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FLYING THE GANTLET: POPULATION CHARACTERISTICS, SAMPLING BIAS, AND MIGRATION ROUTES OF EARED GREBES DOWNED IN THE UTAH DESERT

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ABSTRACT.—In January 1997, an estimated 35,000 Eared Grebes (*Podiceps nigricollis*), about 3% of the population that stages at Great Salt Lake, Utah, were downed by snowstorms while migrating between Great Salt Lake and Mexico. Another 920 grebes crashed on the northbound migration in late March 1997. We examined 1,500 carcasses to determine the characteristics of the population during fall versus spring migration with regard to age and sex ratios, body mass, plumage abnormalities, presence of parasites, and morphological defects. In many cases, large samples derived from mass downings provide a reasonable index of the composition of birds aloft. However, we found important differences in sex ratios between two samples derived from the same flight, which indicates that assumptions regarding unbiased sampling require testing. The possibility that regular catastrophic events in central and southern Utah have influenced the evolution of migration routes in Eared Grebes deserves further consideration. *Received 19 December 1997, accepted 22 June 1998.*

BIRDS KILLED DURING A MIGRATORY FLIGHT can be an important source of information on many aspects of migration, including energetics, body composition, migration routes, timing of migration by sex and age class, and the relation of molt to migration (e.g. Tordoff and Mengel 1956; Stoddard and Norris 1967; Jenni and Jenni-Eiermann 1992; Jehl 1993, 1994, 1996). Data from large mortality events can also provide insights into various population characteristics, such as sex ratio or the frequency of morphological defects.

One species regularly afflicted by mass mortality is the Eared Grebe (*Podiceps nigricollis*), which in fall stages at hypersaline lakes in the western United States, remains until food runs out, and then flies nonstop to wintering areas in southern California and Mexico (Jehl 1988). The routes are inherently hazardous because they cross hundreds of miles of desert that offer few places to land in an emergency. For grebes that stage at Great Salt Lake, Utah, the southward route that parallels the Wasatch Front in central and southern Utah is particularly hazardous because it constitutes a migratory gantlet—a location where frequent winter storms take regular swipes at the nocturnal migrants attempting to pass overhead. Downings of hundreds and even thousands of grebes have been reported in this area for decades (e.g. Cottam 1928, Jehl 1996). Caught under conditions of poor visibility from fog or snowstorms, migrating grebes become disoriented, home in on bright lights along highways or in towns, and crash (Jehl 1993, 1994, 1996, 1997, 1998).

In January 1997, bad weather in southern Utah resulted in several downings within an 11-day span that involved approximately 35,000 Eared Grebes moving southward from Great Salt Lake. Three months later, in an unprecedented spring event, at least 920 grebes flying northward toward Great Salt Lake were downed in the same area. In both cases, many birds were badly injured and hundreds were killed. We examined 1,500 specimens from these events to compare population characteristics of birds during southward and northward migrations, presuming that large samples derived from catastrophic events would provide an unbiased index of the population migrating overhead. We also considered whether high mortality incurred in localized but regular downings might influence the grebes' use of staging areas and migration routes.

BACKGROUND AND METHODS

Downings of southbound migrants.—Eared Grebes killed in central and southern Utah during winter are derived from the population that stages at Great Salt Lake, which remains ice-free year-round owing to its high salinity. Other than Mono Lake, Califor-

