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Massive Collapse and Rapid Rebound: Population Dynamics of Eared Grebes (*Podiceps nigricollis*) During an ENSO Event

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Abstract.—In autumn, >99% of North American Eared Grebes (*Podiceps nigricollis*) stage at Mono Lake, California, and Great Salt Lake, Utah, creating an exceptional opportunity to measure population trends in a common and otherwise widely distributed species. Aerial photocounts showed that numbers at both lakes fluctuated in parallel, from a total of ~3.56 million in 1997, then crashing to 1.60 million in 1998. The decline was coincident with a major El Niño, during which hundreds of thousands starved in the Gulf of California. The population rebounded to 3.27 million by 2000, illustrating the species' potentially high survivorship throughout the year. Catastrophic events are evidently the major factors affecting proximate changes in population size. Factors that set the ultimate limit to the population can be clarified through long-term studies at staging areas.

Resumen.—En otoño, >99% de los individuos de *Podiceps nigricollis* se congregan en el Lago de Mono, California, y el Gran Lago de Sal, Utah, lo que crea una oportunidad excepcional para medir las tendencias poblacionales de esta especie común pero normalmente extensamente distribuida. Conteos mediante fotografías aéreas mostraron que los números poblacionales en ambos lagos fluctuaron en paralelo, de un total de ~3.56 millones en 1997, disminuyendo luego drásticamente a 1.60 millones en 1998. La disminución fue coincidente con un evento El Niño importante, durante el cual cientos de miles murieron de inanición en el Golfo de California. La población aumentó a 3.27 millones en el año 2000, lo que ilustra la potencialmente alta supervivencia de esta especie a lo largo del año. Evidentemente los eventos catastróficos son los mayores factores que afectan a los cambios proximales del tamaño poblacional. Los factores que imponen los límites decisivos sobre las poblaciones pueden ser clarificados a través de estudios a largo plazo en áreas de escala.

Saline lakes are preferred breeding and staging habitat for a small but important assemblage of North American birds. By far the most numerous of those is the Eared Grebe (*Podiceps nigricollis*; Jehl 1994) In autumn, the great majority of the North American population shifts to Mono Lake, California, and Great Salt Lake, Utah, to molt, stage, and exploit the enormous biomass of aquatic invertebrates (Jehl 1988, Jehl et al. 1999). Timing of the movement varies little from year to year (Jehl and Johansson 2002). Postbreeding adults begin to arrive in late July, and adults and juveniles continue to arrive through the fall, reaching peak numbers by late October. Grebes remain continuously until food supplies are depleted (typically in late November–December), then shift to wintering areas in the southern United States and Mexico (Jehl 1998, Jehl and McKernan 2002, Jehl et al. 2002,).

The number of birds involved is very large, and obtaining accurate estimates requires aerial photography techniques (Boyd and Jehl 1998). In this article, we document numbers at staging areas in 1996 through 2000, present estimates of the North American population, show that it experienced a massive collapse in the winter of 1997–1998 but then rebounded quickly, and discuss factors that affect population size.

Methods.—We made aerial photocounts of Eared Grebes staging at Mono Lake on or about 15 October from 1996 through 2000 and at Great Salt Lake from 1997 through 2000. By 15 October, >95% of the migrants have arrived (Jehl and Johansson 2002). Transects were flown at altitudes higher than would cause grebes to dive or engage in other evasive behavior. At Mono Lake (180 km^2), transects were spaced 0.75 km apart and covered the entire lake. Vertical photos were taken every 10 s, with the first of each transect at the lake edge. Landmarks were photographed to provide a scale. Bird images were counted on prints and converted to densities, which were than extrapolated to determine lakewide population size. We used topographic maps and satellite photos to determine the area of Mono Lake. (For details on methods, see Boyd and Jehl 1998.)

The protocol at Great Salt Lake was similar (D. Paul et al. unpubl. report; D. Paul unpubl. data). Because that lake is far too large (2,610 km^2) to allow complete coverage, the Utah Division of Wildlife Re-

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TABLE 1. Photocounts (in millions) of Eared Grebes staging at Mono Lake, California, and Great Salt Lake, Utah.

