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Spring Downings Clarify the Migration Biology of Eared Grebes (*Podiceps nigricollis*)

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Abstract.—Eared Grebes (*Podiceps nigricollis*) staging at the Great Salt Lake, Utah, USA, sometimes experience weather-induced downings where many individuals are killed. Downings of Eared Grebes moving south during the fall have been reported for decades; however, spring downings are rare and underrepresented in the literature. On 15 April 2013, 13,500 Eared Grebes flying northward encountered inclement weather, were attracted to lights on Dugway Proving Ground, and downed. This spring downing was documented, and population characteristics were compared with those observed in previous downings. An estimated 38% were killed outright. Rescue efforts promoted the survival of 88% of those not killed on impact. Grebes that were 9-10 months old were, on average, 10% lighter than adults in the same flight, perhaps indicating slow growth or age differences in foraging efficiency. Adults dominated all downings, supporting previous information that adults and young migrate on different schedules. The sex ratio in the North American population appears to be 1:1. Downings occur when Eared Grebes encounter inclement weather and are attracted to lights. Knowledge of the route, migration period, and flight speed of Eared Grebes allows predictions about when and where downings are likely to occur. Reducing the number and intensity of lights on snowy nights in high risk areas may decrease mortality. *Received 20 January 2016, accepted 19 March 2016.*

Key words.—downing, Eared Grebe, Great Salt Lake, migration, mortality, *Podiceps nigricollis*.

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Migration involves trade-offs between potential benefits available in separate regions vs. risks associated with the journey between areas. In many species of migratory birds, adverse weather during migration can be a major cause of annual mortality (Newton 2007). While birds do not typically depart under poor weather conditions (Richardson 1990), they have little defense when encountering storms en route, which can result in mass mortality events for some species.

Great Salt Lake, Utah, and Mono Lake, California, USA, are the major fall staging areas for Eared Grebes (*Podiceps nigricollis*) in North America, together supporting nearly all of the species' population at that season (Jehl *et al.* 1999). Postbreeding birds begin to arrive in late summer (adults, late July-early September; juveniles, mid-August-October), remain until food runs out, then fly overnight to wintering areas in southern California and Mexico (Cullen *et al.* 1999; Jehl *et al.* 2003). The departure period spans 4-5 weeks between mid-November and early January. When Eared Grebes return northward in spring, large numbers have historically staged at the Salton Sea, California, before continuing further north (Jehl and McKernan 2002).

Eared Grebes typically leave fall staging areas shortly after sunset on evenings when the winds are light and cloud cover is low (Jehl *et al.* 2012; Williams and Laird 2013). The migration route is particularly hazardous for those that use the Great Salt Lake because their non-stop, overnight flight requires them to cross long stretches of Great Basin desert that lack water bodies suitable for stopover in case of severe weather. Small downings occur almost annually. Large events involving hundreds to thousands are infrequent but notable, because they sometimes result in significant mortality. Downings of Eared Grebes in Utah have

been reported for decades and occur when migrants lose their bearings in snow or fog. Eared Grebes often crash near bright lights associated with anthropogenic features. Most downings have occurred between mid-December and early January in areas slightly to the west of the Wasatch Front between the towns of Delta and Cedar City, Utah (Fig. 1). Spring downings are infrequent because the main northward movement occurs after the storm season has passed.

Detailed studies of fall downings (Cottam 1928; Jehl 1993, 1994, 1997; Jehl *et al.* 1999, 2012; Roberts *et al.* 2014), or of Eared Grebes departing from normal migration (Jehl and Johansson 2002; Jehl and Henry 2010), have provided a wealth of information on various aspects of migration biology. This information includes timing, route, meteorology associated with migration and downing events, population composition, causes of mortality, and flight energetics (Cullen *et al.* 1999; Jehl and Bond 1983; Jehl *et al.* 2003). Carcasses salvaged from fall downings have allowed ancillary studies of phenotypic flexibility (Jehl and Henry 2013; Jehl *et al.* 2015), seasonal and annual variability in timing of migration across age classes (Jehl and Henry 2010), and toxicology (Jehl *et al.* 2003; Burger *et al.* 2013). In contrast, Eared Grebe biology during the spring is virtually unstudied. To address this lack of information, we took advantage of an exceptional event on 15 April 2013, in which ≈13,500 Eared Grebes crashed in and around English Village, Dugway Proving Ground (DPG), Utah, during an unseasonable snowstorm. Here, we present an overview of the downing phenomenon in Utah, document the DPG event, and interpret the findings in relation to fall downings.