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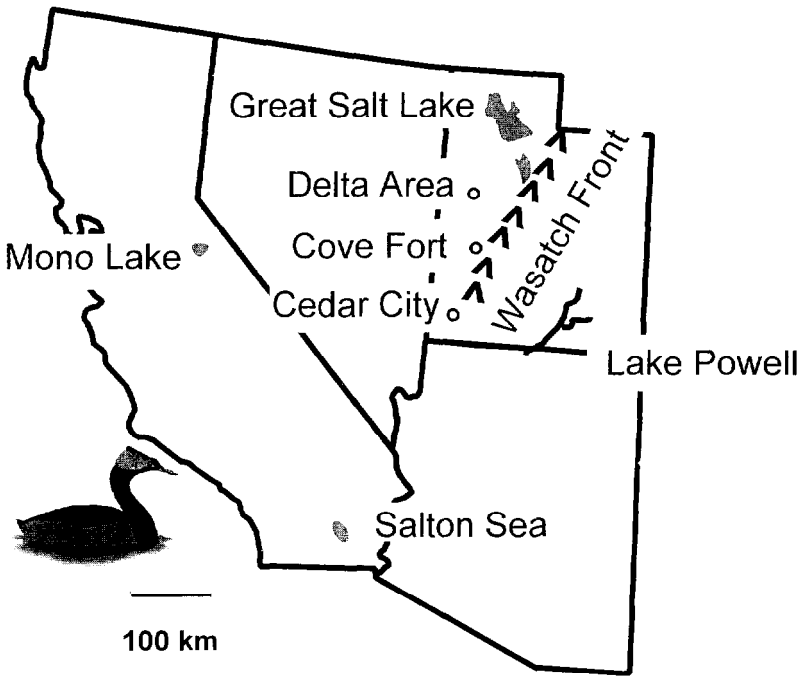

FIG. 1. The southwestern United States, showing the major localities mentioned in the text.

nia, 1,000 km to the west, no other large body of water in the interior is capable of holding any significant number of staging grebes into early winter.

In the first January 1997 downing, about 1,000 grebes crashed in the Cove Fort area on several snowy nights between 5 and 11 January (see Fig. 1). Nearly all were found at and along the brightly lighted intersection of interstate highways I-15 and I-70. Local observers reported that most of the birds were downed on the night of 8 to 9 January. State game officers and local residents salvaged 770 live grebes, which they released on nearby ponds and lakes, and retrieved 182 dead; at least 60 more dead were not retrieved (Table 1). The second event occurred on 13 to 14 January, when more than 7,200 birds were downed by a snowstorm in the Delta area (including Holden and Hinkley), 85 km north of Cove Fort. Near Delta 3,650 birds were found along local roads and in adjacent upland areas; of these, 148 (4.1%) dead were salvaged. Concurrently, 3,600 crashed on or immediately around a 20-ha pond at the Intermountain Power Project plant (IPP) 35 km west of Delta; 1,600 (44.4%) of these birds died. Two nights later, on 15 to 16 January, 10,000 more landed at IPP, and 16,500 more were seen at Lake Powell, about 280 km SE of Delta, on the morning of 16 January (Rosenberg and Benesh 1997). The latter group may have become disoriented by snowstorms, because Lake Powell is east of the expected migratory route.

Downings of northbound migrants.—On the night of 31 March to 1 April 1997, at least 920 grebes were downed at the WECCO Corporation plant (WECCO), 24 km west of Cedar City; 663 were found alive on two ponds and 50 more on land nearby; 207 were dead. This event was also associated with the passage of a cold front during which about 2 cm of snow fell at Cedar City. This sample almost surely originated at the north end of the Salton Sea, California, which is a major spring staging area.

Methods.—Birds were salvaged within one to two days of each downing by conservation officers of the Utah Division of Wildlife Research. Because all events occurred when the ground was covered with snow, the carcasses were naturally refrigerated. They were then transported to Cedar City and frozen. Division of Wildlife Research personnel provided 1,500 carcasses for further study. We examined all of them, but owing to limitations of manpower and the condition of some carcasses (e.g. some had been crushed by cars), data on all characteristics were not always obtainable.

We determined the age of January specimens by iris color (bright red in adults, brown to pale orange in juveniles; Storer and Jehl 1985, Jehl 1988); those whose iris color was in transition were considered "unknown." We recognized two age groups in March. One-year-olds (i.e. those hatched the previous summer) were identified by a combination of the pattern of white on the primaries (Storer and Jehl 1985) and the presence of a bursa $\geq$10 mm in length;

TABLE 1. Location, dates, and numbers of Eared Grebes affected in 1997 downings.

