis*) stages at GSL each fall
(Roberts et al. 2013). During their stay at GSL, eared grebes feast primarily on adult
brine shrimp (*Artemia franciscana*), which are abundant in the lake throughout most of
the staging period (Roberts and Conover 2013). As water temperature and primary
production in the lake decrease in late fall, adult brine shrimp densities also decrease and
ultimately collapse. In December, eared grebes increase their consumption of brine
shrimp cysts as the density of brine shrimp adults declines (Roberts and Conover 2013).
Concomitantly, brine shrimp cysts are collected by commercial harvesters, but
disturbance to eared grebes caused by harvesting is minimal (Roberts et al. 2013). In
addition to brine shrimp, eared grebes consume brine fly (Ephydridae) larvae, but
throughout the staging period brine fly larvae comprise a relatively small portion of
Eared grebes are the last migratory birds to depart from GSL each fall. Migration is especially challenging for eared grebes as they are poor fliers; their wings are small relative to their body mass, and they must take a running start from the water to become airborne (Jehl et al. 2003). During some years, migrating eared grebes encounter inclement weather that forces them to crash-land. These events are known as downings and can affect thousands to tens of thousands of birds (Jehl 1996). On some occasions, grebes will mistake the glow of lights on wet pavement for a body of water and will land in parking lots or on roads, which is a fatal error. Many grebes that land on hard surfaces die on impact (Jehl 1993), while others are killed by exposure to the elements and an inability to become airborne again. Thus, migration is risky for eared grebes and departure timing can directly affect survival.

The influence of prey availability on the timing of eared grebe departure from GSL has been debated in previous studies. During the staging period, eared grebes temporarily lose the ability to fly because their flight muscles atrophy while their digestive organs increase in size and mass (Jehl 1997). Eared grebes must then rebuild their flight muscles before departing for their wintering grounds. Jehl (1988) posited that eared grebes staging at Mono Lake, California, delayed migration until brine shrimp adults fell to a density of about 3,000 shrimp/m² (converted to 0.5 shrimp/L by Caudell and Conover (2006)). Caudell and Conover (2006) tested the hypothesis of a critical shrimp limit at GSL, but found that early departure from the lake was not correlated with low brine shrimp densities. Instead, eared grebes responded to low shrimp densities by increasing time spent foraging. Jehl (2007) refuted these conclusions and argued that the
data of Caudell and Conover (2006) did indicate an earlier migration in years with lower shrimp densities, and estimated that a density of 1.2 shrimp/L would trigger eared grebe departure from GSL.

Like many migrating birds, eared grebes depart at night and therefore cannot be observed directly (Jehl et al. 2003), but their migrations can be seen on local weather radar. Radar cannot typically distinguish among species of birds, but because grebes depart after other species, radar data can be used to determine exact departure times of eared grebes from GSL. Using radar to detect migrations has become common in studies of nocturnal migrants. Examples include determining the stopover locations of migrants (Buler and Dawson 2014), understanding how migrating birds navigate (O’Neal et al. 2015), and examining the effects of weather on migration (Gagnon et al. 2011).

For this study, I considered factors that may influence the timing of the eared grebe migration period, as well as factors that may influence the likelihood of eared grebe departure on a given night. While weather variables have often been considered in migration studies, I am only aware of one study to consider the effects of both prey availability and weather on the timing of departure. Studds and Marra (2011) examined rainfall and arthropod biomass as factors related to the departure dates of migrating American redstarts (Setophaga ruticilla). Decreased arthropod biomass and decreased rainfall in the month of March were both correlated with earlier departure dates of redstarts (Studds and Marra 2011). Weather conditions are a well-known influence on whether birds depart on a given night as well (Richardson 1990). In particular, previous studies on the effects of weather have indicated the importance of wind, precipitation, and cloud cover on nightly departure decisions (Åkesson and Hedenström 2000, Schaub
et al. 2004, Van Belle et al. 2007, Gagnon et al. 2011, Sjöberg et al. 2015). In addition to weather, Sjöberg et al. (2015) considered the effect of body condition on migration; fatter birds completed migration faster. However, the study did not examine differences in the timing of departure between fat and lean birds.

I had 3 objectives for this research. The first was to use Doppler radar to determine the timing of eared grebe fall migration from GSL from 1999 through 2014. From this data, I sought to examine factors that were correlated with interannual variation in the first, median, and last days of migration, as well as the span of the migration period. I predicted that departures would occur earlier in years with lower densities of brine shrimp adults, because brine shrimp are the primary prey of eared grebes during the staging period. My second objective was to use Doppler radar data and local weather data to evaluate the influence of weather conditions on the likelihood that eared grebes would depart from GSL on any given night during their potential migration period. I hypothesized that eared grebes would be more likely to depart from GSL on nights with low winds, no precipitation, and high barometric pressures. My third objective was to examine whether departure timing was triggered by a shrimp threshold (with all departures occurring after densities of brine shrimp adults fell to a certain level), and whether departure on a given night was limited by a wind threshold (with no departures occurring on nights when winds were above a certain speed). I predicted that a shrimp threshold would exist, but that it would be lower than the 1.2 shrimp/L suggested by Jehl (2007), due to increased foraging by eared grebes as prey densities decrease. Without much biological basis for my hypothesis of a wind threshold, I predicted that no eared grebes would depart from GSL when there were unfavorable winds >5 m/s.
METHODS

Study Area

Great Salt Lake is a large (4,400 km²), terminal lake in northern Utah, USA. Great Salt Lake is shallow, with an average depth of 4.9 m when the lake elevation is at its historic average of 1,283 m above sea level. The average annual lake level fluctuated over the period of years included in this study, from a high of 1,281 m in 1999 to a low of 1,278 m in 2014 (U.S. Geological Survey 2015). Two causeways cross the lake and restrict water flow; this flow restriction combined with the clumped distribution of freshwater inflow results in a variety of salinities throughout the bays of GSL. Salinity affects brine shrimp distribution and therefore eared grebe distribution (Roberts et al. 2013). Before migration departures begin, eared grebes are most abundant in central and southern Gilbert Bay (Fig. 4-1).

The National Oceanic and Atmospheric Administration (NOAA) Doppler radar station for Salt Lake City, KMTX, is located north of Gilbert Bay on a peninsula called Promontory Point (Fig. 4-1). Stansbury Island and Antelope Island border Gilbert Bay on the west and east, respectively, while the Stansbury and Oquirrh mountain ranges are located south of GSL. These geographic features interfere with the radar signal from KMTX to some degree. Antelope Island blocks much of the low-elevation signal from reaching Farmington Bay, but eared grebes do not typically spend time in that bay before migrating (Roberts and Conover 2014). The mountain ranges south of the lake also block low-elevation signals, so that eared grebes on radar appear as a tight column between these ranges. In reality, migrating grebes probably fly closer to the mountains than
indicated on radar, but this did not affect detection of flocks.

**Data Collection**

*Radar Data.*—Archived radar data for KMTX are free and publicly available from 1995 to present day. I examined data for migration seasons from 1999–2014, because data on GSL brine shrimp densities and lake temperatures were not available prior to 1999. Within each year, I obtained radar data for 02 November through 20 January. For each day, I examined data from 0000 hours to 0459 hours Greenwich Mean Time (GMT), which corresponded with 1700 hours to 2359 hours Mountain Standard Time (MST) for the dates of 01 November through 19 January. I chose these dates and times to encompass the entire time period over which eared grebes may potentially be migrating (i.e. the potential migration period).

I visualized radar images using NOAA’s Weather and Climate Toolkit (Ansari 2015). Each radar sweep collects several types of data. Base velocity data represent the speed of airborne objects relative to the radar station. I used base velocity images to visualize flocks of eared grebes, which fly directly south of KMTX. I examined base velocity data from the 0.5° radar sweep, which is the lowest angle available at this station. Even though higher-resolution (256 Level) data became available in 2010, I used lower-resolution 16 Level data for all years so that visualization of data was consistent.

To identify nights when eared grebes departed from GSL, I first looked for images showing a column of birds moving south or southwest. Eared grebes migrate in large flocks that are conspicuous on the radar. A date criterion was considered next, because migrations of other birds, such as waterfowl, were common before 18 November
and could not always be distinguished from eared grebes. I subsequently narrowed the search to start on 18 November of each year. Thus, a few early eared grebe departure days may have been excluded from the analysis, but the sample size was large enough that this should not have affected the results. The third criterion for identifying eared grebe departure was that the flock pattern had to originate from Gilbert, Carrington, or Ogden Bays (Fig. 4-1). Finally, the flock had to appear in two consecutive images and be greater than four color blocks in size (airborne objects detected by radar are represented by a pixel of color when visualized; individual birds cannot be distinguished from any other airborne object). Very small flocks of grebes that departed from GSL would have been excluded by this criterion, but I was unable to confidently distinguish those flocks from other aerial objects. I created a binary variable for departure, with “0” for days without a departure and “1” for days with a departure.