Location	Date	Count (± % SE)	Adjusted, diving[a]	Percent lake surveyed (estimated percent encountered)	Adjusted, 100% coverage, mid-October	Maximum expected population[b]
Mono Lake	15 Oct 96	1.495 (4.0)	1.734	100 (100)	1.734	1.821
	15 Oct 97	1.623 (4.8)	1.882	100 (100)	1.865[c]	1.976[c]
	16 Oct 97	1.592 (4.2)	1.847	100 (100)	—	—
	15 Oct 98	0.825 (6.0)	0.975	100 (100)	0.957	1.005
	17 Oct 99	1.077 (5.3)	1.249	100 (100)	1.249	1.311
	18 Oct 00	1.583 (7.5)	1.836	100 (100)	1.836	1.928
Great Salt Lake	14–15 Oct 97	1.237	1.435	10 (95)	1.507	1.582
	14 Oct 98	0.442	0.513	24 (90)	0.569	0.598
	13 Oct 99	0.855	0.992	27 (80)	1.240	1.302
	16–17 Oct 00	0.995	1.154	27 (90)	1.281	1.345

[a] Count × 1.16.
[b] Adjusted coverage × 1.05 for later arrivals.
[c] Mean of 15–16 October 1997.

sources made boat and plane surveys on the South Arm through the autumn to locate major concentrations (currently the North Arm does not support either grebes or prey). In mid-October, photo-transects were flown at intervals of 1.8 km, except in regions of very low bird density, where they might be expanded to as much as 10 km. Photographic techniques and counting procedures were as at Mono Lake. The area encompassed by transects was determined by GPS readings and measured by computer using ARCVIEW software. Boat and plane parties (above) estimated numbers in areas in which photography was not feasible or precluded by lake or sun conditions (D. Paul et al. unpubl. report).

Because photocounts were made when Eared Grebes consituted >99% of the birds on Mono Lake and in the areas surveyed on Great Salt Lake, all images were considered to represent grebes unless determined otherwise. To allow for submerged birds, we used data from 17 h of monitoring radiotagged grebes at Mono Lake and Great Salt Lake over three periods in 1996 (22–24 September, 14–16 October, and 28–29 October). It was found that grebes were spending 14–19% of the day under water (Boyd and Jehl 1998), similar to estimates from direct observations at Mono Lake (Jehl 1988). We used 16% in our calculations.

At Mono Lake, aerial transects covered the entire lake, so no further adjustments to calculate total numbers were necessary. At Great Salt Lake, transect routes encountered 90 to 95% of the population, except in 1999, when the rate was only 80%, due to greater dispersal in a period of low brine shirmp numbers (DSP). To determine total numbers were adjusted count data proportionately, assuming 100% detection. Finally, to estimate the maximum staging population at each lake we increased the corrected totals by 5% to allow for birds that might arrive after 15 October (Jehl and Johansson 2002).

To roughly model population trends after the 1997–1998 die-off, we used counts from Mono Lake (which are more precise; see below) and made the following assumptions: (1) grebes return to the same staging area each year; (2) mortality during staging is trivial (Jehl 1988, 2001); (3) annual mortality is low (Cullen et al. 1999)—we estimated 5%; (4) age of first breeding is 1 year; that is suspected for nearly all females, at least some males (Jehl 1988), and is further indicated by the very low numbers of nonbreeding individuals encountered at staging lakes in summer (Jehl unpubl. data); (5) all surviving birds are capable of breeding; and (6) recruitment averages 0.8 fledglings per pair (Cullen et al. 1999; recruitment rate can be considered similar to fledging success because of low juvenile mortality; Jehl 1988, 2001). Thus, the number of pairs available to breed in any year ($-_p$) can be estimated as $N_p = 0.95\ N_f/2$, where N_f is the size of the fall peak. The projected size of the population at staging lakes the subsequent fall is

$$N_{f\ +1} = 0.8\ N_p + 2N_p.$$

Results.—Adjusted mid-October photocounts for Mono Lake in 1986 through 2000 ranged between 0.96 and 1.86 million, and for Great Salt Lake in 1987 through 2000 between 0.57 and 1.51 million (Table 1). The accuracy of the Mono Lake counts was indicated by their replicability (the difference in unadjusted counts on two consecutive days in 1997 was 2%), and low standard errors (Boyd and Jehl 1998). Error estimates for high density areas of Great Salt Lake were similar, but were not attempted lakewide because of the extrapolations required.