METHODS

We reviewed the literature on downings in Utah and surrounding areas and visited most localities at which notable events had occurred (Table 1; Fig. 1) to assess conditions that may have influenced downings by Eared Grebes at specific locations. With reference to the 15 April 2013 downing, Eared Grebes were found only in the immediate area of the DPG entrance and in Skull Valley, Utah, some 12 km to the north. A sample that died on impact (n = 192) was salvaged within 2 days and moved to local freezers; the remainder were disposed of at a local landfill. Eared Grebes that appeared to have no major injuries (e.g., broken bones, bleeding from mouth) were released at two water treatment ponds at DPG. Follow-up monitoring on 29 April and 5 May 2013 involved counting Eared Grebes remaining on the ponds as well as walking the perimeter to count and collect carcasses (n = 42). We also examined 23 Eared Grebes killed in southern Utah on 16 April 2013, the night following the DPG downing.

We classified Eared Grebes as adult or first-year juvenile by plumage and soft-part coloration (Storer and Jehl 1985). We determined sex anatomically and weighed Eared Grebes on a digital scale to the nearest 1.0 g. Weights of muscles or organs were determined to the nearest 0.1 g after removal of surface fat. We determined the weight of stomach contents to the nearest 0.1 g and made a detailed examination of the stomach contents of 20 individuals. We also recorded the location and extent of external and internal injuries. Five carcasses were sent to the National Wildlife Health Center, Madison, Wisconsin, USA, to test for infectious diseases. We used t-tests to compare body, organ, and muscle mass by sex between Eared Grebes that died on impact compared to those retrieved later in ponds and also between males and females. We used Fisher's exact test to determine if our sample was unequal in respect to age or sex. All analyses were done in statistical program R (R Development Core Team 2012), and we set $\alpha = 0.05$ for all statistical tests. Meteorological data were gathered at weather station ID# DPG07 from MesoWest online.

RESULTS

Summary of 2013 Spring Downing

On the nights of 15 and 16 April 2013, a series of downings occurred at several localities in Utah. The largest was at DPG and vicinity (≈13,500, 15 April) with smaller numbers (n = 671) in central and southwest Utah the following night (Table 1). At DPG, Eared Grebes were observed falling to the ground, some bouncing several times between 04:30 hr and 05:15 hr. Additionally, Eared Grebes were observed calling from the air and ground. The downing occurred during a period of reduced visibility due to snow and fog. Snow accumulated to approximately 25 mm by 06:00 hr. Between 03:00 hr and 07:00 hr, relative humidity was 100%, the average temperature was -0.9 °C, and the average wind speed was 27 kmph from the north.

At DPG, downed Eared Grebes were concentrated around the brightly lighted en-

Table 1. Location, date, and number of Eared Grebes (*Podiceps nigricollis*) affected in Utah and Nevada downings reported in the literature or gleaned from records of the Utah Division of Wildlife Resources (UDWR), 1928-2013. All locations are in Utah unless indicated.

