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Abundance, Distribution and Migration Patterns of North American Eared Grebes (*Podiceps nigricollis*)

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Abstract.—Most North American Eared Grebes (*Podiceps nigricollis*) undertake a post-breeding migration to two hypersaline lakes in the USA: Mono Lake in California and Great Salt Lake in Utah. Single air photo surveys were conducted in mid-October at Mono Lake from 1996-2012 and multiple fall surveys were conducted from 2013-2018, the latter to determine variation in abundance patterns within and across years. In four of the six years with multiple fall surveys, peak abundance occurred in mid-October as expected. However, in 2014 and 2015, Eared Grebe numbers declined dramatically soon after arrival, coinciding with low levels of their primary food, brine shrimp (*Artemia monica*). Abundance remained low from 2016-2018, and this could have been due to a shift to Great Salt Lake or to a massive mortality event. In 2017 and 2018, Eared Grebes breeding in south-central British Columbia, Canada were marked with Very High Frequency (VHF) radio transmitters and light-level geolocator (GLS) tags. Contrary to 1996, when the majority of VHF-tagged birds were molting/staging on Mono Lake, our 2017-2018 telemetry data indicated that most individuals were on Great Salt Lake. Our study provides insight into the variable abundance patterns at Mono Lake and novel information on Eared Grebe migration patterns. *Received 24 April 2020, accepted 25 September 2020.*

Key words.—Abundance, Eared Grebes, Great Salt Lake, Mono Lake, *Podiceps nigricollis*

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Two hypersaline lakes in the USA, Mono Lake in California and Great Salt Lake in Utah, support one of the most impressive concentrations of a single bird species anywhere in the world. Almost all North American Eared Grebes (*Podiceps nigricollis*) molt and/or stage on these lakes in fall (Jehl *et al.* 2002). Once their primary food declines to a critical level, they continue southward to wintering areas in coastal areas of Mexico and southern California, USA (Jehl 1988; Jehl 1993; Cullen *et al.* 1999).

Eared Grebes (hereafter grebe) are difficult to survey on the breeding grounds because they are secretive and difficult to monitor using conventional methods (i.e., air-ground surveys). However, counts at Mono Lake and Great Salt Lake during fall migration have been considered an effective approach to estimating the size and trend of the entire North American population. Boyd and Jehl (1998) developed a survey protocol using air photos to accurately estimate grebe abundance on Mono Lake, and the protocol has been used at both lakes since 1996. The survey occurs in mid-October when abundance is assumed to be relatively constant and at a peak level (Jehl 1988; Boyd and Jehl 1998; J. R. Jehl, unpubl. data). However, the Mono Lake counts from 1996 and 2012 yielded some unlikely increases over short time intervals that could not be explained by normal population fluctuations. We therefore conducted multiple, within-year surveys over several consecutive years to: (1) determine the degree to which the level and timing of peak abundance at Mono Lake varied across years; (2) assess the extent to which that variation might explain the unlikely numerical increases when only mid-October counts were conducted; and (3) use the results to design a robust, long-term monitoring program. We also repeated a telemetry study using Very High Frequency (VHF) transmitters, supplemented with light-level geolocator (GLS) tags, to determine if fall connectivity patterns of Eared Grebes breeding in south-central British Columbia, Canada changed since 1996, and to generate novel information on migration patterns.

Methods

Air Photo Surveys

We conducted multiple, within-year air photo surveys at Mono Lake, California, USA (38° 00′ N, 119°02′ W) during the fall molting/staging period from 2013 to 2018, using the protocol described in Boyd and Jehl (1998). In summary, the survey consists of 16 east-west transects spaced every 0.75 km over the surface of Mono Lake; vertical photos are taken every 10 sec along each transect at an altitude of 400 m above lake level (approximately 450 photos total, < 5% of the area of Mono Lake); fixed landmarks at the lake edge are photographed to calculate photo scale and Eared Grebe density per photo; and then images are counted manually. Five surveys were conducted each year except 2017 (six surveys). The surveys occurred every 2-3 weeks from mid-September through mid-November (2013-2015) and from mid-August through mid-November (2016-2018).

Telemetry Surveys

We used gill nets to capture adult Eared Grebes on ponds at or near Riske Creek (52° 00′ N, 122° 30′ W) in south-central British Columbia, Canada (see Boyd *et al.* 2000). This area has hundreds of palustrine wetlands, several of which traditionally support nesting colonies ranging from a few to hundreds of Eared Grebes (for description, see Boyd and Savard 1987).