Location	Date	Live (released)	Dead (retrieved)	Dead (not retrieved)	Minimum mortality (%)
	Southbound migrants				
Cove Fort	5–9 Jan.	770	182	>60	18.0
Delta/Hinkley/Holden	13–14 Jan.	3,502	148	unknown	4.1
IPP Power Plant	13–14 Jan.	2,000	1,600	unknown	44.4
IPP Power Plant	15–16 Jan.	10,000	0	0	0.0
Lake Powell	15–16 Jan.	16,500	0	0	0.0
Total January downings		32,772	1,930	>60	5.6
	Northbound migrants				
WECCO	31 Mar.–1 Apr.	713	207	unknown	22.5

all others were considered adults. In opening the body cavity to determine sex, we also looked for any obvious infestations of parasitic worms. All specimens were examined for evidence of plumage abnormalities, foot deformities, and parasitic infestation of the ankle joint. Body mass was measured on a digital scale to the nearest 1.0 g. Mass of birds obtained from two independent samples from the downing of 13 to 14 January was compared using *t*-tests.

RESULTS

Age and sex ratios.—In the January sample, 88.0% of 979 specimens were classified as adults, 4.0% as juveniles, and 8% as unknown (juveniles or subadults; Table 2). In late March, 95.5% of 199 specimens were adults and 4.5 % were first-year birds.

The sex ratio in the combined January downings was approximately equal (48.9% males, 51.1% females; $P = 0.568$; see Table 2). The sample from 5 to 9 January, however, was significantly male biased (62.6%; $P = 0.001$). The composition of the sample from 13 to 14 January was slightly in favor of males (52.7%; $P = 0.511$) at Delta but significantly in favor of females (54.4%, $P = 0.009$) at IPP. In March females outnumbered males (52.3%, $P = 0.523$).

Foot deformities, plumage, and parasites.—Four of 1,301 birds examined in January had foot defects that consisted of minor notches excised from the toe lobes (one bird lacked an entire toe). None of 199 birds examined in March showed any irregularity. No bird showed any plumage abnormality or evidence of leucism (see Jehl 1985). A nematode, *Pelecitus fulicaeatrae,* that inhabits the ankle joint of grebes was observed in one leg of a January specimen. We found no obvious helminth infestations in the body cavity; however, in most cases, we did not examine the intestinal tract where the vast majority of grebe parasites occur. Intestinal parasites are "mostly less than 1 mm long and thread-like" and are easily overlooked (R. W. Storer pers. comm.).

Body mass.—Within sexes, there was no significant difference in body mass of grebes killed at Delta and IPP on the nights of 13 to 14 January (males, $t = 0.66$, df = 305, $P = 0.51$; females, $t = -0.42$, df = 288, $P = 0.68$), con-

TABLE 2. Sex and age ratios (%) of Eared Grebes downed in Utah in 1991 and 1997.

Date	Location	Males	Females	*n*	χ^2	*P*	Adults	Juveniles	Unknown	*n*
			1991							
10–11 Dec.	Minersville/Cedar City	54.5	45.5	109	0.82	0.366	97.0	3.0	0.0	139
			1997							
5–9 Jan.	Cove Fort	62.6	37.4	171	1.81	0.001	75.6	8.9	15.5	168
13–14 Jan.	Delta/Hinkley/Holden	52.7	47.3	148	0.43	0.511	91.9	5.4	2.7	148
13–14 Jan.	IPP Power Plant	45.6	54.5	867	6.84	0.009	90.4	2.4	7.2	663
Total January	All locations	48.9	51.1	1,186	0.33	0.568	88.0	4.0	8.0	979
31 Mar.–1 Apr.	WECCO	47.7	52.3	199	0.41	0.523	95.5	4.5	0.0	199

TABLE 3. Body mass of Eared Grebes downed in Utah in 1997.