I considered 3 time variables related to eared grebe departure: year of migration (YOM), Day, and Week. Because digital radar data collection began in 1995, I defined 1995 as YOM 0 so that each YOM could easily be calculated by subtracting 1995 from the year. Day 1 was defined as 18 November. In the final data analysis, I removed all days past the last day on which I observed a departure. Therefore, each year had a different total number of days. Week 1 began on 18 November each year, so that Week 1 corresponded to Days 1 – 7, Week 2 corresponded to Days 8 – 14, etc.

Weather Data---I obtained weather data from 2 weather stations at GSL, 1 on Hat Island and 1 on the south shore of Gilbert Bay. The data from these stations were available for the full study period. I obtained the following weather measurements: temperature (°C), ground-level wind speed (m/s), ground-level gust speed (m/s), wind
direction (°), barometric pressure (mmHg), precipitation (cm), and precipitation (ordinal, with higher numbers indicating more intense precipitation). These weather stations approximately bordered the area of the lake where most eared grebes were located before departing. For most days, values were available from both stations, so I averaged the values. On days when data were only available from one station, I used that one set of data. The precipitation (cm) data were sparse and not meaningful, so I combined these data with the precipitation (ordinal scale) data to create a binary variable representing occurrence of precipitation, where “0” indicated no precipitation and “1” indicated occurrence of some form of precipitation. For each weather measurement except precipitation, I created 3 variables: the value at 1700 MST (i.e. “sunset”), the average value of the weather factor 12 hr prior to sunset, and the average value of the weather factor 24 hr prior to sunset. I created the 12 and 24 hr variables to examine whether there were any lags in the effect of weather on departure. For precipitation, I created 2 variables, for occurrence of precipitation 1 hr and 3 hr before sunset.

*Brine shrimp density data.*---Utah Division of Wildlife Resources (UDWR) collected data on the densities of all life stages of brine shrimp in GSL throughout the year for all years of the study. The surveys were conducted by the Great Salt Lake Ecosystem Program (GSLEP) at 17 sites across GSL. Data were collected approximately once per week during the staging period of eared grebes. From these data, I examined adult brine shrimp densities (shrimp/L) and cyst densities (cysts/L). I interpolated densities linearly between collection days. I also created variables for lags in density of adult brine shrimp to test the hypothesis that eared grebes depart from staging areas after rebuilding their flight muscles in response to a threshold density of brine shrimp adults
(Jehl 2007). Jehl (1988) noted a substantial increase in the flying ability of eared grebes on Mono Lake over a span of 2 weeks, concomitant with exercise behavior to increase flight muscles, and therefore estimated that 2 weeks is the average amount of time eared grebes need to regrow their flight muscles before departing for migration. To account for uncertainty and variation in the time needed for eared grebes to regain flight ability, I considered lags of 7, 14, and 21 days.

Other environmental data.---I considered 3 additional environmental variables that may have affected eared grebe departure. Lake temperature (°C) was collected by GSLEP during shrimp surveys, and I used the average value from the 17 sites they measured. As with shrimp data, I interpolated lake temperature linearly between collection days. Because eared grebes migrate at night, I considered the effect of moon illumination on departure. To create the moon variable, I obtained the percentage of moon illumination on each night and determined whether the moon was present in the sky during or within 4 hr after eared grebe departure (Astronomical Applications Department 2015). If the moon was in the sky during departure or within 4 hr after, the value I used for the moon variable was the percentage of illumination, although it should be noted that this value does not account for cloud cover. If the moon had already set or had not yet risen during departure, I coded the variable as 0. Finally, I created a “storms” variable to consider in analyzing the length of the migration span. I considered a night to be stormy if there were unfavorable (120–240°) or slightly unfavorable (90–120° or 240–270°) winds greater than 5 m/s, unfavorable or slightly unfavorable gusts greater than 10 m/s, and/or any precipitation. This was a binary variable, with “0” for non-stormy nights and “1” for stormy nights.
**Statistical Analysis**

All statistical analyses were conducted in R (R Core Team 2016). Explanatory variables were continuous and linear except YOM (categorical, treated as a random component), precipitation (binary), and wind direction, which was circular and was analyzed using package circular (Ulric Lund 2013). I calculated mean first and last dates of departure, median departure day, and average migration span (i.e. the number of days from the first to the last departure within the potential migration period). To examine interannual variability in first, median, and last departure days, I built linear models that considered the effects of brine shrimp adult density, brine shrimp cyst density, and water temperature. I also built linear models to examine the variation in migration span relative to brine shrimp adult density, brine shrimp cyst density, number of nights with storms, and the first day of migration departure. All variables were standardized by taking the difference between the measurement for that year and the measurement on the mean response day (e.g., the difference between lake temperature on day of first departure in 1999 and lake temperature on the mean day of first departure across all years). Negative values therefore indicate a lower-than-average measurement, while positive values indicate that the measurement was higher than average. Likewise, negative day values indicate an earlier-than-average departure, while positive day values indicate a departure that was later than average. I compared models with second-order Akaike’s Information Criterion (AICc) using package MuMIn (Bartoń 2015).

To examine differences between departure and non-departure nights, I conducted t-tests to compare departure with each of the explanatory variables. For modeling, I only included variables that were not significantly correlated \( (\alpha \geq 0.10) \) with other variables in
the model; I obtained correlations with package Hmisc (Harrell 2014). I used logistic regression to examine departure differences among YOM and Week, to determine whether these time variables should be included in the models. To account for both wind speed and direction in my models, I multiplied wind speed by 1 for “favorable” wind (from the north and with eared grebe migration, 300–60°), by -1 for “unfavorable” wind (from the south and against eared grebe migration, 120–240°), by 0.1 for “slightly favorable” wind (60–90° or 270–300°), or by -0.1 for “slightly unfavorable” wind (90–120° or 240–270°). I termed this variable “wind velocity,” even though it was not a true velocity measure. I modeled departure likelihood with logistic regression, and compared models with Akaike’s Information Criterion (AIC) using package MuMIn (Bartoń 2015).

Two additional analyses of interest were the potential threshold values for wind speed and brine shrimp densities. In addition to comparing the magnitude of the differences in these values between departure and non-departure nights, I determined the maximum (wind) and minimum (shrimp) values when departures occurred. Where appropriate throughout the results, means are given as mean ± SE.

RESULTS

Interannual Variations in Migration Timing

The mean day when eared grebes first departed from GSL was 02 December. The earliest day of first departure was 18 November (the first day of sampling), which occurred both in 1999 and in 2014. The latest day of first departure was 19 December, observed in 2012. The best model for variation in first day of departure included lake temperature (-4.5 ± 1.1, \( P = 0.001 \)), density of brine shrimp adults 14 days before first
migration (-6.1 ± 3.9, \( P = 0.15 \)), and density of brine shrimp cysts (0.1 ± 0.04, \( P = 0.01 \); Fig. 4-2). This model explained 64\% of the variance in first day of departure. A second model was competitive (\( \Delta AIC_c \leq 2 \)) and contained only the term for lake temperature (Table 4-1).

Median day of departure was not correlated with YOM (\( r = 0.15, \ P = 0.58 \)). Variation in median departure day was best represented by lake temperature, which was negatively correlated with the variation in median departure day (-3.0 ± 0.8, \( P = 0.003 \); Fig. 4-3). The top model explained 47\% of the variation in median day of departure. The second-ranked model was included density of brine shrimp adults 14 days before median departure in addition to lake temperature (Table 4-2), but this additional parameter was uninformative (Arnold 2010).

The mean day when eared grebes were last observed departing from GSL was 02 January. The earliest day of last departure was 18 December, observed in 1999, while the latest day of last departure was 19 January, observed in 2002. None of the models for the variation in last departure day were strong: 5 models were competitive and none were significant against a null model (Table 4-3). The top model included only the density of brine shrimp adults 21 days before last departure, which was weakly negatively correlated with the variation in day of last departure (-12.7 ± 9.9, \( P = 0.22 \), Fig. 4-4). This model explained 10\% of the variation in day of last departure.

On average, eared grebes departed from GSL on 17 nights each year. In 2009, just 8 departures were observed, while there were 31 departures in 2014 (Fig. 4-5). The migration span was 31 days on average. The shortest migration span occurred in 2012 and lasted just 14 nights. The longest migration span occurred in 2002 and covered 54
nights (Fig. 4-6). The best model of interannual variation included only the day of first
departure that year (Table 4-4). Migration span was negatively related to day of first
departure (-0.5 ± 0.2, \( P = 0.04 \)), meaning that migration span was shorter in years when
the first migration occurred later (Fig. 4-7). No models were competitive with the top
model and the top model explained 28% of the variation in migration spans among years.

**Effect of Weather on Departure Likelihood**

I evaluated departures over 734 nights from 1999 to 2014. On 19 nights, I could
not discern whether a departure had occurred, leaving 715 nights for analysis. All
departures began after sunset and ended no later than 2330 hours each night. All of the
weather variables, except wind direction at sunset and mean wind direction over 24 hr
prior to sunset, were significantly different between departure and non-departure nights,
likely due to the large sample size (Table 4-5). Moon illumination was not different
between departure and non-departure nights. Many of the continuous weather variables
were highly correlated with one another (Table A-6). For modeling, I removed
observations with any missing variables, leaving 652 observations. I compared models of
departure likelihood with AIC because the sample size was large relative to the estimated
number of parameters (Burnham and Anderson 2002).