Year	Date	Map Code and Location	Size	Conditions	Source
South (post-staging) migration					
1928	12-13 Dec	1. Iron/Washington Counties (Modena vicinity); Lincoln County (Caliente, Nevada, vicinity)	Many thousands (15,000?)	Snow	Cottam 1928
1981	9 Dec	2. Utah County (Provo)	2,000	Snow	UDWR; Jehl and Bond 1983
1981	24-Dec	3. Millard County (Cove Fort)	1,000	Snow	UDWR; Jehl and Bond 1983
1982	9, 25 Dec	4. Beaver County (Minersville)	> 3,000	Snow	UDWR; Jehl 1996
1991	10-11 Dec	5. Utah County (Provo); Millard County (Holden); Iron County (Cedar City)	14,000-15,000	Snow	Jehl 1993, 1994, 1997
1993	19-Dec	6. Iron County (Brian Head)	1,500	Snow	Jehl 1996, 1997
1997	5-11 Jan	7. Millard County (Cove Fort vicinity)	1,000	Snow	Jehl *et al.* 1999
1997	13-16 Jan	7. Millard County (Delta vicinity)	15,000	Snow	Jehl *et al.* 1999
1997	15-16 Jan	8. Kane County (Lake Powell). Same flight as 7; birds drifted eastward	16,500	Snow	Rosenberg and Benesh 1997; Jehl *et al.* 1999
2008	18 Dec	9. Millard County (Cove Fort)	105	Snow	UDWR; K. Day, pers. commun.
2011	11-12 Dec	10. Iron County (Cedar City vicinity)	> 7,000 (total flight 50,000)	Snow	Jehl *et al.* 2012; Roberts *et al.* 2014
2012	25-Dec	11. Iron County (Brian Head)	135	Snow	UDWR; K. Day, pers. commun.
North (spring) migration					
1997	31 Mar- 1 Apr	12. Iron County, (west of Cedar City)	> 900	Snow	Jehl *et al.* 1999
2005	31-Mar	13. Iron County (Newcastle)	>30	Snow	UDWR; K. Day, pers. commun.
2013	15-Apr	14. Tooele County (Dugway vicinity)	13,500	Snow, fog	this study
2013	16-Apr	14. Iron County (west of Cedar City)	76	Snow	UDWR; K. Day, pers. commun.
2013	16-Apr	14. Beaver County (northeast of Milford)	595	Snow	UDWR; K. Day, pers. commun.

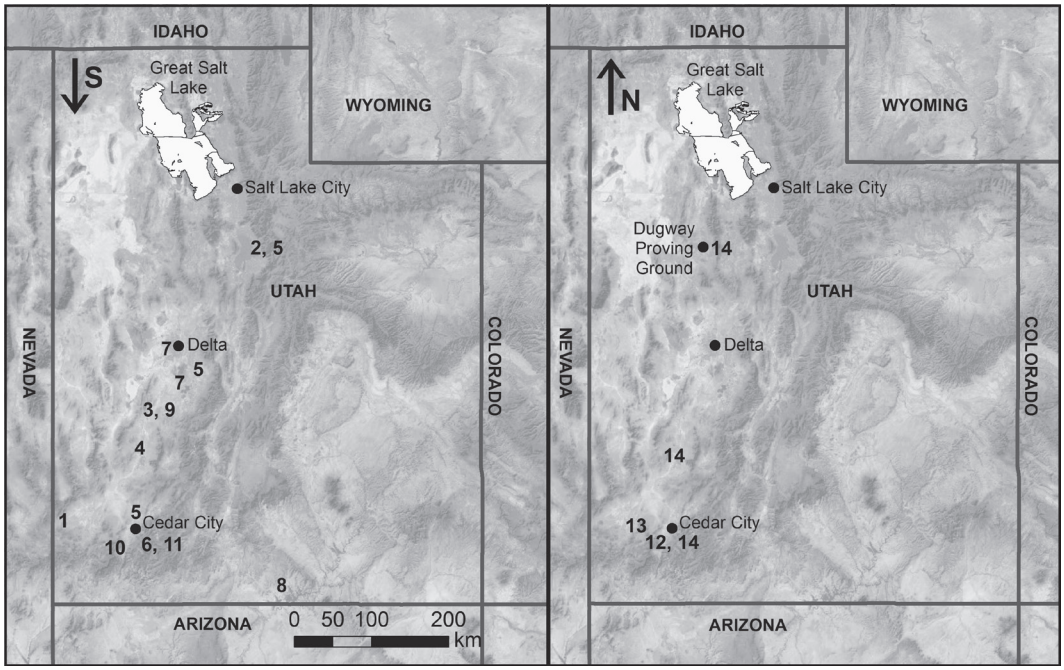

Figure 1. Eared Grebe (*Podiceps nigricollis*) downing locations from south migration (post-staging; left panel) and north migration (spring; right panel) in Utah, 1928-2013. Numbers correspond with locations described in Table 1.