Location	Males			Females		
	$\bar{x} \pm$ SD	Range	n	$\bar{x} \pm$ SD	Range	n
Southbound migrants						
Cove Fort	446.1 ± 38.3	256–521	87	406.3 ± 30.6	324–477	48
Delta/Hinkley/Holden	417.1 ± 39.6	333–502	78	367.5 ± 28.1	284–449	70
IPP Power Plant	413.8 ± 36.6	195–507	229	369.1 ± 27.8	281–438	220
Total January downings	421.6 ± 39.7	195–521	394	374.1 ± 31.1	281–477	338
Northbound migrants						
WECCO	361.1 ± 26.7	303–421	95	318.5 ± 27.5	246–376	104

firming that these two samples were derived from the same flight. Birds in that flight, however, were significantly lighter than those killed in Cove Fort the previous week (males, $t = -4.89$, df = 392, $P < 0.001$; females, $t = -9.45$, df = 336, $P < 0.001$). Northbound migrants downed in this area in March averaged about 60 g lighter than southbound migrants (Table 3), partly because they had flown at least 220 km farther before being downed (the distance between the Salton Sea and Cedar City is 220 km farther than that between Great Salt Lake and Delta), and partly because spring migrants depart at a lighter mass (Jehl 1997). In all downings, females averaged about 11% lighter than males (Table 3).

DISCUSSION

The fall migration of Eared Grebes is perhaps the latest of that of any North American bird. As a result, the high representation of adults in January 1997 (88%; vs. 95% in December 1991; Jehl 1993) was not surprising, because adults migrate later than juveniles (Jehl 1988, 1993, 1997). Likewise, the high percentage of adults in March (>95%) also was expected, because northward migration starts in March, and breeders migrate earlier than nonbreeders (i.e. 1 to 2 years old), whose major movements take place in April to May (Jehl 1988).

Even though grebes are hosts for a large and diverse fauna of internal parasites (see Storer 1998), we found none in these samples. Their apparent absence in birds leaving Great Salt Lake paralleled findings from birds at Mono Lake. If the harsh chemistry of hypersaline lakes helps purge grebes of parasites accumulated on the breeding grounds (Jehl 1988), one would expect higher parasite loads in spring migrants that had wintered in the "normal" sea water of the Gulf of California. However, that did not seem to be the case, at least so far as macroparasites were involved. The question could be resolved by comparative studies at different phases of the annual cycle that incorporated detailed examination of intestinal contents.

The incidence of major foot injuries in the January/March 1997 downings (1 of 1,500 had a missing toe), although trivial, was lower than that among birds banded or examined at Mono Lake in fall (5 of about 4,000; missing foot, dislocated ankle, crippled leg, club foot). Such a trend would be expected. Badly crippled grebes can survive for long periods at hypersaline lakes because prey is abundant and easily obtained from the surface (Jehl 1988). But in late fall, when brine shrimp numbers dwindle and diving becomes the principal form of foraging, crippled birds are likely to be eliminated.

Bias in an "unbiased" sample.—How representative are data from downings? A snowstorm that disorients and precipitates everything attempting to fly through it would seem to be the perfect way to obtain an unbiased sample of migrants aloft. However, discordant data on sex ratio from two samples from the flight of 13 to 14 January indicate that unbiased sampling cannot be assumed. At Delta there were more males than females (52.7%), whereas only 35 km away, at IPP, males were significantly (45.6%) scarcer. A second difference was the much higher mortality rate at the IPP ponds (44.4%) than at Delta (4.4%). We have no reason to suspect differences in the distribution of the sexes overhead and, therefore, attribute our findings to differential mortality among the birds forced to earth. Jehl (1998) argued that the higher mortality at IPP was incurred as dis-