Differences in the likelihood of departure by YOM were marginally significant
\( (\chi^2_1 = 3.25, P = 0.07) \), so I included YOM as a random term in all models. There was also
a significant difference in departure likelihood by Week \( (\chi^2_1 = 60.47, P < 0.001) \); plotting
this variable revealed that the trend was quadratic, so I included Week and the square of
Week in all models. I chose to use the variable for average barometric pressure over the
12 hr prior to departure as a starting point for my models; I could then include other variables in the model that were more likely to affect eared grebes immediately before departure. I tested 5 models (Table 4-6). Other than the time variables, the top model included only a weak positive relationship between departure likelihood and barometric pressure ($\beta_{\text{pres12}} = 1.00 \pm 0.12$). The top model outperformed a null model ($\chi^2_3 = 163.05$, $P < 0.001$).

**Wind and Shrimp Thresholds**

The mean ground-level wind speed at sunset on departure nights was 2.3 ± 0.1 m/s, while the mean wind speed at sunset on non-departure nights was higher, 3.3 ± 0.1 m/s ($t_{670} = 5.30$, $P < 0.001$). Eared grebes preferred to depart on nights with calmer winds; most (94%) departures occurred when the wind speed was <5.0 m/s, while wind speed at sunset was <5.0 m/s for 82% of all non-departure nights. However, I did not find a threshold value above which eared grebes would not depart (Fig. 4-8). On 2 occasions, eared grebes departed from GSL when the wind speed at sunset was >16.0 m/s. Of the departure nights with wind speeds ≥5.0 m/s, 60% had a favorable wind direction. Of the non-departure nights with wind speeds ≥5.0 m/s, only 41% had favorable winds.

Shrimp densities decreased before and during the potential migration period each year, but I did not find a clear shrimp-density threshold. The mean density of brine shrimp adults 14 days before first departure was 0.72 ± 0.11 shrimp/L, and the mean density of brine shrimp adults 14 days before median departure was 0.42 ± 0.08 shrimp/L (Fig. 4-9). I also calculated the mean densities 21 days before first and median departure, to examine whether eared grebes were responding to a threshold that occurs earlier
relative to when they begin physiological changes. The mean density of brine shrimp adults 21 days before first departure was $0.80 \pm 0.13$ shrimp/L, while the mean density of brine shrimp adults 21 days before median departure was $0.57 \pm 0.10$ shrimp/L.

**DISCUSSION**

Migration is a costly undertaking for any species, and the timing of migration can have a broad range of consequences on migrants (Bauer et al. 2016). Eared grebes staging at GSL forage for months to gain sufficient mass before their fall departure; knowing the factors that influence the timing of departure can help managers protect the resources that eared grebes need to complete a successful migration. Previous research has indicated that some, but not all, species of waterfowl have delayed the timing of their fall migrations over recent years, possibly due to climate change (Lehikoinen and Jaatinen 2012). In my study, eared grebe migration over the past 16 years showed a slight trend toward later migration, but this relationship was not significant. Yearly variations in eared grebe departures should continue to be monitored to determine whether migrations are occurring later.

An important caveat in this study is that the brine shrimp densities I used were an average value from samples taken across GSL. However, considerable differences in the distribution of brine shrimp likely exist throughout GSL. If brine shrimp densities decrease in one area of the lake, eared grebes may move to another area of the lake rather than depart. Sites with low densities of shrimp pull down the overall lake average, but eared grebes may not be using these areas and may instead spend time at sites with sufficient prey. Eared grebe movements on GSL during the staging period are largely
unknown, but one study has indicated that changes in distribution of eared grebes on GSL can be predicted by prey availability (Roberts et al. 2013). Further research on the movements of eared grebes during the staging period relative to prey availability could contribute substantially to the understanding of multiple aspects of eared grebe migration.

Day of first departure was related to lake temperatures and prey availability (brine shrimp adults plus brine shrimp cysts). However, some of the relationships were in the opposite direction of what I expected. While earlier departure initiation was correlated with lower densities of brine shrimp cysts, early first departure was also correlated with higher lake temperatures and weakly correlated with higher densities of brine shrimp adults. Rather than lingering at staging areas as long as possible (Jehl 1988), my data suggest that eared grebes at GSL may begin migration departures when prey are still readily available. When temperatures are relatively warm and densities of brine shrimp adults are relatively high, eared grebes may be able to gain sufficient mass for migration more quickly, and may take advantage of favorable weather conditions relatively early in the potential migration period. Conversely, when brine shrimp adults are sparse, eared grebes may need to spend more time foraging to gain sufficient mass, as suggested by Caudell and Conover (Caudell and Conover 2006). Another consideration, however, is that brine shrimp adults are not the only source of prey for eared grebes at GSL. In October and November, eared grebes primarily consume brine shrimp adults, but about 9% of their diet consists of brine fly larvae throughout the staging period (Roberts and Conover 2013). In December, eared grebes increase their intake of brine shrimp cysts to around 44%. Availability of brine shrimp cysts as a prey item may be an important factor in the timing of eared grebe migration departures, which corresponds with the positive
relationship between timing of first departure and density of brine shrimp cysts.

By remaining on the lake longer when lake temperatures are lower, eared grebes may face thermoregulatory challenges. Heat loss to water is of particular concern because the thermal conductance of diving birds can be >2 times that of swimming birds (de Vries and van Eerden 1995). However, the amount of energy needed by eared grebes to keep warm before departure is unknown. The thermal neutral zone (TNZ) of eared grebes ranged from 15.0 to 38.1°C for eared grebes that were captured and tested in air temperature-controlled chambers in late summer/early fall (Ellis and Jehl 2003). While the water temperatures experienced by eared grebes on GSL are considerably colder than the air temperatures for which TNZ was measured, winter plumage and fat stores may reduce the thermo-energetic costs to eared grebes of remaining at GSL until they are ready to depart. Regardless of thermoregulatory costs, the general decrease in lake temperatures – which, on average, fell 2°C from first day of departure to median day – may be an important cue to eared grebes to depart from GSL.

In all of the models for departure timing, I included models of the densities of brine shrimp adults 21, 14, and 7 days before departure. For the models that included the brine shrimp cyst and lake temperature variables, however, I only included the 14-day lag in my a priori set. I did not test all lags with all variables to keep the number of a priori models small in light of my small sample size (Burnham and Anderson 2002). Post hoc, I tested the 21- and 7-day lags in a model with all variables. The model of first departure day that included brine shrimp cysts, lake temperature, and the 7-day lag outperformed the model with the 14 days lag. However, the top model for last day of departure included only the 21 days lag variable. One explanation for these variations is that grebes cue to
different lag times throughout the potential migration period. Another explanation is that the time needed for eared grebes to regrow their flight muscles may vary by individual, depending on a grebe’s ability to successfully forage, and by year, depending on prey availability. None of the lags that I tested post-hoc were significantly better than the others, which would be expected if the time need to regrow flight muscles was variable and if eared grebes can supplement their diets with other prey (brine fly larvae and brine shrimp cysts) before departure.

Rather than lake temperature or brine shrimp densities, the strongest predictor of migration span was the day on which first migration occurred. The migration span tended to be longer when the first migration occurred earlier and shorter when the first migration occurred later in the potential migration period. When eared grebes do not begin to migrate until later in the year, they may need to depart relatively quickly, as the weather tends to worsen later in the year. On the other hand, when departures begin early, grebes can depart at a more leisurely pace. A potential cause of differences in migration span that I did not investigate was differences in age class. Smaller birds lose body heat more quickly than do larger birds of the same species (de Vries and van Eerden 1995). As lake temperatures decrease, adult eared grebes may be able to delay migration for a longer period of time than juveniles. An alternative hypothesis is that, conversely, adults may be able to gain mass more quickly and depart earlier than juveniles. Differences in migration span could therefore be related to age class differences in ability to successfully attain sufficient mass. Future studies should investigate the ratio of juvenile to adult eared grebes present on GSL throughout the migration period to test this hypothesis.

Barometric pressure was a strong indicator of departure likelihood on a given
night, although the influence of barometric pressure on departure was unlikely to be
direct (Gagnon et al. 2011). Birds migrating south and southwest are more likely to
depart when pressure is high and rising (Richardson 1990). High pressures are strongly
correlated with low wind speeds, low gust speeds, and lower incidence of precipitation,
which are more likely to impact eared grebe departure than barometric pressure per se.

