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A salt lake under stress: Relationships among birds, water levels, and invertebrates at a Great Basin saline lake

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ABSTRACT

Saline lakes are threatened globally and provide critical habitat for a diverse array of migratory and breeding waterbirds. The ability of large numbers of waterbirds to profitably use saline lakes is primarily dependent upon concentrations of invertebrate fauna that are only present within a narrow range of salinities. Additionally, waterbirds themselves can incur steep physiological costs as their salt loads increase, meaning that they are especially sensitive to changes in salinity. Nonetheless, relatively little is known about ecosystem function within natural saline lakes or how birds will respond to fluctuations in salinity across time, hindering efforts to maintain ecologically functional saline ecosystems. To help address this gap, we coupled data from waterbird surveys undertaken across 25 years at Lake Abert, Oregon, USA with data on lake area (a proxy for salinity) and invertebrate abundance to document how waterbird numbers changed in response to variation in lake area and the presence of their invertebrate prey. We found that as the area of Lake Abert decreased and salinity increased, both invertebrate and waterbird numbers declined, with especially high salinities associated with the presence of few waterbirds and invertebrates. However, we also found that at high lake levels and low salinities the abundance of most waterbirds and invertebrates either plateaued or declined as well. Our study reinforces physiological studies showing that both invertebrates and waterbirds can only tolerate a narrow range of salinities, and is among the first to document the effects of this tolerance range at the ecosystem level. As anthropogenic water usage increases and snowfall decreases in the coming century, Great Basin saline lakes are projected to increasingly face water shortages and high salinities. Conserving saline lake ecosystems thus requires mitigating these losses and maintaining water levels and salinities within the normal range of inter-annual variation. When conditions outside of this range occur too frequently or persist too long, they can result in dysfunctional ecosystems with deleterious consequences for the species that rely on them.

1. Introduction

The invertebrate fauna of endorheic saline lakes provide critical resources for a diverse array of waterbirds worldwide (Jellison et al., 2008). In some cases, these lakes and associated wetlands provide breeding habitat for thousands of waterbirds, as well as stopover habitat that millions of migrants use to molt and refuel each year (Jehl Jr., 1994; Kingsford and Porter, 1994; Jehl Jr. and McKernan, 2002; Shuford et al., 2002; Frank and Conover, 2017). Some species even rely on saline lakes for nearly the entirety of their annual cycle. For instance, many Wilson's Phalaropes (*Phalaropus tricolor*) breed on or near saline lakes throughout western North America, then stage during their southward migration on a handful of saline lakes in central Canada and the Great Basin of the United States, before spending the nonbreeding season on saline lakes in South America (Jehl Jr., 1988). Nonetheless, the long-term population dynamics of waterbirds relying on saline lakes have been little studied away from a few well-characterized sites (e.g., Great Salt Lake: Frank, 2016; Mono Lake: Wrege et al., 2006; Western Australia Wheatbelt: Lyons et al., 2007), creating a significant gap in our understanding of the biology of this widespread,

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but relatively rare ecosystem that makes up ~3% of global lake volume (Wurtsbaugh et al., 2017).

Saline lakes have always been characterized by a degree of ephemerality (Keister Jr., 1992; Williams, 1996; Jellison et al., 2008; Bedford, 2009; Wurtsbaugh, 2014). However, the cumulative effects of the anthropogenic threats currently facing saline lakes — which range from the diversion of water to support agricultural practices and urban expansion to the direct effects of droughts resulting from global climate change (Jellison et al., 2008; Jeppesen et al., 2015; Wurtsbaugh et al., 2017) — are being superimposed on this natural variability. Such changes can lead to hypersalinization, disrupting the tight osmotic balance required of birds living in saline environments (Rubega and Robinson, 1996; Anderson et al., 2007; Gutiérrez, 2014). Even species acclimated to saline environments must raise their metabolic rate, suppress their immune function, and alter other aspects of their physiology to adjust to increases in salinity (Gutiérrez et al., 2011, 2012, 2013). These costs must subsequently be offset by increases in energy consumption. However, the size and nutritional quality of saline lake invertebrates also decline at high salinities, limiting the ability of birds to meet their heightened energetic requirements (Herbst, 2006). Hypersalinization can thus potentially initiate reversible state effects (sensu Senner et al., 2015) that adversely influence performance (Masero et al., 2017), as well as aggravate disease outbreaks (Shuford et al., 1999; Caskey et al., 2007).

Complicating matters is the fact that hypersalinization is not the only potential conservation threat facing saline lakes. In fact, the inverse — the incursion of high levels of freshwater — can also be detrimental and result in reductions in the invertebrate food resources on which waterbirds rely (Herbst, 2001; Beutel et al., 2001). There is thus a trade-off among salinity, invertebrate diversity and abundance: Low salinities tend to result in higher overall invertebrate diversity, but reduced abundance. As salinities increase, there is a decline in invertebrate diversity and an increase in the abundance of a few saline-tolerant species until a point above which few, if any, invertebrates can survive (Herbst, 2006; Brown, 2010). As an example, optimal salinity levels for *Ephydra* spp. (brine flies) and *Artemia* spp. (brine shrimp) — two common saline lake invertebrates — occur between 3 and 8% salinity, with salinities being too low or too high for these species to survive outside the range of 2.5–15% (Brown, 2010). As a result, evidence from artificial saltpans suggests that both invertebrate and waterbird abundance peak at intermediate salinities (Warnock et al., 2002). However, without more detailed knowledge concerning the effects of fluctuations in water and salinity levels in natural saline lakes on bird populations and their prey, it is difficult to identify priority conservation and management strategies that can be implemented to help conserve these ecosystems (Stralberg et al., 2011).