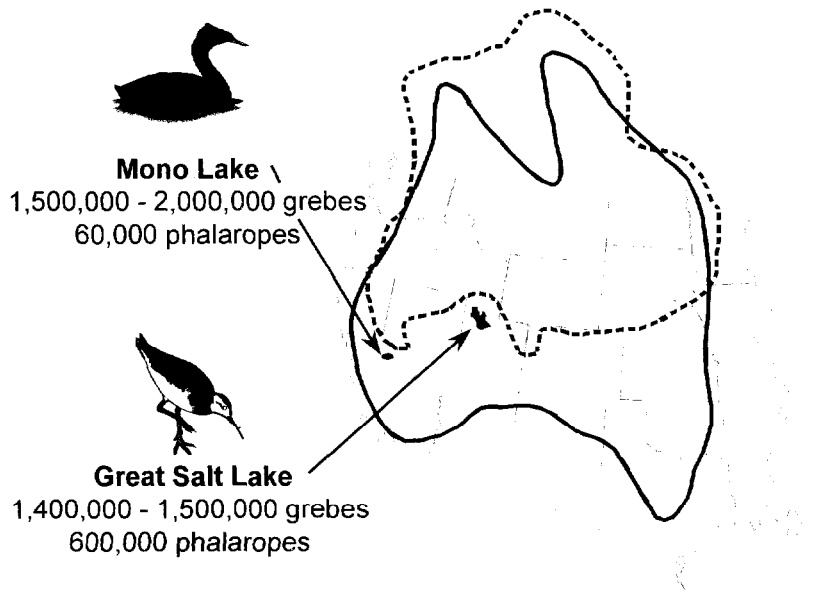

FIG. 2. The western United States, showing the major breeding ranges of Eared Grebe (solid line) and Wilson's Phalarope (hatched line), and peak population sizes for each species at Great Salt Lake and Mono Lake.

oriented birds massed over the pond and crashed into one another in flight as they tried to land. Because females are smaller, they are more likely to suffer injury in collisions, which would explain their higher representation in the IPP sample. Regardless of the validity of this interpretation, the different characteristics represented in two samples from a single flight show that unbiased sampling in mass downings cannot be assumed.

Mass downings and the choice of staging area.—Eared Grebes and Wilson's Phalaropes (*Phalaropus tricolor*) are the two bird species most characteristic of and reliant on hypersaline lakes in North America. They have similar breeding ranges, and more than 90% of the entire grebe and adult phalarope populations are thought to stage at Mono Lake and Great Salt Lake (Jehl unpubl. data). Banding information has shown that grebes from the easternmost and westernmost breeding areas are not confined to one staging area, but may occur at either Mono Lake or Great Salt Lake (Jehl and Yochem 1986, S. Boyd pers. comm.); comparable data do not exist for phalaropes. Because Great Salt Lake is larger and more centrally located, it offers the most direct route for birds moving between the major mid-continental breeding areas and wintering areas in Mexico (grebes) or South America (phalaropes). Thus, one might expect it to be the major staging area for both species. Indeed, peak numbers of phalaropes are an order of magnitude larger at Great Salt Lake than at Mono Lake (Jehl 1988, unpubl. data; Fig. 2). Contrary to expectation, however, grebes at Mono Lake outnumber those at Great Salt Lake (J. Jehl, S. Boyd, and D. Paul unpubl. data).

Phalaropes migrate in summer, when weather-induced downings are not a problem. Grebes typically remain at staging areas into December or later, when winter storms are frequent. Since 1980, we know of only one significant downing that may have involved grebes originating at Mono Lake. In contrast, downings of hundreds to thousands of grebes that originated at Great Salt Lake seem to be an annual occurrence in southern Utah (Jehl 1996, unpubl. data). Although some birds survive, the numbers that may be downed are not inconsequential. In 1997, downings affected at least 3% of the population staging at Great Salt Lake. Can it be that selection resulting from the frequency and severity of catastrophic events experienced by birds flying the southern Utah gantlet in winter helps tip the balance in favor of Mono Lake as a staging site?

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