Migrating birds are affected by weather conditions all along their routes, not just at the
locations from which they depart. The average barometric pressure 12 hr before sunset
may be a better indicator of suitable weather conditions on the journey than the
conditions immediately before departure at the departure site. In my models, the pressure
model outperformed the model with both wind velocity and precipitation. However, there
are a few other reasons why the model with wind velocity and precipitation may have
performed poorly. Wind “velocity,” as I measured it here, was not an exact description of
the wind conditions on the lake. Additionally, I used wind speed and wind direction data
for surface conditions, which eared grebes only experience briefly while climbing to a
higher cruising altitude. Treating precipitation as a binary variable was also not a perfect
representation of conditions. The likelihood that eared grebes will depart may vary with
precipitation intensity, not just occurrence of precipitation. For all nights, I averaged the
weather measurements from 2 stations at GSL, but the conditions at these 2 stations often
varied. In particular, wind speeds tended to be higher at the Hat Island weather station
relative to the South weather station. Eared grebes staging in south Gilbert Bay, near the
South weather station, might experience slightly different conditions than grebes staging
in Carrington Bay, near the Hat Island station.

Interestingly, there was no difference in moon illumination on nights with and
without migration departure. My variable for moon illumination did not account for wind cover, which may have affected this result. However, the similarity in moon illumination on nights with and without departure suggests that eared grebes may not rely on the moon for navigation or improved visibility. Weather conditions that directly impact flying ability are probably more important to eared grebes than whether the moon is giving additional light for navigation.

Juvenile and adult eared grebes may respond differently to the same weather conditions, thus influencing variations in departure likelihood. Juvenile savannah sparrows (*Passerculus sandwichensis*) departed for fall migration when tailwinds were less supportive of their travel, compared with the wind conditions under which adult savannah sparrows departed (Mitchell et al. 2015). Juvenile eared grebes may depart under slightly different weather conditions than adults. Mitchell et al. (2015) suggested that juveniles may depart under less favorable conditions if the risks of predation or costs of thermoregulation exceed the increased energetic cost of flying with a less supportive tailwind. Thermoregulation costs might also spur juvenile eared grebes to depart earlier. Another explanation for the departure of juveniles under less favorable conditions is that juveniles lack the experience of adults to discern which nights are best for departure.

I did not detect a wind speed threshold above which eared grebes would not depart. The highest wind speed on a departure night was 17 m/s. Wind direction on that night was from the west, which could possibly pose a challenge to eared grebes at higher wind speeds. Why depart under such unfavorable conditions? This particular departure occurred late relative to other departures that year. Additionally, brine shrimp densities were especially low in the year that this departure occurred – just 0.02 shrimp/L. The cost
to the grebes of flying in high winds may have been low relative to the cost of remaining at GSL with virtually no prey.

Conover and Caudell (2009) estimated that eared grebes at GSL require at least 0.38 shrimp/L to satisfy their daily energy needs. Of the years that I measured, the density of brine shrimp adults 14 days before median departure was ≥0.38 shrimp/L for 44% of the years; eared grebe departure from GSL was underway before the densities of brine shrimp fell below critical levels almost half of the time. However, in all but 2 years of this study, the average shrimp densities 14 days before departure were below the threshold of 1.2 shrimp/L suggested by Jehl (2007). My research indicates that there is not a lake-wide brine shrimp density that triggers eared grebe departure from GSL, but decreasing prey availability is probably still a key signal to eared grebes to begin physiological changes. Future work should examine eared grebe departures in relation to the spatial heterogeneity of shrimp densities. Most likely, departure initiation is influenced by multiple factors. Lake temperature, weather patterns, individual variations in fitness, and (spatially heterogeneous) prey availability may all contribute to the departure decisions of eared grebes on GSL and affect the synchrony and consistency of migrations (Bauer et al. 2016). Structural equation models may be useful in future work to analyze the factors that contribute to the timing of eared grebe departure.

While many studies have examined the effects of weather on bird migration, the temporal duration of this research (16 years) exceeded that of previous studies and incorporated the effect of prey densities in the examination of interannual variability of migration timing. Archived radar and weather data are valuable tools that will support numerous future research projects regarding migration, especially as radar data continue
to improve. This study contributes to previous evidence that weather conditions influence the departure timing of migrating birds in the fall. My research also indicates that departure timing may be impacted by non-weather environmental factors, such as prey availability. In particular, brine shrimp cysts and brine fly larvae availability may influence eared grebe departure in addition to availability of brine shrimp adults. Other factors that may relate to departure – such as age class of migrants, body condition, and resource heterogeneity – should be investigated in future research to further improve understanding of the impetuses behind migration.

LITERATURE CITED


Ansari, S. 2015. NOAA’s Weather and Climate Toolkit. National Climatic Data Center, Asheville, North Carolina, USA.


http://cran.r-project.org/web/packages/MuMIn/index.html


TABLE 4-1. Linear regression models of the first day of eared grebe migration departures from Great Salt Lake, 1999–2014. All variables were calculated relative to the mean for that variable on the mean first day of migration and were standardized to an approximately normal distribution. Variables included: density of brine shrimp adults 14 days prior to first departure (shrimp/L; BSA14), density of brine shrimp cysts (cysts/L; Cyst), water temperature on day of first departure (°C; LakeTemp), density of brine shrimp adults 21 days prior to first departure (shrimp/L; BSA21), and density of brine shrimp adults 7 days prior to first departure (shrimp/L; BSA7). The sign in parentheses indicates whether the parameter estimate was negative or positive. K is the number of the parameters estimated in the model. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights to determine which variable(s) were most strongly related to variation in the first day of migration.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weight</th>
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<td>(-) BSA14 (+) Cyst (-) LakeTemp</td>
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<td>7.97</td>
<td>0.011</td>
</tr>
<tr>
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</tr>
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<td>9.92</td>
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TABLE 4-2. Linear regression models of the median day of eared grebe migration departures from Great Salt Lake, 1999–2014. All variables were calculated relative to the mean for that variable on the mean median day of migration and were standardized to an approximately normal distribution. Variables included: density of brine shrimp adults 14 days prior to median departure (shrimp/L; BSA14), density of brine shrimp cysts (cysts/L; Cyst), water temperature on day of median departure (°C; LakeTemp), density of brine shrimp adults 7 days prior to median departure (shrimp/L; BSA7), and density of brine shrimp adults 21 days prior to median departure (shrimp/L; BSA21). The sign in parentheses indicates whether the parameter estimate was negative or positive. K is the number of the parameters estimated in the model. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights to determine which variable(s) were most strongly related to variation in the median day of migration.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
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<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weight</th>
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TABLE 4-3. Linear regression models of the last day of eared grebe migration departures from Great Salt Lake, 1999–2014. All variables were calculated relative to the mean for that variable on the mean last day of migration and were standardized to an approximately normal distribution. Variables included: density of brine shrimp adults 21 days prior to last departure (shrimp/L; BSA21), density of brine shrimp adults 7 days prior to last departure (shrimp/L; BSA7), water temperature on day of last departure (°C; LakeTemp), density of brine shrimp cysts (cysts/L; Cyst), and density of brine shrimp adults 14 days prior to last departure (shrimp/L; BSA14). The sign in parentheses indicates whether the parameter estimate was negative or positive. K is the number of the parameters estimated in the model. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights to determine which variable(s) were most strongly related to variation in the last day of migration.

<table>
<thead>
<tr>
<th>Models</th>
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<th>ΔAICc</th>
<th>AICc weight</th>
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</tbody>
</table>
TABLE 4-4. Linear regression models of the span of eared grebe migration departures from Great Salt Lake, 1999–2014. All variables were calculated relative to the mean change in that variable over all migration spans and were standardized to an approximately normal distribution. Variables included: standardized day of first departure (difference between day of first departure and the 16-year mean day of first departure; FirstDep), change in density of brine shrimp adults from 7 days prior to first departure to 7 days prior to last departure (shrimp/L; dBSA7), change in density of brine shrimp cysts from day of first departure to day of last departure (cysts/L; Cyst), change in water temperature from day of first departure to day of last departure (°C; LakeTemp), and number of storms that occurred during the potential migration period (unfavorable or slightly unfavorable winds greater than 5 m/s, unfavorable or slightly unfavorable gusts greater than 10 m/s, and/or any precipitation; Storms). The sign in parentheses indicates whether the parameter estimate was negative or positive. K is the number of the parameters estimated in the model. LogLik is the log likelihood of the model and AICc is the second-order Akaike’s Information Criterion. Models were compared using AICc weights to determine which variable(s) were most strongly related to variation length of the migration span.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>(-) FirstDep</td>
<td>4</td>
<td>-54.6</td>
<td>117.3</td>
<td>0.00</td>
<td>0.718</td>
</tr>
<tr>
<td>(+) dBSA7</td>
<td>4</td>
<td>-56.9</td>
<td>121.7</td>
<td>4.46</td>
<td>0.077</td>
</tr>
<tr>
<td>(+) dCyst</td>
<td>4</td>
<td>-57.1</td>
<td>122.2</td>
<td>4.92</td>
<td>0.061</td>
</tr>
<tr>
<td>(-) dLakeTemp</td>
<td>4</td>
<td>-57.2</td>
<td>122.3</td>
<td>5.07</td>
<td>0.057</td>
</tr>
<tr>
<td>(-) Storms</td>
<td>4</td>
<td>-57.2</td>
<td>122.4</td>
<td>5.14</td>
<td>0.055</td>
</tr>
<tr>
<td>(+) dBSA7 (-) Storms</td>
<td>5</td>
<td>-56.6</td>
<td>124.8</td>
<td>7.52</td>
<td>0.017</td>
</tr>
<tr>
<td>(+) dBSA7 (-) dLakeTemp</td>
<td>5</td>
<td>-56.8</td>
<td>125.3</td>
<td>8.00</td>
<td>0.013</td>
</tr>
<tr>
<td>(+) dBSA7 (-) dLakeTemp (-) Storms</td>
<td>6</td>
<td>-56.5</td>
<td>129.1</td>
<td>11.79</td>
<td>0.002</td>
</tr>
</tbody>
</table>
TABLE 4-5. Mean values with standard errors for weather variables measured on nights with and without departures of eared grebes from Great Salt Lake during the potential migration periods of 1999–2014. Welch’s $t$-test was used to compare measurements on nights with and without departure for all variables except wind direction. Differences in wind direction for nights with and without departure were compared using 1-criterion analysis of variance for circular data. The designations “12” and “24” indicate variables for 12 and 24 hours prior to sunset, respectively. Wind speed, gust speed, and wind direction were measured at ground level. “Precipitation 1” and “Precipitation 3” indicate the occurrence of precipitation summed over 1 and 3 hours prior to sunset, respectively.