trance to the facility. Additional Eared Grebes accumulated elsewhere around the base, but always in the immediate vicinity of illuminated areas. Hundreds more fell at a church 300 m from the base entrance; the density of bodies decreased outward in a 40-m radius from the 10-m high illuminated steeple, which appeared to be the focal point of collisions. Several hundred additional Eared Grebes were found at a vacated gas station 12 km north of the DPG gate, one of the only other lighted areas in the region. Rescue operations at DPG started immediately and continued for several days, until no more dead or injured Eared Grebes were reported. Of the individuals examined, 38% died on impact. The 62% judged capable of survival were released on nearby water treatment ponds. Of those Eared Grebes, 88% appeared to have left successfully, as only 876 carcasses were recovered when ponds were resurveyed on 29 April and 112 more on 5 May.

Population Characteristics

We examined 234 Eared Grebes that died on impact and 42 that died later in the water treatment ponds. Adult males averaged 30.4 g (12%) heavier than females (t = 8.44, $P < 0.01$); adult males and females averaged 35.9 g (10%; t = 2.38, P = 0.02) and 23.4 g (11%; t = 2.48, P = 0.01) heavier than juvenile males and females, respectively (Table 2). After controlling for sex and age, we found no difference in weight between Eared Grebes that died on impact or later at treatment ponds: body (t = 0.65, P = 0.51), pectoral muscle (t = 1.04, P = 0.30), heart (t = -0.57, P = 0.56), liver (t = 0.07, P = 0.94), and stomach (t = -0.79, P = 0.43) (Table 3). The sex ratio of our sample was not different from 1:1 (47.9% males and 52.1% females; P = 0.41; Table 4). There was no difference in the sex ratio between Eared Grebes that died on impact or in ponds (P = 0.83), nor were there differences in the proportion of juveniles that died in ponds or on impact for either sex (P_{male} = 0.46; P_{female} = 0.42).

Stomach Contents

All grebes (Podicipedidae) eat their own feathers, which when regurgitated contain remnants of undigestible food items. Because

Table 2. Mean (SE) and Range of body weights (grams wet weight) from Eared Grebes (*Podiceps nigricollis*) collected after spring downing events at Dugway Proving Ground, Utah, on 15 April 2013 and at the WECCO Corporation plant, Cedar City, Utah, on 31 March-1 April 1997.

		Males			Females		
Age	Location of Death	$\bar{x}$ (SE)	Range	*n*	$\bar{x}$ (SE)	Range	*n*
Dugway (2013)							
Adult	Impact	332.6 (4.0)	261-420	78	304.1 (3.4)	221-389	76
Juvenile	Impact	298.9 (8.5)	240-339	13	275.4 (6.3)	225-351	25
Adult	Pond	336.2 (7.1)	237-378	20	303.9 (6.8)	268-367	14
Juvenile	Pond	298		1	285.9 (6.6)	250-303	7
Total		333.0 (3.2)	237-420	112	296.9 (2.8)	221-389	122
WECCO (1997)							
Total		361.1 (2.7)	303-421	95	318.5 (2.7)	246-376	104

pellets are cast prior to migrating, the residual stomach contents of migrants are small but not nil; wet weight averaged 0.97 ± 0.42 g (Range = 0.43-1.99, *n* = 31). Stomachs examined in detail (*n* = 20) contained feather fragments and algae. Seventeen of these stomachs contained traces of one or more of the following potential food items: Coleoptera (12), Hymenoptera (5), Hemiptera (3), Mollusca (1), annelid worm (1), and traces of plant material (3). One stomach also contained 3 live nematodes (Nematoda). Grit was absent.