In 2017 we deployed VHF transmitters and GLS tags, in 2018 we deployed GLS tags only and recaptured grebes tagged in 2017, and in 2019 we recaptured grebes tagged in 2017 and 2018. All capture/recapture events occurred over a 10-day period in June. Each grebe was marked with a Bird Banding Lab metal leg band and culmen length was used to predict sex (Jehl *et al.* 1998). As in 1996, we tagged mostly male grebes because they were larger and heavier than females and therefore more capable of carrying implant transmitters. We avoided marking females if they had eggs in their oviducts.

We used the same type of intra-coelomic VHF transmitter as in 1996 (Holohil Ltd.; 5.3 cm long x 1.5 cm diameter, 12 g, 12-month battery life). The transmitters were implanted by an experienced wildlife veterinarian using the protocol of Korschgen *et al.* (1996) except that each transmitter and its antenna were fully encased within a cylinder. The GLS tags (Migrate Technology Ltd.; model Integeo-C65, 1 g, 16-month battery life) were glued and zap-strapped to the metal leg bands.

In early October 2017, we conducted VHF telemetry surveys at Riske Creek to determine if any tagged grebes died before migrating south. We conducted aerial telemetry surveys at Great Salt Lake on 18 and 19 October 2017 in a Cessna 172 at 400 m above lake level (15 hrs total). Most of Great Salt Lake was flown but our transects were concentrated in an area known to have the large majority of grebes (500 km^2, approximately from the north tip of Fremont Island south to Highway 80 and from Antelope Island to 10 km farther west; J. Neill and J. Luft, Utah Division of Wildlife Resources, pers. commun.).

We conducted eight aerial VHF surveys at Mono Lake in 2017 in conjunction with the air photo surveys that year (from 31 August to 22 November, 20 hrs total). Seven boat-based surveys were carried out to record individual dive/pause data (seven surveys from 23 September to 22 November, 20 hrs total). The dive/pause data were used to determine the average percent of time Eared Grebes were underwater and not visible on the photos, and, by extrapolation, the total number of birds molting/staging on the lake (see Boyd *et al.* 2000 for methods).

GLS Tags and Analysis

A GLS tag is an archival tracking device used to estimate migration routes and identify important wintering, breeding and staging areas (McKinnon and Love 2018). The device records solar irradiance and solar noon which are used to estimate latitude and longitude, respectively, with location accuracies on the order of 100-200 km (Rakhimberdiev *et al.* 2015). For more information on GLS tags and interpretation see Lisovski *et al.* 2019.

Our GLS data were analyzed in program R (R Core Team 2019) using multiple packages. Tag data were first drift-adjusted and log-transformed in preparation for analysis. Twilight events were identified autonomously using the package *GeoLight* (Lisovski and Hahn 2012), and then manually edited to remove clearly erroneous twilight events. Following this, light-level data for each tag were calibrated using a combination of rooftop and on-bird calibration using the package *FLightR* (Rakhimberdiev *et al.* 2015). Calibration periods varied, but were generally at least 30 days and lasted until the grebe left its capture pond. A spatial mask was applied to limit movements to within known areas of grebe occurrence plus a large buffer zone (between 150° and 50° west, between 0° and 70° north, and no farther than 200 km out to sea from the nearest shoreline). Following this, we used *FLightR* to generate probable migration tracks using the '*run.particle.filter*' function (n particles = 1e6, precision.sd = 100, check.outliers = TRUE) and to identify likely overwintering areas and stopover sites for each bird using the '*stationary.migration.summary*' function (using the parameters Meanlat, Meanlon and Q.50 Arrival/Departure). We generated maps depicting the migratory paths for each grebe using the '*map.FLightR.ggmap*' function of *FLightR* (see Rakhimberdiev *et al.* 2015 for more details).

Results

Grebe Abundance Patterns

As noted, the number of Eared Grebes on Mono Lake estimated in mid-October from 1996 to 2012 yielded some unlikely numerical increases over short time intervals that are difficult to explain based on average survival/recruitment rates (Fig. 1). For example, in only two years (1998-2000) abundance increased from 1.0 million to 1.6 million and over four years (2008-2012) it went from 0.2 million to 1.0 million.