<table>
<thead>
<tr>
<th>Factor</th>
<th>$n$</th>
<th>No departure</th>
<th>Departure</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature ($^\circ$C)</td>
<td>690</td>
<td>2.0 ± 0.2</td>
<td>0.1 ± 0.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperature 12</td>
<td>709</td>
<td>0.8 ± 0.2</td>
<td>-0.3 ± 0.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperature 24</td>
<td>705</td>
<td>0.9 ± 0.2</td>
<td>-1.2 ± 0.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Wind speed (m/s)</td>
<td>709</td>
<td>3.3 ± 0.1</td>
<td>2.3 ± 0.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Wind speed 12</td>
<td>728</td>
<td>3.4 ± 0.1</td>
<td>2.9 ± 0.1</td>
<td>0.001</td>
</tr>
<tr>
<td>Wind speed 24</td>
<td>724</td>
<td>3.3 ± 0.1</td>
<td>2.9 ± 0.1</td>
<td>0.001</td>
</tr>
<tr>
<td>Gust speed (m/s)</td>
<td>661</td>
<td>5.1 ± 0.2</td>
<td>3.4 ± 0.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Gust speed 12</td>
<td>689</td>
<td>5.5 ± 0.2</td>
<td>4.3 ± 0.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Gust speed 24</td>
<td>695</td>
<td>5.3 ± 0.1</td>
<td>4.4 ± 0.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Barometric pressure (mmHg)</td>
<td>641</td>
<td>869.7 ± 0.3</td>
<td>874.9 ± 0.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Barometric pressure 12</td>
<td>611</td>
<td>870.0 ± 0.4</td>
<td>875.6 ± 0.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Barometric pressure 24</td>
<td>618</td>
<td>870.1 ± 0.4</td>
<td>874.2 ± 0.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Precipitation 1</td>
<td>693</td>
<td>0.1 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Precipitation 3</td>
<td>697</td>
<td>0.2 ± 0.0</td>
<td>0.1 ± 0.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Wind direction ($^\circ$)</td>
<td>690</td>
<td>84.4 ± 0.1</td>
<td>94.5 ± 0.1</td>
<td>0.29</td>
</tr>
<tr>
<td>Wind direction 12</td>
<td>709</td>
<td>157.4 ± 0.0</td>
<td>149.1 ± 0.1</td>
<td>0.05</td>
</tr>
<tr>
<td>Wind direction 24</td>
<td>705</td>
<td>160.7 ± 0.0</td>
<td>160.7 ± 0.0</td>
<td>0.99</td>
</tr>
<tr>
<td>Moon illumination</td>
<td>715</td>
<td>38.5 ± 1.9</td>
<td>38.7 ± 2.5</td>
<td>0.93</td>
</tr>
</tbody>
</table>
TABLE 4-6. Logistic regression models describing the likelihood that eared grebes would depart from Great Salt Lake on any given night, 1999–2014. Variables tested in the models included: average barometric pressure over the 12 hr prior to sunset (mmHg; Pres12), wind velocity (m/s multiplied by -1 for unfavorable winds, -0.1 for slightly unfavorable winds, 1 for favorable winds and 0.1 for slightly favorable winds, see text for specifications; WindV), and occurrence of precipitation 1 hr prior to sunset (binary; Precip1). Week (Week), and week squared (Wk2) were included in all models, as was a random term for year of migration (YOM). In all models, the parameter estimates were positive for Pres12 and Week, and negative for WindV and Wk2. K is the number of the parameters estimated in the model. LogLik is the log likelihood of the model and AIC is the Akaike’s Information Criterion. Models were compared using AIC weights to determine which variable(s) were most strongly related to variation length of the migration span.

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>logLik</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>AIC weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pres12 + Week + Wk2</td>
<td>20</td>
<td>-293.6</td>
<td>625.3</td>
<td>0.00</td>
<td>0.613</td>
</tr>
<tr>
<td>Pres12 + WindV + Week + Wk2</td>
<td>21</td>
<td>-293.1</td>
<td>626.2</td>
<td>0.92</td>
<td>0.387</td>
</tr>
<tr>
<td>Precip1 + Week + Wk2</td>
<td>20</td>
<td>-323.8</td>
<td>687.6</td>
<td>62.34</td>
<td>0.000</td>
</tr>
<tr>
<td>WindV + Precip1 + Week + Wk2</td>
<td>21</td>
<td>-325.1</td>
<td>688.3</td>
<td>63.00</td>
<td>0.000</td>
</tr>
<tr>
<td>WindV + Week + Wk2</td>
<td>20</td>
<td>-334.3</td>
<td>706.5</td>
<td>81.22</td>
<td>0.000</td>
</tr>
</tbody>
</table>
FIG. 4-1. Map of Great Salt Lake, UT, including major bays, causeways, freshwater inflow, and islands. KMTX radar station is represented by a solid circle and weather stations are represented by asterisks.
FIG. 4-2. Variation in day of first migration departure of eared grebes leaving from Great Salt Lake, 1999–2014, compared with variation in a) density of brine shrimp adults 14 days before first departure \( (r = -0.14, P = 0.62) \), b) density of brine shrimp cysts \( (r = 0.30, P = 0.26) \), and c) lake temperature \( (r = -0.60, P = 0.02) \). All explanatory variables were standardized by subtracting the mean value of that variable on the mean first day of migration departure, 02 December.
FIG. 4-3. Variation in day of median migration departure of eared grebes leaving from Great Salt Lake, 1999–2014, compared with variation in a) density of brine shrimp adults 14 days before median departure ($r = -0.16, P = 0.56$), and b) lake temperature ($r = -0.68, P = 0.004$). The lake temperature values plotted are the difference between the lake temperature in a given year and mean value of lake temperature on the average median day, 17 December.
FIG. 4-4. Variation in day of last migration departure of eared grebes leaving from Great Salt Lake, 1999–2014, compared with variation in density of brine shrimp adults 21 days before last departure ($r = -0.32, P = 0.22$). The explanatory variables were standardized by subtracting each year’s values from the value of that variable on the mean last day of departure, 02 January.
FIG. 4-5. Number of nights on which eared grebes departed from GSL each year during the fall migration, 1999–2014. Data are based on radar scans during the potential migration period (18 November – 20 January).
FIG. 4-6. Variation in eared grebe fall migration departures from Great Salt Lake by year, 1999–2014. Peaks indicate a single departure while plateaus indicate multiple consecutive days with departures. Valleys show a day or days where no departures occurred. Breaks indicate missing data.
FIG. 4-7. Variation in the length of the migration span of eared grebes leaving from Great Salt Lake, 1999–2014, relative to the first day of departure that year (r = -0.53, P = 0.04).
FIG. 4-8. Number of eared grebe migration departures from Great Salt Lake that occurred at various wind speeds, relative to the number of nights when no departures occurred, when wind direction was a) favorable, b) slightly favorable, c) unfavorable, and d) slightly unfavorable, 1999–2014 (see text for definitions of wind directions).
FIG. 4-9. Density of brine shrimp adults (shrimp/L) in Great Salt Lake 14 days prior to a) first departure and b) median departure over 16 years, 1999–2014. On each graph, the dashed line indicates the 1.2 shrimp/L threshold estimated by Jehl (2007) and the solid line indicates Caudell and Conover’s (2006) foraging efficiency threshold of 0.38 shrimp/L.
CHAPTER V
CONCLUSIONS AND FUTURE WORK

CONCLUSIONS

Managing a complex resource like Great Salt Lake (GSL) requires an understanding of the system and its inner workings. My research contributed to the knowledge and, therefore, the management of GSL through investigations into the relationship between invertebrate prey and ecology of staging waterbirds. I had three objectives for this research: 1) determine the habitats of GSL that are primarily used by phalaropes and evaluate the factors associated with phalarope use of those habitats, 2) investigate phalarope foraging behavior in relation to prey availability, and 3) examine the factors related to the interannual variation of eared grebe departure from GSL and determine whether migration departure is triggered by decreasing prey availability.