Five Eared Grebes tested negative for avian influenza viruses, pathogenic bacteria, and organophosphate pesticides. No abnormalities other than trauma were found. In our sample of those that died on impact, the majority suffered broken bones or other injuries in the anterior part of the body (head, neck, shoulder girdle, wings).

DISCUSSION

As in previous large events, the DPG downing occurred during a period of poor visibility, which likely caused the Eared Grebes to become disoriented. Birds have several methods to navigate during migration including magnetic-compass, sun-compass, star cues, and topography (Martin 1990; Berthold 2001; Wiltschko and Wiltschko 2009). Whereas all of these are likely available to Eared Grebes, the importance of celestial clues was suggested in the Cedar City 2011 event; > 7,000 individuals had already crashed when a break in the clouds allowed tens of thousands more to immediately reorient and turn back toward the Great Salt Lake (Jehl *et al.* 2012).

Table 3. Mean (SE) weight (g) of body, muscle, and organs from Eared Grebes (*Podiceps nigricollis*) collected after a spring downing at Dugway Proving Ground, Utah, on 15 April 2013.

Mass (g)	Males	*n*	Females	*n*
Body weight	333.0 (3.2)	112	296.9 (2.8)	122
Pectoral muscle	22.6 (0.6)	29	20.0 (0.6)	28
Heart	3.1 (0.1)	29	3.5 (0.1)	28
Liver	8.7 (0.2)	36	7.6 (0.2)	41
Stomach	8.0 (0.1)	29	7.3 (0.2)	28

The exact site of downings is sometimes associated with the presence or illusion of open water, as created by wet highways. However, the only factor common to major events (Table 1) was the attractive presence of the bright lights of towns or industry. The historical concentration of downings in the Delta-Cedar City, Utah, region is likely related to topographic features, namely the proximity of the mountains to the east, which block westerly winds and allow snow and fog to linger in the area (Jehl and Bond 1983; Jehl *et al.* 2012).

A review of all downings provided no indication that the sexes are migrating at different times in either spring or fall. Although unequal sex ratios were detected at two of three sites in early January 1997 and in two samples from Cedar City in 2011, this unequal sex ratio disappeared when samples were merged (Table 4). Fall downings (Table 2) were dominated by adults. This occurs

Table 4. Sex and age ratios (%) from samples of Eared Grebes (*Podiceps nigricollis*) downed in Utah in 1991, 1997, 2011, and 2013. * = sexed by bill length (adult only).

Date	Location of Downing	*n*	Males (%)	Females (%)	*P*	*n*	Adult (%)	Juvenile (%)	Unknown	Reference
Spring downings										
31 Mar-1 Apr 1997	WECCO	199	47.7	52.3	0.52	199	95.5	4.5	0	Jehl *et al.* 1999
15 Apr 2013	Dugway	234	47.9	52.1	0.41	234	83.3	16.7	0	this study
16 Apr 2013	South and Central Utah	20	45.0	55.0		24	83.3	16.7	0	this study
Fall downings										
10-11 Dec 1991	Cedar City	109	54.5	45.5	0.37	139	97.0	3.0	0	Jehl *et al.* 1999
5-9 Jan 1997	Cove Fort	171	62.6	37.4	< 0.01	168	75.6	8.9	15.5	Jehl *et al.* 1999
13-14 Jan 1997	Delta/Hinkley/Holden	148	52.7	47.3	0.51	148	91.9	5.4	2.7	Jehl *et al.* 1999
13-14 Jan 1997	IPP Power Plant	867	45.6	54.5	< 0.01	663	90.4	2.4	7.2	Jehl *et al.* 1999
13 Dec 2011*	Cedar City	98	35.7	64.3	< 0.01	101	99.0	1.0	0	Roberts *et al.* 2014
13 Dec 2011	Cedar City	80	60.0	0.40	0.02	95	78	15	2	J. R. Jehl, unpubl. data