Our multiple, within-year photo counts from 2013 to 2018 showed the extent to which the level and timing of peak abundance varied across years. In 2013, the number of Eared Grebes on the lake surface increased as expected, from 1.0 million in mid-September to 1.1 million in early October and then to 1.2 million in mid-October before declining (Fig. 2). In 2014, however, 1.0 million Eared Grebes were estimated in mid-September but, instead of increasing, abundance decreased by 287,000 by the end of September and by another 403,000 by mid-October. Similarly, in 2015, 0.8 million Eared Grebes were estimated on the lake in mid-September but abundance decreased by 235,000 by the end of September and by another 245,000 by mid-October. The patterns in 2016, 2017 and 2018 were similar to one another but they differed considerably from the previous three years; counts were consistently low, reaching only about one-third of the maximum number estimated in 2013.

The numbers in Table 1 and Fig. 2 do not account for birds that would have been underwater when the photos were taken. Our dive/pause data, recorded for three VHF-tagged grebes from September through November 2017, indicated that Eared Grebes were submerged about 30% of the time (range: 27-32%). Applying this correction factor to the surface estimates, the total number of Eared Grebes molting/staging on Mono Lake peaked at about 1.7 million in 2013, 1.5 million in 2014, 1.2 million in 2015, and 0.4-0.5 million in 2016, 2017, and 2018.

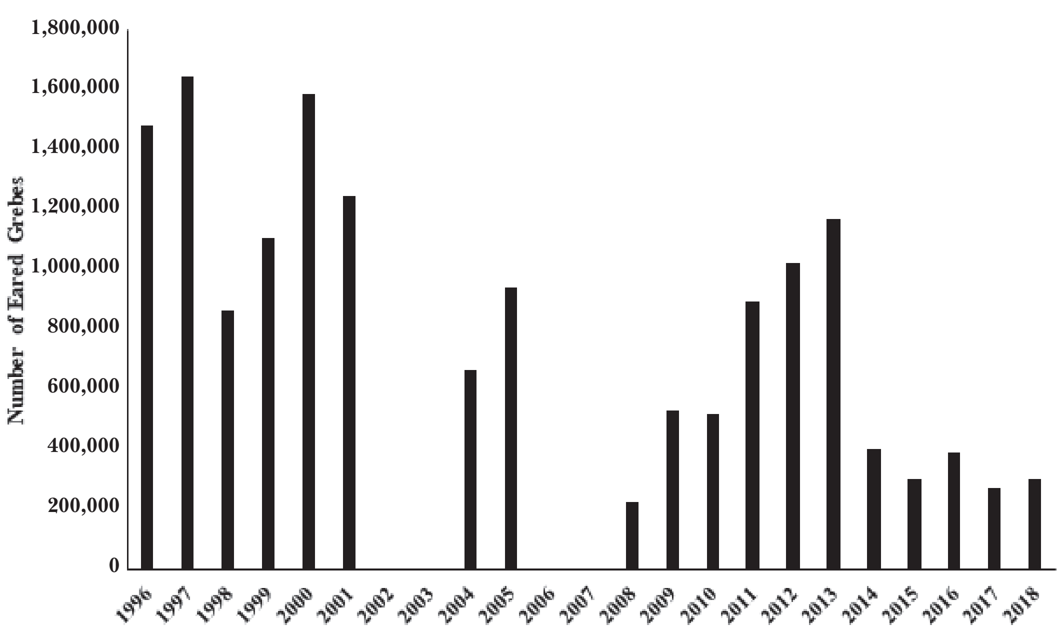

Figure 1. Abundance of Eared Grebes (*Podiceps nigricollis*) on Mono Lake, California, USA in mid-October, 1996-2018 (surface birds only). Surveys were not conducted in 2002, 2003, 2006, and 2007.