As in many ecosystems, a substantial threat to the health of the GSL ecosystem is habitat loss. Staging birds visit GSL each year because the lake and its surrounding habitats provide food resources that allow migratory birds to gain sufficient mass to migrate successfully to their wintering grounds. Therefore, maintaining suitable habitat at GSL for staging birds requires a bottom-up examination of factors that affect the food resources birds need. Several different issues have impacted invertebrate prey resources at GSL and therefore the suitability of staging bird habitat at GSL. A substantial driver of habitat loss at GSL was the construction of the railroad causeway between Gunnison and Gilbert Bays in 1959 and the subsequent increase in the salinity of Gunnison Bay (White et al. 2015). Since the early 1960s, the salinity of Gunnison Bay has been above the
tolerance levels of brine shrimp and brine flies. Solar evaporation ponds constructed around GSL have also reduced bird habitat by increasing the salinity of these ponds beyond the tolerance level of aquatic invertebrates. In both cases, bird habitat was lost because high salinity levels made the habitat unsuitable for use by aquatic invertebrates and therefore by birds. Recent threats to GSL habitat have primarily been related to the loss of water altogether. Inter- and intra-annual fluctuations in lake elevation at GSL are natural, but have been exacerbated by anthropogenic water use (Wurtsbaugh et al. 2016). Not only do low lake levels directly reduce habitat for birds by shrinking the size of the lake, but salinity increases as the elevation of GSL falls as well.

My research quantified the importance of invertebrate prey to three species of birds that stage at GSL. Wilson’s phalaropes, red-necked phalaropes, and eared grebes rely on GSL to provide them with sufficient prey to gain mass before their fall migrations each year. Migration is an energetically costly endeavor, so staging birds need a consistent prey resource that allows them to gain body mass before departure (Warnock 2010). Phalaropes and eared grebes each use different specific prey resources and different lake habitats at GSL, but habitat loss affects all three species. In addition to the importance of brine shrimp, brine flies and high-salinity bays, my research has demonstrated that Farmington Bay and its brackish-water invertebrates are important for staging phalaropes.

Phalarope habitat use at GSL was related to two key components lake-wide: water depth and density of aquatic invertebrates other than brine shrimp, such as brine fly larvae, brine fly pupae, chironomid larvae, and corixids. In Carrington Bay, large, dense phalarope flocks were found more often at sites with high biomasses of brine fly larvae
and pupae. Associations between phalarope presence and habitat variables in Farmington Bay were less clear, but an additional consideration in this area was the importance of salinity, which has been shown in laboratory experiments to affect the survival of the invertebrates found in Farmington Bay (Barnes and Wurtsbaugh 2015).

Examination of phalarope behaviors throughout GSL provided a clearer picture of the importance of invertebrate prey to phalaropes at GSL. Phalaropes foraged most frequently in Carrington Bay, which had the highest accumulations of brine fly adults, and in Farmington Bay, which had the highest densities of benthic macroinvertebrates. Additionally, I detected differences in the specific foraging behaviors used by the two species of phalaropes. Red-necked phalaropes were more likely than Wilson’s phalaropes to forage by surface picking, while Wilson’s phalaropes were more likely to forage by spinning. Overall, surface picking was the most common foraging behavior observed by both species, although I observed the full suite of foraging behaviors that have been described for phalaropes in other studies.

My research on eared grebes at GSL added to previous work on the resources needed by grebes during their staging period (Conover and Caudell 2009, Roberts and Conover 2013), by examining which factors were related to the departure of eared grebes at the end of their staging period. I analyzed eared grebe departures on two time scales, interannual and nightly. Interannual variation in the timing of eared grebe departures was most strongly correlated with lake temperature. First and median departure days occurred earlier in the year when lake temperatures were warmer. The span of eared grebe migrations was most strongly related to the timing of first departure day, with early departure initiation related to longer migration spans. Nightly variation in the likelihood
that eared grebes would depart from GSL was most strongly related to barometric pressure. Eared grebes were more likely to depart from GSL on nights when the average barometric pressure over 12 hours prior to sunset was high. Eared grebes generally departed when wind speeds were <5 m/s, but I did not detect a threshold wind speed above which grebes would not depart. I also did not detect a lake-wide shrimp threshold that triggered migration departures.

The uniqueness of GSL makes the ecosystem essential for birds migrating through the arid Great Basin region. Maintaining the GSL ecosystem as a suitable resource for migratory birds should be a top management priority. Phalaropes and eared grebes are present on GSL both in large numbers and in large proportions of their continental populations. While the overall population of eared grebes is high, the reliance of eared grebes on just two staging areas (GSL and Mono Lake, California) makes them vulnerable to any changes that reduce habitat suitability in those areas (Roberts et al. 2013). The continental populations of both species of phalaropes also depend on GSL resources, which are especially important in light of wetland habitat loss throughout the U.S. (Rittenhouse et al. 2012). Not only is GSL itself an important site for migratory birds, but the entire GSL ecosystem provides a critical matrix of wetland habitats that benefit many species. Managing wetlands on a landscape scale is important for all wetland birds (Naugle et al. 2001, Ma et al. 2010), and maintaining wetland connectivity is especially important for migratory birds that face a suite of challenges throughout their journeys (Iwamura et al. 2013). Management and conservation efforts should protect the Great Salt Lake ecosystem so that this critical staging area can continue to contribute to the global well-being of wetland bird populations.
FUTURE RESEARCH

The data provided in this study can guide management of the GSL ecosystem, particularly by encouraging the maintenance of sufficient water levels in GSL. However, additional studies are needed to refine our understanding, management, and conservation of the GSL ecosystem. Future studies related to the conservation of phalaropes at GSL should look beyond the lake itself and focus on the broader GSL ecosystem. In particular, little is known about roost sites used by phalaropes in the wetlands surrounding GSL, or about freshwater resources used by phalaropes. Breeding eared grebes also use the wetlands of GSL early in the year, and this use should be investigated. A major gap in current knowledge about staging eared grebes is how much grebes move throughout the bays of GSL during their staging period. Because eared grebes lose their ability to fly for several weeks during the staging period, research is needed regarding their ability to move throughout GSL in relation to heterogeneous prey resources. Site-specific studies of eared grebe populations in relation to prey densities may also provide a clearer picture of the factors that affect eared grebe fall migration departure.

Early concepts of energy transfer in GSL largely viewed the high-salinity bays as having two weakly linked food chains: one benthic (brine fly larvae) and the other pelagic (brine shrimp; Belovsky et al. 2011). Research on the prey consumed by wintering and migratory birds has revealed that some birds consume both benthic and pelagic invertebrates, linking the ecosystems more tightly (Vest and Conover 2011, Roberts and Conover 2013). Recent observations have suggested that the benthic and pelagic zones of GSL are also closely linked by the invertebrates themselves. Bioherms may contribute to brine shrimp survival and contribute substantially to the yearly life
cycle of these pelagic invertebrates (G. Belovsky, University of Notre Dame, personal communication). Keeping bioherms underwater and productive may therefore be even more critical to the health of GSL than just providing habitat to brine fly larvae. Research projects to investigate these linkages at the invertebrate level would improve management by providing an understanding of the foundation of GSL’s food web. Future research is also needed regarding brine flies. In particular, future work should examine how densities of brine fly larvae vary spatially and temporally at GSL.

To complete the invertebrate prey picture, and to expand the understanding of resources needed by a greater number of birds, Farmington Bay invertebrates should be studied more thoroughly. I am aware of only one study that address some aspects of the ecology of corixids and chironomids from Farmington Bay (Barnes and Wurtsbaugh 2015). Many bird species that use Farmington Bay also prey upon these invertebrates, including globally important species such as American avocets (*Recurvirostra americana*), black-necked stilts (*Himantopus mexicaus*), and green-winged teal (*Anas crecca*; Barber and Cavitt 2012). In addition to the threats to GSL habitat as a whole, Farmington Bay faces threats such as eutrophication that may further impact its invertebrates and therefore birds.

**LITERATURE CITED**


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APPENDIX
Supplemental Tables

Table A-1. Comparison of prey and environmental measurements at sites with and without phalaropes in the high-salinity bays of Great Salt Lake during the staging period, 2014–2015.