In any year fewer birds staged at Great Salt Lake (average 77%, range 59–99%). The similar numbers

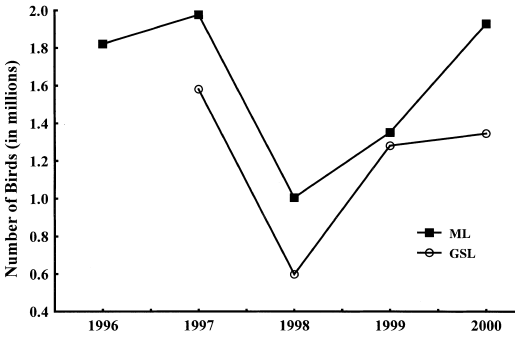

FIG. 1. Maximum fall staging populations of Eared Grebes at Mono Lake, California (ML), and Great Salt Lake, Utah (GSL). 1996–2000. See Table 1 for details.

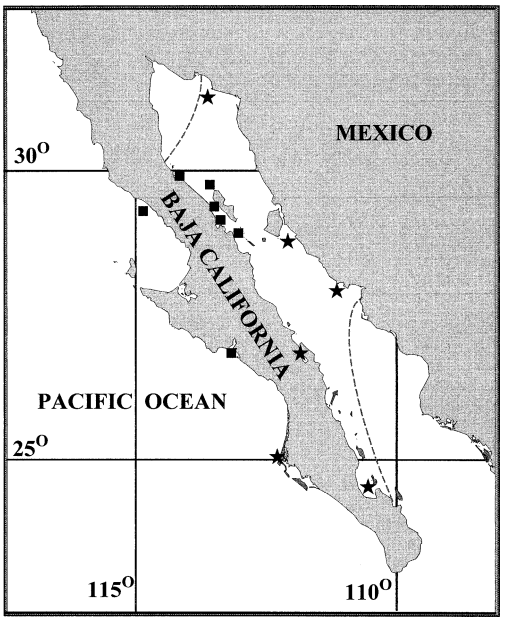

FIG. 2. In the winter of 1997–1998, large numbers of Eared Grebes were found dead in the areas bordering Baja California and mainland Mexico. Stars indicate areas where heavy mortality was reported to or observed by D.W.A. Squares indicate areas where beach or boat surveys were made. Dotted lines enclose the area in the Gulf of California where high mortality was encountered.

to Mono Lake in 1999 are probably anomalous due to the high adjustment used in that year. Over our study numbers at both lakes varied in parallel (Fig. 1). They were high in 1997 (and in 1996 at Mono Lake), then plummeted in 1998, before rebounding in 1999 and, at Mono Lake, returning to near pre-crash size by 2000.

Discussion.—Numbers of fall staging Eared Grebes at Mono Lake and Great Salt Lake exhibited great annual differences between 1996–1997 and 2001, dominated by a massive decline after the winter of 1997–1998. The reality of that decrease was indicated by other evidence as well.

(1) Radar observations of grebes leaving Great Salt Lake in 1997–2000 indicated that departure flights were smaller and fewer in 1998 than in other years (S. Gauthreaux and J. Jehl unpubl. data).

(2) Only 25% as many grebes were encountered at a monitored site near Green River, Wyoming (see Jehl and Johansson 2002) in autumn 1998 as in 1997 (J. Jehl unpubl. data).