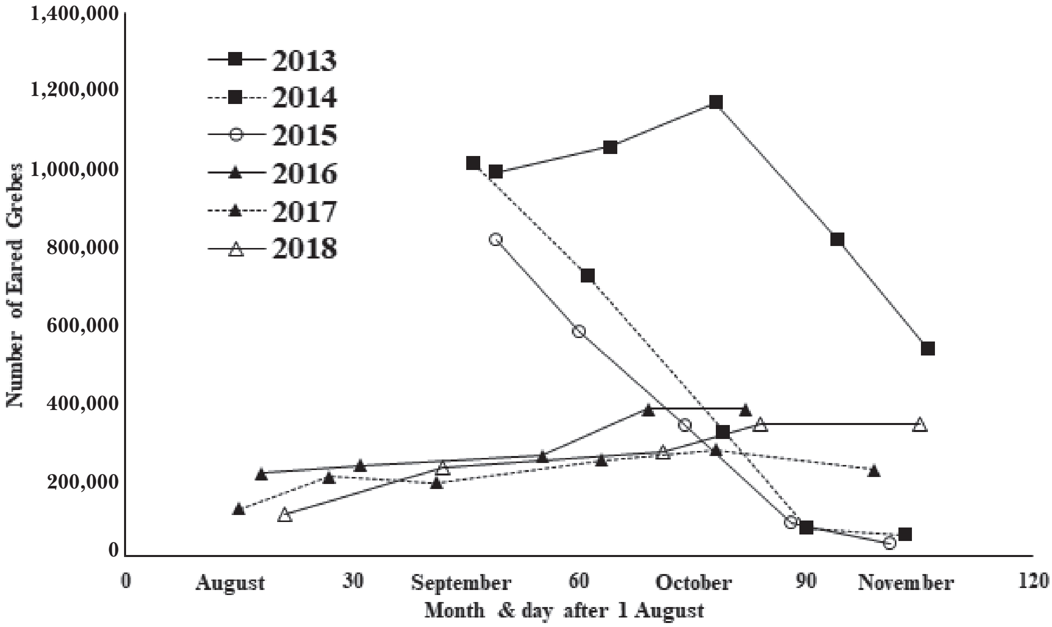

Figure 2. Abundance of Eared Grebes (*Podiceps nigricollis*) on Mono Lake, California, USA during the molting/staging period, 2013-2018 (surface birds only). Month and day after 1 August are shown on the x-axis. SE for individual counts varied from 6-26% and averaged 11% (see Table 1).

VHF and GLS Patterns

We marked 30 Eared Grebes at or near Riske Creek in 2017 with both VHF transmitters and GLS tags and an additional 30 individuals in 2018 with GLS tags only (Table 2). At least three tagged birds died at Riske Creek in 2017, so a maximum of 27 individuals carrying both VHF transmitters and GLS tags migrated south that year. In fall 2017, we detected nine VHF-tagged males on Great Salt Lake and three on Mono Lake, two females on Great Salt Lake and none on Mono Lake, and one individual of unknown sex on Great Salt Lake and one on Mono Lake.

We carried out aerial and boat-based surveys at Mono Lake throughout the 2017 fall molting/staging period (Table 3). We detected four VHF-tagged Eared Grebes and of these, three (VHF tag numbers 165.184, 165.305, and 165.332) were detected multiple times. VHF tag 165.969 was detected only once by each survey method; this individual may have migrated away from the lake, the tag may have failed, or it was present but simply went undetected. The latter scenario is entirely possible based on aerial telemetry results at Mono Lake in 1996 (W. S. Boyd, unpubl. data) and at Great Salt Lake when some transmitters went undetected from one day to the next.

We conducted aerial telemetry surveys on two consecutive days at Great Salt Lake in 2017 (18 and 19 October) and detected 12 to 16 VHF-tagged Eared Grebes (Table 4). This latter estimate of 16 VHF-tagged individuals is based on detection differences across the two days: three transmitters identified on 18 October were not heard on 19 October and two detected on 19 October were not heard on 18 October. Hence, some tagged Eared Grebes went undetected each day even though the same area of Great Salt Lake was surveyed at the same intensity. A simple mark-recapture analysis suggested that up to four tagged individuals could have been present over and above the 12 definite detections (S. Wilson, unpubl. data).

Eared Grebes tagged on the same ponds migrated to either Mono Lake or Great Salt Lake in the same fall (Table 4). Of the seven Eared Grebes tagged with VHF transmitters

Table 1. Abundance of Eared Grebes (*Podiceps nigricollis*) (± %SE) on Mono Lake, California, USA counted on air photos during the molting/staging period, 2013-2018 (surface birds only).