<table>
<thead>
<tr>
<th></th>
<th>Non-phalarope sites</th>
<th>Phalarope sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water temperature (°C)</td>
<td>24.5 ± 0.4</td>
<td>24.7 ± 0.5</td>
</tr>
<tr>
<td>Wind speed (m/s)</td>
<td>1.9 ± 0.2</td>
<td>1.7 ± 0.2</td>
</tr>
<tr>
<td>Water depth (m)</td>
<td>5.6 ± 0.6</td>
<td>3.8 ± 0.8</td>
</tr>
<tr>
<td>Biomass of brine fly larvae/pupae (mg/m²)</td>
<td>8.7 ± 3.9</td>
<td>39.2 ± 33.3</td>
</tr>
<tr>
<td>Accumulation of brine fly adults (mg/m²/10 min)</td>
<td>375.9 ± 147.8</td>
<td>1022.7 ± 444.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Non-phalarope sites</th>
<th>Phalarope sites</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2013–2015</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water temperature (°C)</td>
<td>26.5 ± 0.8</td>
<td>23.5 ± 1.4</td>
</tr>
<tr>
<td>Wind speed (m/s)</td>
<td>1.2 ± 0.2</td>
<td>1.3 ± 0.1</td>
</tr>
<tr>
<td>Water depth (m)</td>
<td>0.3 ± 0.1</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td>Water salinity (%)</td>
<td>2.9 ± 1.2</td>
<td>2.1 ± 0.4</td>
</tr>
<tr>
<td>Biomass of benthic macroinvertebrates (mg/m²)</td>
<td>327.7 ± 109.2</td>
<td>346.3 ± 83.0</td>
</tr>
<tr>
<td><strong>2014–2015</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water temperature (°C)</td>
<td>26.4 ± 0.9</td>
<td>25.1 ± 1.0</td>
</tr>
<tr>
<td>Wind speed (m/s)</td>
<td>1.4 ± 0.2</td>
<td>1.1 ± 0.1</td>
</tr>
<tr>
<td>Water depth (m)</td>
<td>0.3 ± 0.1</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td>Water salinity (%)</td>
<td>2.6 ± 1.4</td>
<td>1.2 ± 0.2</td>
</tr>
<tr>
<td>Biomass of benthic macroinvertebrates (mg/m²)</td>
<td>464.4 ± 105.3</td>
<td>297.9 ± 103.8</td>
</tr>
</tbody>
</table>
Table A-3. Mixed-effects logistic regression models of phalarope presence in a low-salinity bay of Great Salt Lake over 3 years, 2013–2015. Total number of phalarope and non-phalarope sites was 43. Variables included water salinity (Salinity; %), water depth (Depth; m), biomass of benthic macroinvertebrates (BnInv; mg/m²), and water temperature (Water; °C). The sign noted in parentheses before each variable indicates whether the coefficient was positive or negative for that parameter. LogLik is the log likelihood of the model and AIC_c is the second-order Akaike’s Information Criterion. Models were compared using AIC_c weights (weight) to determine which variable(s) were most related to the likelihood of phalarope presence at a site. The model set tested was the same as for the 2014–2015 data.

<table>
<thead>
<tr>
<th>Model parameters</th>
<th>K</th>
<th>logLik</th>
<th>AIC_c</th>
<th>Δ AIC_c</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>(-) Salinity</td>
<td>4</td>
<td>-15.9</td>
<td>38.8</td>
<td>0.00</td>
<td>0.326</td>
</tr>
<tr>
<td>(-) Depth</td>
<td>4</td>
<td>-15.9</td>
<td>38.8</td>
<td>0.01</td>
<td>0.324</td>
</tr>
<tr>
<td>(+) BnInv</td>
<td>4</td>
<td>-16.8</td>
<td>40.6</td>
<td>1.80</td>
<td>0.132</td>
</tr>
<tr>
<td>(+) BnInv (-) Depth</td>
<td>5</td>
<td>-15.8</td>
<td>41.5</td>
<td>2.71</td>
<td>0.084</td>
</tr>
<tr>
<td>(-) BnInv (-) Salinity</td>
<td>5</td>
<td>-15.8</td>
<td>41.6</td>
<td>2.77</td>
<td>0.082</td>
</tr>
<tr>
<td>(+) BnInv (-) Water</td>
<td>5</td>
<td>-16.8</td>
<td>43.4</td>
<td>4.62</td>
<td>0.032</td>
</tr>
<tr>
<td>(+) BnInv (-) Depth (+) BnInv*Depth</td>
<td>6</td>
<td>-15.7</td>
<td>44.5</td>
<td>5.67</td>
<td>0.019</td>
</tr>
</tbody>
</table>
Table A-4. Mean percentages of non-foraging phalaropes engaged in each pre-defined non-foraging behavior at Great Salt Lake during the staging periods of 2014 and 2015, by site and species. See text for definitions of behaviors.

<table>
<thead>
<tr>
<th></th>
<th>Alert</th>
<th>Preen</th>
<th>Interaction</th>
<th>Movement</th>
<th>Inactive</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Wilson’s phalaropes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrington</td>
<td>34.0%</td>
<td>4.2%</td>
<td>0.2%</td>
<td>2.8%</td>
<td>5.9%</td>
</tr>
<tr>
<td>Gilbert</td>
<td>64.4%</td>
<td>1.3%</td>
<td>0.0%</td>
<td>13.4%</td>
<td>7.5%</td>
</tr>
<tr>
<td>Farmington – deep</td>
<td>17.6%</td>
<td>18.2%</td>
<td>0.0%</td>
<td>12.2%</td>
<td>11.8%</td>
</tr>
<tr>
<td>Farmington – shallow</td>
<td>5.6%</td>
<td>29.4%</td>
<td>1.4%</td>
<td>8.7%</td>
<td>8.8%</td>
</tr>
<tr>
<td><strong>Red-necked phalaropes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrington</td>
<td>77.2%</td>
<td>4.2%</td>
<td>0.0%</td>
<td>0.5%</td>
<td>0.5%</td>
</tr>
<tr>
<td>Gilbert</td>
<td>35.9%</td>
<td>0.7%</td>
<td>0.0%</td>
<td>6.2%</td>
<td>8%</td>
</tr>
<tr>
<td>Farmington – deep</td>
<td>10.1%</td>
<td>31.2%</td>
<td>2.2%</td>
<td>12.3%</td>
<td>9.1%</td>
</tr>
<tr>
<td>Farmington – shallow</td>
<td>16.7%</td>
<td>33.3%</td>
<td>33.3%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
</tbody>
</table>
Table A-5. Mean percentages of foraging phalaropes engaged in each pre-defined foraging behavior at Great Salt Lake during the staging periods of 2014 and 2015, by site and species. See text for definitions of behaviors.

<table>
<thead>
<tr>
<th></th>
<th>Surface pick</th>
<th>Spin</th>
<th>Air pick</th>
<th>Dunk</th>
<th>Bob</th>
<th>Search</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Wilson’s phalaropes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrington</td>
<td>50.0%</td>
<td>9.3%</td>
<td>3.1%</td>
<td>1.7%</td>
<td>3.3%</td>
<td>32.6%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Gilbert</td>
<td>50.4%</td>
<td>1.4%</td>
<td>2.6%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>45.6%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Farmington deep</td>
<td>14.7%</td>
<td>42.0%</td>
<td>0.1%</td>
<td>16.9%</td>
<td>0.1%</td>
<td>26.2%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Farmington shallow</td>
<td>41.3%</td>
<td>16.8%</td>
<td>0.1%</td>
<td>33.2%</td>
<td>0.0%</td>
<td>8.6%</td>
<td>0.0%</td>
</tr>
<tr>
<td><strong>Red-necked phalaropes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrington</td>
<td>89.4%</td>
<td>0.4%</td>
<td>0.0%</td>
<td>0.2%</td>
<td>0.0%</td>
<td>10.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Gilbert</td>
<td>77.9%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>22.1%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Farmington deep</td>
<td>44.5%</td>
<td>4.6%</td>
<td>0.4%</td>
<td>0.5%</td>
<td>0.0%</td>
<td>50.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Farmington shallow</td>
<td>39.6%</td>
<td>1.0%</td>
<td>1.6%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>57.8%</td>
<td>0.5%</td>
</tr>
</tbody>
</table>
Table A-6. Correlations among continuous weather variables measured during the potential migration period of eared grebes from Great Salt Lake, 1999–2014. Numbers above the gray diagonal are correlation values (Pearson’s r) and numbers below the gray diagonal are the corresponding \( P \)-values.