because juveniles move south earlier (mid-November to mid-December) and are mostly gone before the season of snows (mid-December to early January) that trap the later-migrating adults (Jehl *et al.* 1999, 2012). The only age data in spring derive from the WECCO downing of 31 March 1997 (≈ 95% adults) and DPG of 15 April 2013 (≈ 83% adults). The higher percentage of adults in March is consistent with the commonplace finding that adults of most species migrate before young in spring (Jehl *et al.* 1999). Of more interest, however, is that the weight differences between adults and young in fall (Jehl 1988) persist into the following spring, with first-year migrants averaging only 90% as heavy as adults in the same flight. This difference may indicate that slow growth is an inherent property of this species. Alternatively, since the age groups likely winter together, it may indicate that young Eared Grebes forage less efficiently than adults for a long time (non-adaptive); or that young are fully competent but, being smaller, require less fat for the same trip (adaptive).

As recently as 2001, the Salton Sea has been a major spring staging area for Eared Grebes and average peak numbers exceeded 500,000 (Jehl and McKernan 2002). At the Salton Sea, pile worms (*Neanthes succinea*) have been Eared Grebes' major food yet have declined in the last decade (Jehl and McKernan 2002; Anderson *et al.* 2007). Mouthparts of pile worms typically occur in the hundreds or thousands in the gizzards of Eared Grebes at the Salton Sea (Jehl and McKernan 2002). The virtual absence of pile worms in the 2013 downings (only one in 20 samples from DPG and none in 12 samples from further south) indicates that the flight originated elsewhere, most likely the Gulf of California. In that case, to reach DPG at 05:00 hr, the Eared Grebes would have to depart around 13:00 hr. In contrast, observations of Eared Grebes in fall migration indicate that the flight does not begin until after sunset (Jehl and Henry 2010). Ecological conditions at the Salton Sea are changing rapidly, which, as its level drops and salinity increases, will eventually become too salty to support worms (Anderson *et al.* 2007;

Hurlbert *et al.* 2007). We encourage studies of stomach contents in future spring downings because they may provide insight into changes in food resources or in staging areas themselves.

Flight costs of Eared Grebes are among the highest in birds (Jehl 1994; Jehl *et al.* 2003). Downings have provided information from which costs can be estimated. Estimation of costs requires information on weight at departure, weight at downing, flight speed, and distance flown. Weight at departure is virtually impossible to get (but see Jehl 1997, 1998), but can be circumvented by determining the weight difference between birds killed at two points of the same flight, in a so-called "double downing." Using this approach, Jehl (1994) calculated fuel consumption in a 400-g Eared Grebe at 7.4 g/hr, subsequently revised (with a model) to 5.4 g/hr (Jehl *et al.* 2003). An estimate of 10 g/hr (Roberts *et al.* 2014) is problematic because it failed to adjust for weight loss in the 2-7 days that elapsed after sampling staging Eared Grebes and before their actual departure [0.71 g/hr, minimum based on basal metabolic rate (Roberts *et al.* 2014) to 1.5 g/hr based on inactive captives (Jehl 1988)]. Unfortunately, the DPG data are of no help, and further estimates await another double-downing.

Mortality at DPG was caused by blunt trauma. Injuries in Eared Grebes that died on impact were concentrated on the anterior part of the body, consistent with observations of birds flying headlong into fixed objects. Further, we did not detect differences in mean weights between crashed and pond Eared Grebes, indicating pond mortality occurred rapidly and also resulted from internal injuries, not starvation. Only two of 42 pond carcasses weighed < 250 g, and only one (190 g) was in the weight range (< 220 g) of Eared Grebes known to have died from starvation (Jehl and Henry 2010). This finding suggests that rescue efforts were highly effective and justified by the survival of thousands of grounded individuals that would otherwise have died.

Eared Grebes guard against downings by flying when weather conditions are favorable. Changes en route cannot be anticipated, and they sometimes encounter bad weather. Based on a review of all Eared Grebe downings, a common factor at the location site is the presence of illuminated features. Additionally, lights from anthropogenic features appear to influence the behavior of some nocturnally migrating birds (Watson *et al.* 2016). The simple act of turning off bright lights along the migration route on snowy evenings between late November and early January may preclude unnecessary mortality.

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