Year	Date	# Grebes	%SE
2013	18 Sep 2013	991,000	7.8
2013	2 Oct 2013	1,056,000	6.8
2013	16 Oct 2013	1,170,000	8.0
2013	1 Nov 2013	819,000	10.0
2013	13 Nov 2013	537,000	8.7
2014	15 Sep 2014	1,012,000	7.0
2014	30 Sep 2014	725,000	7.0
2014	17 Oct 2014	322,000	8.8
2014	28 Oct 2014	75,000	10.3
2014	10 Nov 2014	57,000	12.5
2015	18 Sep 2015	815,000	7.6
2015	29 Sep 2015	580,000	6.8
2015	12 Oct 2015	335,000	6.0
2015	26 Oct 2015	85,000	12.2
2015	9 Nov 2015	31,000	26.0
2016	18 Aug 2016	214,000	17.0
2016	1 Sep 2016	236,000	12.8
2016	24 Sep 2016	260,000	10.3
2016	7 Oct 2016	381,000	10.9
2016	20 Oct 2016	380,000	9.0
2017	15 Aug 2017	123,000	12.0
2017	11 Sep 2017	205,000	12.0
2017	25 Sep 2017	190,000	11.9
2017	16 Oct 2017	248,000	8.4
2017	31 Oct 2017	276,000	8.8
2017	21 Nov 2017	224,000	15.6
2018	21 Aug 2018	108,000	13.0
2018	11 Sep 2018	230,000	10.5
2018	9 Oct 2018	270,000	8.0
2018	22 Oct 2018	340,000	8.5
2018	12 Nov 2018	340,000	13.3

on McMurray Lake (25 km north of Riske Creek), three were detected on Mono Lake and four were detected on Great Salt Lake in fall 2017. Of the three Eared Grebes captured on Pond #6 (one of the capture ponds at Riske Creek), one was detected on Mono Lake and two were detected on Great Salt Lake. In addition, one VHF-tagged Eared Grebe (165.520) detected on Great Salt Lake on 18 and 19 October 2017 was also heard at Mono Lake during aerial surveys on 21 August and 21 September in 2018.

We retrieved 11 (18%) of the 60 deployed GLS tags, nine of which provided migration and wintering data (Online Appendix Fig. 1A) and two that failed (Tables 2 and 4). One Eared Grebe originally tagged in 2017 (BG343) was recaptured in 2018 and marked with a new GLS tag (BK173). Our relatively small number of retrievals was due to the following: (1) Previously tagged grebes were alert to the gill net and capture protocol and, compared to naïve grebes, were difficult to recapture; and (2) It was almost impossible to recapture any of the 15 tagged grebes on McMurray Lake and Pond #6 because these waterbodies are relatively large (0.75 km^2 and 0.25 km^2, respectively) and have several hundred nesting Eared Grebes each.

The functional GLS tags we retrieved yielded some potentially valuable information on the migratory behavior of Eared Grebes (Table 4; Online Appendix Table 1A, Fig. 1A):

1) Six Eared Grebes with GLS tags deployed in 2017 (BG314, BG334, BG343, and BG352) and in 2018 (BK160 and BK170) migrated to Great Salt Lake in fall and remained there for an average of 3.5 months (mean: 105 days, range: 80-140 days), suggesting that all six individuals likely molted there. Five of these six birds overwintered in the Sea of Cortez.

2) GLS data for two Eared Grebes (BG329 and BG331) indicated fall and overwintering locations in California but not at Mono Lake. The latter was confirmed by the fact that the VHF transmitters carried by these individuals were never detected.

Table 2. Summary of Very High Frequency (VHF) radio transmitters and light-level geolocation (GLS) tags deployed on Eared Grebes (*Podiceps nigricollis*) at and near Riske Creek, British Columbia, Canada plus VHF detections in fall and GLS recaptures in 2018 and 2019.

Year Tagged	VHF Deployed	GLS Deployed	Confirmed Mortalities	VHF Detected Fall 2017	GLS Recaptures (2018)	GLS Recaptures (2019)
2017	30	30	3	16	6	2
2018	0	30	n/a	n/a	n/a	3[1]

[1]One individual originally tagged in 2017 (BG343) was subsequently captured/re-tagged in 2018 (BK173).

Table 3. Eared Grebe (*Podiceps nigricollis*) Very High Frequency (VHF) radio transmitters detected by boat and aircraft telemetry at Mono Lake, California, USA in 2017.

Date	VHF frequencies (165.xxx)
VHFs detected by boat:	
23 Sep 17	305, 332
27 Sep 17	305, 969
14 Oct 17	184
18 Oct 17	184, 305, 332
26 Oct 17	184, 305
02 Nov 17	184, 305
22 Nov 17	184
VHFs detected by aircraft:	
31 Aug 17	305
11 Sep 17	305, 332
12 Sep 17	305, 332
26 Sep 17	969
17 Oct 17	184, 305, 332
31 Oct 17	332
01 Nov 17	184, 305, 332
22 Nov 17	184

3) Two Eared Grebes (BG314 and BG343) provided GLS data spanning two annual cycles (2017-2019) and both birds more-or-less followed the same migration route each year. Both individuals were on Great Salt Lake through the fall period and both overwintered in the Sea of Cortez.