<table>
<thead>
<tr>
<th></th>
<th>Temp(^a)</th>
<th>Temp12</th>
<th>Temp24</th>
<th>Wind(^b)</th>
<th>Wind12</th>
<th>Wind24</th>
<th>Gust(^c)</th>
<th>Pres(^d)</th>
<th>Pres12</th>
<th>Pres24</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp</td>
<td></td>
<td>0.70</td>
<td>0.91</td>
<td>-0.01</td>
<td>0.01</td>
<td>-0.11</td>
<td>0.02</td>
<td>-0.13</td>
<td>-0.07</td>
<td>0.00</td>
</tr>
<tr>
<td>T12</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T24</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
<td>0.11</td>
<td>-0.01</td>
<td>-0.21</td>
<td>0.13</td>
<td>-0.22</td>
<td>-0.20</td>
<td>-0.11</td>
</tr>
<tr>
<td>Wind</td>
<td>0.69</td>
<td>0.02</td>
<td>0.00</td>
<td></td>
<td>0.22</td>
<td>0.05</td>
<td>0.96</td>
<td>-0.01</td>
<td>-0.05</td>
<td>-0.05</td>
</tr>
<tr>
<td>Wind12</td>
<td>0.76</td>
<td>0.05</td>
<td>0.73</td>
<td>0.00</td>
<td></td>
<td>0.39</td>
<td>0.20</td>
<td>0.17</td>
<td>0.15</td>
<td>0.13</td>
</tr>
<tr>
<td>Wind24</td>
<td>0.00</td>
<td>0.01</td>
<td>0.00</td>
<td>0.16</td>
<td>0.00</td>
<td></td>
<td>0.03</td>
<td>0.27</td>
<td>0.30</td>
<td>0.24</td>
</tr>
<tr>
<td>Gust</td>
<td>0.63</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.52</td>
<td></td>
<td>-0.02</td>
<td>-0.05</td>
<td>-0.04</td>
</tr>
<tr>
<td>Pres</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.77</td>
<td>0.00</td>
<td>0.00</td>
<td>0.56</td>
<td></td>
<td>0.94</td>
<td>0.72</td>
</tr>
<tr>
<td>Pres12</td>
<td>0.07</td>
<td>0.00</td>
<td>0.00</td>
<td>0.18</td>
<td>0.00</td>
<td>0.00</td>
<td>0.21</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pres24</td>
<td>0.95</td>
<td>0.03</td>
<td>0.01</td>
<td>0.25</td>
<td>0.00</td>
<td>0.00</td>
<td>0.33</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

\(^a\)Temp = air temperature (°C), \(^b\)Wind = ground-level wind speed (m/s), \(^c\)Gust = ground-level wind gust speed (m/s), \(^d\)Pres = barometric pressure (mmHg). A 12 or 24 after a weather abbreviation indicates that the value tested was the mean of the measurements over the 12 or 24 hours prior to sunset.
CURRICULUM VITAE

Maureen G. Frank
5230 Old Main Hill, Logan, UT 84322
Phone: (303) 547-6503
Email: mgfrank12@gmail.com

Education

Ph.D., Wildlife Biology                        August 2016 – Present
Utah State University, Logan, Utah
Dissertation: Migratory waterbird ecology at a critical staging area, Great Salt Lake, Utah
Cumulative GPA: 3.96

Bachelor of Science, Wildlife and Fisheries Sciences      May 2012
Texas A&M University, College Station, Texas
Cumulative GPA: 3.92, Summa Cum Laude

Professional Experience

Ph.D. Research Assistant, Utah State University             August 2012 – Present
Advisor: Dr. Michael Conover
Long-term monitoring of waterbird use of Great Salt Lake through aerial surveys; created flight plans and performed population estimates. Designed and conducted field research for studies of phalarope diet, invertebrate abundance, phalarope habitat use, and phalarope behavior. Compiled data from various sources, including radar images, to study timing of fall eared grebe migration. Managed, coordinated, and supervised lab technicians: 13 total, up to 6 at a time. Managed and analyzed data using various statistical methods. Wrote annual reports for funding agency. Presented results of study for scientific advisory groups, university symposia, and professional conferences.

Teaching Assistant, Utah State University          Spring 2014, 2015
Supervisor: Dr. Michael Conover
WILD 3300 – Animal Behavior/Communications Intensive
Created and managed online materials to teach grammar, composition, and editing skills for clear scientific writing. Gave in-class review lectures on grammar skills.
Prepared quizzes and exams to test students’ knowledge. Graded animal behavior quizzes, helped write exams, and conducted other classroom management.

Research Assistant, Texas A&M University

Advisor: Dr. Thomas DeWitt

September 2010 – May 2012

Undergraduate Program in Biological and Mathematical Sciences funded by the National Science Foundation

Conducted original research to analyze geometric morphometrics of isopods, *Ligia* spp. Compiled and managed a digital image database. Digitized consistent, repeatable morphometric points on images.

Relevant Volunteer Experience

Extension Volunteer, Utah State University

Supervisor: Tiffany Kinder

Natural Resource Field Days

Led educational activities designed for 4th grade students from Cache Valley. Taught students about aquatic macroinvertebrates and basic plant identification.

Research Assistant (Volunteer), Operation Wallacea

Supervisors: Peter Taylor, Jonathan Kolby, Dr. Merlijn Jocqué, Miguel Uribe

Honduras Expedition, Cusuco National Park, Honduras

Assisted with amphibian and reptile population surveys, bird point counts and mist netting, bat mist netting, small mammal trapping, sorting insects, and rainwater filtering for presence of *Batrachochytrium dendrobatidis*. Basic jungle survival training and jungle ecology course. Worked and lived in a remote area with sparse amenities, biting/stinging insects, venomous snakes, and weather hazards.

Peer-Reviewed Publications


Master Naturalist, Utah State University Extension. http://digitalcommons.usu.edu/


Weblog Publications


Research Presentations


Frank, M. G., and M. R. Conover. 24 Mar 2015. Thank goodness they got all the dragons: wildlife damage management through the ages. Increasing connections between IPM and wildlife damage management. 8th International Integrated Pest Management Symposium.


Frank, M. G., and M.R. Conover. 14 Aug 2013. It’s a bird, it’s a plane, it’s… an enormous migration! Radar data show winter departure of eared grebes from the Great Salt Lake. Annual Conference. Central Mountains and Plains Section of The
Wildlife Society.


Frank, M. G., and M.R. Conover. 21 Mar 2013. It’s a bird, it’s a plane, it’s… an enormous migration! Radar data show winter departure of eared grebes from the Great Salt Lake. Annual Conference. Utah Chapter of The Wildlife Society.


Invited Presentations

Phalarope reliance on brine flies and concomitant use of bioherm habitat. 11 May 2016. Invited speaker, 2016 Great Salt Lake Issues Forum. Salt Lake City, Utah.


Media and Other Presentations


The Amazon in your backyard. Utah State University Ignite!, Maureen Frank. 10 Apr 2015. https://www.youtube.com/watch?v=atNFLMeDxGA

Research Skills, Relevant Training, and Certifications

Educational Certifications
   Project WILD Basic (2011)
   Project WILD – Science and Civics (2011)

Technical Certifications
   Wilderness First Aid/CPR (2014 – current)
   SCUBA Open Water Diver – PADI (2005 – current)
Wildlife survey techniques
Technical: aerial surveys, radio telemetry, spotlight surveys, radar ornithology
Avian: point counts, behavior surveys, mist netting, bird banding
Reptiles and amphibians: capture, handling, and identification
Other: small mammal trapping, pond seining, invertebrate sampling, vegetation sampling

Grant writing
Getting started as a successful proposal writer and academician (two-day seminar)

Computer programs
Proficient use of Microsoft Office, ArcGIS, R, NOAA Toolkit (visualizing radar data)
Experience with SAS, Program MARK, tpsDig, tpsRelwarp

Languages
Spanish: Conversant in Spanish, able to read and write proficiently

Professional Service and Affiliations

Utah State University Graduate Student Council 2013 – 2016
Wildland Resources Graduate Student Representative (2015 – 2016)
Ecolunch Chair (Spring 2015)
Central Mountains and Plains Section of The Wildlife Society 2012 – present
Program Chair (2013 Annual Conference)
Human-Wildlife Interactions 2012 – present
Reviewer and page proofing
The Wildlife Society 2008 – present
Conservation Education and Outreach Working Group
Communications Committee (2015 – present)
Texas A&M University Student Chapter of The Wildlife Society 2008 – 2012
President (2010 – 2012)
Conclave Team (2010 – 2012)
Secretary (2009 – 2010)
Wildlife and Fisheries Science Department, Texas A&M University 2011 – 2012
Undergraduate Representative to the Department Head Search Committee

Awards and Grants

Robins Award Nominee Utah State University 2016
International Travel Award ($400) Utah State University, Office of Research and Graduate Studies 2015
Travel Award Match ($400) 2015
Utah State University, Department of Wildland Resources

Presidential Doctoral Research Fellowship ($20,000/yr) 2012 – 2016
Utah State University, Department of Graduate Studies
One of ten fellows chosen during the first year of the award

First Place Undergraduate Oral Presentation ($300) 2012
Texas A&M University
Student Research Week/Ecological Integration Symposium Dual Competition

Senior Merit Award 2012
Texas A&M University, College of Agriculture and Life Sciences

Outstanding Student Award 2010 and 2012
Texas Chapter of The Wildlife Society

References

Dr. Michael Conover (Major Professor)
Department of Wildland Resources, Utah State University
Phone: (435) 797-2436, Email: mike.conover@usu.edu

Dr. Karin Kettenring
Department of Watershed Resources, Utah State University
Phone: 435-797-2546, Email: karin.kettenring@usu.edu

John Luft
Great Salt Lake Ecosystem Program Manager, Utah Division of Wildlife Resources
Phone: (801) 985-3700, Email: johnluft@utah.gov

Dr. Thomas Lacher, Jr.
Wildlife and Fisheries Science Department, Texas A&M University
Phone: (979) 845-5750, Email: tlacher@tamu.edu