(3) At Eagle Lake, a major colony in central California, Shaw (1998) found 3,260 nests in 1997; in 1998 D. W. Anderson (unpubl. data) estimated 1,040 nests, a reduction of 68%. Eared Grebes are known to shift colony sites from year to year (Cullen et al. 1999), but numbers at Eagle Lake seem to have been stable prior to 1998 (D. W. Anderson unpubl. data).

(4) The Gulf of California is the Eared Grebe's principal wintering area (Jehl and McKernan 2002). For many years, D. W. Anderson (unpubl. data) has conducted standarized beached bird counts at that location as part of long-term research on seabird populations. In most years, relatively few birds are found. In the winter of 1997–1998, however, coincident with a major El Niño–Southern Oscillation (ENSO), he encountered thousands of dead grebes. Mortality was especially intense in the north and midriff areas, but was widespread and even observed on the west coast of Baja California, north at least to Santa Rosaliita (Fig. 2). In the midriff area, densities (representing carcasses deposited on shore between December 1997 and January–February 1998) were much greater in winter 1997–1998 (8.0/100 m ± 4.0 [95% CI]) than in the non-ENSO winters of 1995–1996 and 1996–1997 (0.2/100 m ± 0.1; $P < 0.001$). Similarly, on pelagic transects in the midriff area D. W. Anderson (unpubl. data) found 1.3 floating carcasses per square kilometer in March 1998 and 0.5 carcasses per square kilometer in May 1998; none was observed in earlier (1995–1996 and 1996–1997) or later (1998–1999, 1999–2000) years. Because strong tides in the gulf transport carcasses, which can sink or be scavenged, there is no way to quantify so large and extensive an event with much precision. In the area where heavy mortality was documented, carcass counts indicated a minimum mortality of about 400,000 individuals (D. W. Anderson unpubl. data). Given the regional nature of the El Niño, and the broad range of the Eared Grebe in the gulf, total mortality was surely higher.

Twelve carcasses recovered in fresh condition were emaciated. Body mass averaged 178 ± 14.0 g (95% CI), instead of the 320–340 g expected in healthy birds at that season (Jehl 1997) and well below the estimated minimal survival weight of about 220 g (Jehl

1988). During ENSO years, surface water temperatures are elevated; in June 1998 they were ~30°C, as opposed to 22–24°C in non-ENSO years (D. W. Anderson pers. comm.). We suspect that this affected food supply (see Cullen et al. 1999) either by killing it or by forcing prey to cooler waters below the efficient foraging depth of grebes. ENSO effects on seabirds in the Gulf of California have been reported before (e.g. Anderson 1973, Mellink 2000). In 1997–1998, however, mortality was virtually restricted to Eared Grebes (D. W. Anderson unpubl. data) whose extreme susceptibility probably stemmed from normal seasonal atrophy in their flight muscles (Jehl 1997). That would have rendered them flightless and unable move to alternative foraging areas, which would not have been the case with volant seabirds.

The maximum number of grebes staging at Mono and Great Salt lakes was 3.56 million in 1997 versus 1.60 million in 1998 (Table 1). If we assume that mortality was low after grebes left the wintering grounds and that juveniles made up roughly 35% of the autumn 1998 flock (suggested by recruitment data [below] and estimates from Mono Lake; J. Jehl unpubl. data), the number of grebes surviving the ENSO event and available to breed and return to Mono and Great Salt lakes in autumn 1998 would have been ~1.04 million (1.60 million stagers–0.56 juveniles). Accordingly, ENSO mortality would have involved ~2.52 million birds, or ~70% of the previous fall's numbers. The percentage of the decline is similar to that detected in breeding birds at Eagle Lake and in migrants in Wyoming and compatible with mortality projections from the Gulf of California. Although that may represent as great a decrease from a natural event as has ever been documented in any common and wide-ranging bird, it was not detected by the Breeding Bird Survey, which found no significant trend in the North American population either between 1997 and 1998 (trend + 7.13%) or over a 5 year span (1996–2000, −8.96%; B. Peterjohn and J. Sauer pers. comm.). The lack of correspondence is not unexpected because roadside surveys are of little use for measuring trends in marsh-nesting species.