4) Of five Eared Grebes (BG314, BG334, BG343, BG352 and BK160) that molted/staged on Great Salt Lake, two (40%) returned there in spring for one to two weeks before flying back to Riske Creek.

5) Finally, three GLS-tagged Eared Grebes (GLS tags BG334, BG343, and BG352) molted/staged on Great Salt Lake through fall 2017. The VHF transmitters carried by these three birds were detected on Great Salt Lake in October 2017, illustrating the effectiveness of using GLS tags to describe Eared Grebe migration patterns.

Discussion

Our multiple counts of Eared Grebes on Mono Lake through the fall molting/staging period showed that both the level and timing of peak abundance varied considerably across years (Fig. 2). This was not anticipated when only mid-October surveys were conducted from 1996 to 2012. The assumption then, based on the results of earlier surveys (Jehl 1988; Boyd and Jehl 1998; J. R. Jehl, unpubl. data), was that abundance peaked by early October and remained stable through late October. If our 2013-2018 surveys had been restricted to mid-October, the results would have been highly misleading with respect to peak counts in 2014 and 2015. In those years, only 0.3-0.4 million grebes were estimated in mid-October compared to the actual peak of 0.8-1.0 million in mid-September. Hence, variable molting/staging patterns within and across years could have been responsible for some of the unlikely numbers when only mid-October surveys were conducted from 1996-2012. These results confirm that multiple fall surveys are needed to estimate peak numbers of Eared Grebes at Mono Lake. Combining these with similar efforts at Great Salt Lake would allow for a highly unique situation where the large majority of North American Eared Grebes could be tracked across years.

In both 2014 and 2015, Eared Grebe abundance at Mono Lake decreased by 287,000 in only two weeks, from mid-September to late September. By mid-October, abundance decreased by another 403,000 in 2014 and 245,000 in 2015. There are two possible reasons for these large, abrupt declines: (1) Eared Grebes departed the lake *en masse* or (2) Massive numbers of Eared Grebes died at the lake. Brine shrimp are the principal food for Eared Grebes at both Mono Lake and Great Salt Lake. Shrimp densities in Mono Lake from August-October 2013 were relatively high (Fig. 3; Los Angeles Department of Water and Power 2019) and this corresponded to a peak accumulation of 1.2 million (surface) Eared Grebes by mid-October. In contrast, shrimp densities in 2014 and 2015 were relatively low (especially in September and October), and this coincided with the large, abrupt declines in Eared Grebe numbers. According to Jehl (2007), when shrimp densities are < 3,000/m^2 or even < 5,000/m^2 (recent analysis by J. R. Jehl and R. Jellison, unpubl.), Eared Grebes are unable to maintain body weight and will de-

Table 4. Detection and recapture results for Eared Grebes (*Podiceps nigricollis*) tagged with Very High Frequency (VHF) radio transmitters and/or light-level geolocator (GLS) tags at Riske Creek, British Columbia, Canada. Only individuals with detections during the post-breeding periods in 2017, 2018 and 2019 are included. (M = McMurray Lake, Riske Creek, British Columbia, Canada; ML = Mono Lake, California, USA; GSL = Great Salt Lake, Utah, USA; SOC = Sea of Cortez, Mexico; NC = Northern California, USA; SC = Southern California, USA).

GLS 2017	VHF 2017	Sex	Capture Pond 2017	Recapture Pond 2018/2019	VHF Fall 2017	GLS Fall 2017	GLS Winter 2017/18	GLS Fall 2018	GLS Winter 2018/19
BF827	165.181	M	6		ML				
BG314	165.895	F	11	11		GSL	SOC	GSL	SOC
BG329	165.357	M	12	11		NC	SC		
BG330	165.305	Unknown	M		ML				
BG331	165.032	M	42	39		NC	SC		
BG332	165.856	M	28		GSL				
BG333	165.782	M	28		GSL				
BG334	165.483	F	11	11	GSL	GSL	NC		
BG340	165.232	F	12		GSL				
BG341	165.406	M	M		GSL				
BG343	165.569	M	11	12	GSL	GSL	SOC	GSL	SOC
BG345	165.520	M	6		GSL				
BG347	165.969	M	M		ML				
BG348	165.618	M	6		GSL				
BG349	165.083	Unknown	M		GSL				
BG350	165.595	M	M		GSL				
BG352	165.720	M	12	12	GSL	GSL	SOC		
BG353	165.281	M	M		GSL				
BG354	165.332	M	M		ML				

GLS 2018	Sex	Capture Pond 2018	Recapture Pond 2019	GLS Fall 2018	GLS Winter 2018/19
BK160	M	35	35	GSL	SOC
BK170	F	35	35	GSL	SOC

Note: VHF 165.520 was also detected on Mono Lake on 21 August 2018.

part early. Jehl (1988) suggested that this was the case in 1986 when shrimp died off early and grebes departed before mid-October.