The Great Basin of the western United States supports approximately 45 saline lakes and wetlands (Grayson, 1993). Lake Abert, in eastern Oregon (Fig. 1), is among the largest of these lakes and is of national and international significance for migratory birds. Hundreds of thousands of shorebirds and waterfowl use the lake annually, especially during fall migration (Boula, 1985; Warnock et al., 1998). During the past three decades, however, water levels have fluctuated dramatically as a result of drought and upstream water withdrawals, causing the lake to approach complete desiccation in some years and leading to more frequent and longer periods with extremely high salinity (Moore, 2016; Fig. 2). These fluctuations have, in turn, shifted the benthic ecosystem away from a regime characterized by higher trophic level invertebrates to one dominated by hypersaline-adapted microbes, with as-of-yet-unknown consequences for birds and other species that rely on the lake (Larson and Eilers, 2014; Larson et al., 2016). Given the importance of Lake Abert to migratory waterbirds and the commonality of these circumstances across saline lakes globally, Lake Abert may serve as a case study that can elucidate how such changes affect birds and their invertebrate prey.

Here we present data on waterbird abundance, lake area (a proxy for salinity, see Moore, 2016), and invertebrate abundance collected over the course of 25 years at Lake Abert, providing one of the first opportunities to examine long-term fluctuations in the relationship between birds, their food resources, and salinity at a endorheic saline lake. Because salinity can be both too high and too low for saline lake invertebrates (Brown, 2010), we predicted that waterbird abundance would respond to invertebrate abundance and peak at intermediate levels of salinity (e.g., 3–8%), but decline at both extremely high (> 15%) and low (< 2.5%) levels. If our predictions hold true, they would indicate that the conservation of saline lakes will require strict management in the face of global change and that even relatively small changes in salinity levels can have potentially large-scale impacts on waterbird populations.

2. Methods

2.1. Study area

Lake Abert is located in the closed hydrologic basins of southcentral Oregon, USA (Fig. 1; 42.626°N, 120.233°W). Land ownership surrounding Lake Abert is mixed, but the lake itself and the watershed immediately to the east of the lake are managed by the Bureau of Land Management (BLM) as an Area of Critical Environmental Concern (BLM, 1996). Land and water use in the Lake Abert watershed are dominated by agriculture and forestry, with only minor rural municipal development occurring in the area. Over the period of our study, 1992–2016, the extent of agricultural lands increased slightly and a new reservoir was constructed upstream of Lake Abert (S.I. Fig. 1), but there has been no major land use transformation.

On average, the lake covers ~170 km^2 at a depth of 1.5 m and is the largest hypersaline lake in the Pacific Northwest (Larson et al., 2016). Historically, salinity levels within the lake averaged 7.5%, but ranged between 2 and 8% depending on the season and influx of freshwater (Phillips and Van Denburgh, 1971; Moore, 2016). Freshwater comes mainly from the Chewaucan River, but is supplemented by two ephemeral creeks (Poison and Juniper) and a series of freshwater seeps and springs that occur along the perimeter of the lake, and especially the eastern shore (Fig. 1b). Following the construction of the reservoir above the lake, diversions from the Chewaucan River for agricultural and other purposes now frequently outstrip the river's flow and have in recent years led to a significant reduction in the size of Lake Abert and dramatic increase in its average salinity (Larson et al., 2016; Moore, 2016). However, the presence of the freshwater seeps and springs has meant that the lake has thus far avoided complete desiccation and, at minimum, retained an area of 6–12 km^2 of water during even the driest periods (Larson et al., 2016).

2.2. Bird surveys

Surveys of waterbirds — including Podicepediformes, Anseriformes, and Charadriiformes — using Lake Abert were conducted by wildlife biologists with the BLM biweekly from March 1992–June 1993 and, after a hiatus, bimonthly from December 1993–June 1996 (Devaurs, 1995, 1996). A second set of surveys was conducted by volunteer citizen scientists with the East Cascades Audubon Society (ECAS) from 2011 to 2016 (http://bit.ly/2s3Kwgt). These surveys followed the BLM methodology and were conducted every 2–3 weeks during shorebird migration (April–September). In total, 256 surveys were carried out, with an average of 12 ± 8 surveys occurring per season and 9 ± 6 days elapsing between surveys within a season.

Identical methods were used for all surveys. Surveys started at ~0700 h and were completed by ~1000 h before heat shimmers appeared. All surveys were conducted from stops along U.S. Highway 395, primarily starting at the southeast corner of Lake Abert and moving north along its eastern shore over a distance of about 25 km. Birds were counted individually or estimated in groups (10s, 100s, etc.). Observers