Despite the loss, grebes rebounded to near 1997 levels by autumn 2000. So rapid a recovery might seem improbable for a single-brooded species with a mean clutch of 3 (Cullen et al. 1999). Yet it is plausible for the Eared Grebe because, except for large but irregular die-offs involving losses to disease and migration (Jehl 1996), annual mortality appears to be low (Cullen et al. 1999). Of critical importance is that the survivorship of juveniles is exceptionally high during the highly vulnerable period when they first become independent of their parents. That is because they move directly from breeding areas to staging lakes where food is superabundant and predators are lacking. Over the several month-long fall staging period, juvenile survivorship evidently exceeds 99.5%, and that of adults is even higher (table 4 in Jehl 1988; 2001, and J. Jehl unpubl. data).

At Mono Lake in 1998 the maximum staging population was 1.005 million, of which at least 653,000 (1.005×0.65) can be considered adults that had survived the die-off. Using the assumptions outlined above, that flock would increase to 1.733 million in 2000; the actual mid-October count was 1.836 million, with maximum expected 1.93 million. (Under the same scenario, fall numbers of 598,000 at Great Salt Lake in 1988 would increase to 1.05 million by fall 2000; the actual mid-October count was 1.28 million, maximum 1.35 million). Both projections are lower than modeled, but the agreement is sufficiently good that we conclude that rapid recovery is feasible.

How many Eared Grebes are there in North America? The regional literature including *North American Birds* (and its antecedents), our observations in the western United States and Canada in autumn, and consultation with local experts indicate that nearly all Eared Grebes leave breeding areas by the third or fourth week of September and move promptly to the main staging lakes (Jehl 1988). In Wyoming, 95% of the passage toward Great Salt Lake is completed by 15 October (Jehl and Johansson 2002). To be sure, not all grebes stage at Mono Lake and Great Salt Lake. Some that probably never move there include a few thousand that winter along the Pacific coast between British Columbia and central California. (Jehl 1988, Contreras 1997), and perhaps smaller numbers from the easternmost part of the range that bypass the Great Basin en route to wintering areas from mainland Mexico eastward. In the interior west, the only fall (15 October–early November) concentrations known to us away from the major concentration points are ~5,000 that sometimes linger on Eagle Lake, California (L. Oring pers. comm.), and, in some years, a few thousand at Lake Abert, Oregon (maximum to 17,250 on 12 November 1997; W. Devaurs pers. comm.). Commercial salt works—the anthropogenic equivalents of hypersaline lakes—attract Eared Grebes in early winter. But in mid-October, which is before the exodus from Mono and Great Salt lakes, numbers in the salinas in South San Francisco Bay and San Diego Bay are typically in the hundreds (Cogswell 1999; Unitt 1984, H. Cogswell pers. comm.), most of which are juveniles that have moved there directly from breeding areas. Indeed, there is no indication that grebes leave staging lakes prior to the main departure period. Even the most generous estimates of grebes elsewhere do not sum to 1% of those staging at Mono and Great Salt lakes. For all practical purposes, the North American population can be estimated at no more than 5% above the mid-October totals at those lakes: 3.73 million in 1997, 1.68 million in 1998, 2.74 million in 1999, and 3.43 million in 2000.

The Eared Grebe is the most numerous grebe in the world, perhaps having attained that status only in the last several thousand years, owing to its ability

to exploit invertebrate resources at hypersaline lakes that formed in North America after the end of the Pleistocene (Jehl 2001). Factors that affect population size on a shorter time scale remain to be determined. The species is capable of increasing rapidly but is also highly susceptible to environmental perturbations that can lead to large die-offs. What, then, sets the upper limit for the species? Would the continental population be larger today if it had not encountered the 1997–1998 El Niño? Photocounts at staging areas and backed by an understanding of the Eared Grebe's natural history throughout its range now make it possible to measure and evaluate changes. Furthermore, if counts can be made through an extended period of high survivorship, it may be possible to determine whether grebes ever become sufficiently common to be limited by density-dependent factors on the breeding or wintering grounds, rather than by irregular catastrophic events.

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