An alternative explanation for the large, abrupt declines in 2014 and 2015 is that massive numbers of Eared Grebes starved to death at Mono Lake. In fact, many Eared Grebes died in both years but the total number of mortalities, estimated at < 20,000 in 2015 (R. Di Paolo, pers. commun.), is an order of magnitude lower than the several hundred thousand that disappeared. Also, in subsequent years (2016-2018), when shrimp densities returned to higher levels, very few or no dead Eared Grebes were recorded. Hence, the most parsimonious explanation is that hundreds of thousands of Eared Grebes departed Mono Lake soon after arrival and prior to molting, and this was likely due to shrimp densities being below a critical level.

After experiencing two consecutive years of low shrimp densities, the Eared Grebes that departed Mono Lake *en masse* may have shifted their fall affiliations to Great Salt Lake. Eared Grebes from the same nesting colonies are known to migrate to either Mono Lake or Great Salt Lake in the same fall (Boyd *et al.* 2000) and a VHF-tagged Eared Grebe that was detected on Great Salt Lake in October 2017 was also detected on Mono Lake in August 2018. These findings suggest that individuals may be familiar with both lakes and may change fall locations if conditions (e.g., shrimp densities) warrant. In 1996, 50% of VHF-tagged Eared Grebes from south-central British Columbia molted/staged on Mono Lake and only 10% were

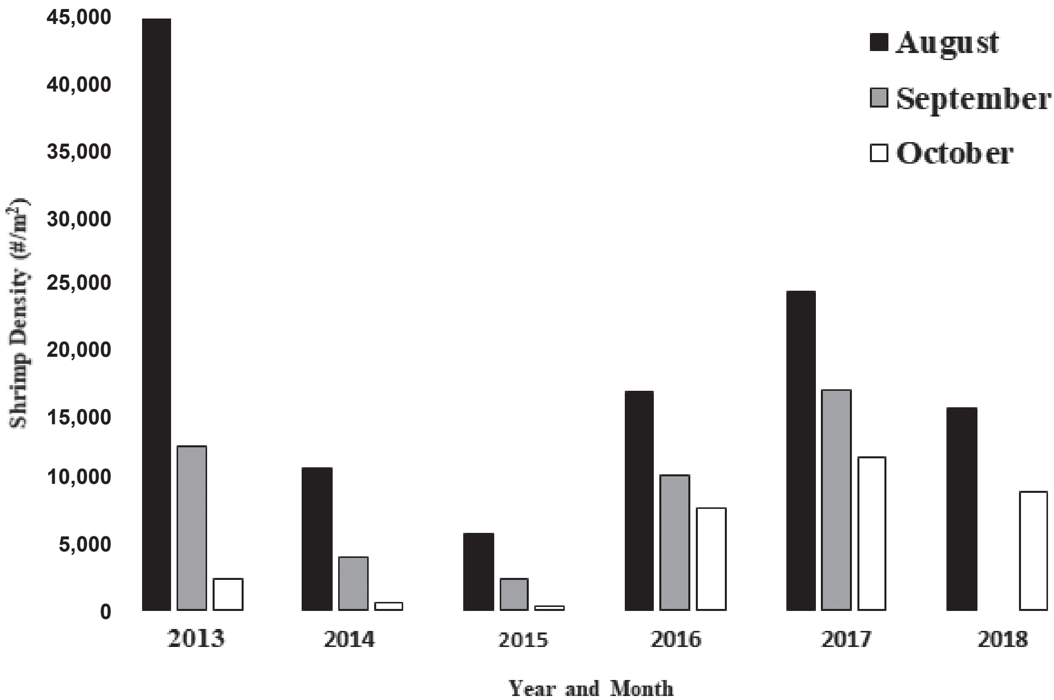

Figure 3. Adult brine shrimp (*Artemia spp.*) densities (#/m²) at Mono Lake, California, USA for the years 2013-2018 (Los Angeles Department of Water and Power, Mono Lake Limnology Report 2019). Densities are average values for 12 stations distributed throughout the lake. Sampling occurred mid-month (no sampling in September 2018). Monthly SEs varied from 9-35% and averaged 19%.

on Great Salt Lake (Boyd *et al.* 2000). However, our fall 2017 telemetry surveys showed the reverse: up to 60% of the VHF-tagged Eared Grebes and 75% of the GLS-tagged Eared Grebes were on Great Salt Lake versus only 15% and 0% on Mono Lake, respectively. It should be noted that this change in molting/staging location for Eared Grebes breeding in south-central British Columbia could have happened any time between 1996 and 2017 and may not represent the movements of other North American Eared Grebes.

It is not unusual for Eared Grebes to succumb to storms during fall migration (Jehl 1996) and intense El Niño (ENSO) events can result in huge die-offs due to starvation (Jehl *et al.* 2002; Roberts *et al.* 2013). Accordingly, the massive decline in abundance at Mono Lake between 2015 and 2016 may have been caused by a very strong ENSO event. Only three such events have ever been recorded (1982-1983, 1997-1998, and 2015-2016) and the first two resulted in massive losses of Eared Grebes (Jehl *et al.* 2002, 2003; J. R. Jehl, pers. commun.). Between October 1997 and October 1998, Eared Grebes at Mono Lake declined by 50% (from about 1.7 million to 0.8 million surface grebes; Fig. 1) and this decline coincided with the 1997-1998 very strong ENSO event when tens of thousands of dead and/or emaciated Eared Grebes were recorded in the Sea of Cortez (Jehl *et al.* 2002, 2003). Jehl *et al.* (2003) estimated that 70% of the entire North American Eared Grebe population starved during that event. Mono Lake Eared Grebes decreased again by 50% (from about 0.8 million to 0.4 million) between 2015 and 2016, and this coincided with the 2015-2016 very strong ENSO event. Therefore, it is entirely plausible that many Mono Lake Eared Grebes overwintering in the Sea of Cortez starved to death during the winter of 2015-2016 but, unfortunately, field data are lacking to verify that possibility.

It is well known that Eared Grebes stop at Salton Sea, California, USA on their southward and northward migrations; Jehl and McKernan (2002) reported > 1 million Eared Grebes in past springs and 300,000 individuals were estimated in late winter/spring 2018. The spring track for BG352 (online Appendix Fig. 1A) suggests that it may have stopped briefly at Salton Sea but the short duration combined with the large error associated with GLS data makes this interpretation difficult. This emphasizes that GLS tags are useful to identify stopover locations and timing for Eared Grebes but only for large waterbodies like Great Salt Lake and Mono Lake, USA, and the Sea of Cortez, Mexico, where numerous data are recorded over weeks or months.

Our study provides valuable information on Eared Grebe abundance patterns at Mono Lake and novel information on migration patterns. The following recommendations would greatly improve our current state of knowledge and provide important information for conservation planning:

1) At least four air photo surveys should be conducted at Mono Lake annually, from early September to mid-November. Combining these surveys with similar efforts at Great Salt Lake would be an effective approach for monitoring abundance and trend patterns of the large majority of North American Eared Grebes. In addition, the relationship between intense ENSO events and abundance patterns at both lakes should be assessed.

2) The relationship between Eared Grebes and shrimp at Mono Lake should be studied in more detail. Further, the interactions between shrimp densities and proximate factors like salinity, algae, and nutrients, and ultimate factors such as freshwater input to the lake, winter snowpack, and climate warming are important to understand. Knowing these ecosystem-level relationships, especially the effects of climate warming, would help wildlife managers predict future scenarios for Eared Grebes molting/staging at Mono Lake.

3) GLS technology is currently the most appropriate one for tracking Eared Grebes. Even though they have relatively large location errors, they are the only external marker accepted by Eared Grebes (Boyd *et al.* 2000; W. S. Boyd, unpubl. data), they are relatively inexpensive, and they can be retrieved at a relatively high rate if restricted to individuals breeding on small ponds. The fact that our VHF detections corroborated the GLS locations at Great Salt Lake illustrates the efficacy of using GLS tags to describe migration patterns at the North American scale. If a sufficiently large number of tags were deployed throughout the breeding range this would: (1) Put the air photo surveys conducted at Mono Lake and Great Salt Lake into a North American perspective, including the proportional split between the lakes; (2) Generate individual arrival and departure information which would allow for the estimation of turnover rates and hence the total number of Eared Grebes moving through each system; and (3) Improve our understanding of Eared Grebe wintering areas, staging sites, migration routes, and timing of movements.

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