

Ecology of migrant Black-necked Grebes *Podiceps nigricollis* at Mono Lake, California

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Autumnal migrant Black-necked or Eared Grebes *Podiceps nigricollis* begin arriving in large numbers at Mono Lake, California, in August. Juveniles appear to arrive later than adults, and the number of grebes at Mono Lake peaks in September and October. The grebes leave by November or December. Stomachs of 73 grebes collected in the Autumns of 1980 and 1981 reveal that brine shrimp *Artemia monica* comprise over 90% of the diet. The remainder of the diet is composed of the larvae, puparia and adults of a brine fly *Ephydra hians* and small numbers of shore bugs *Saldula arenicola* and *S. opiparia* and other terrestrial arthropods. The grebes do not feed at night but rest instead in large nocturnal aggregations over deep water. Grebe fat stores and total body-weight increase from August to October, and adults moult their regimes in August and September. In late autumn brine shrimp densities decline dramatically and the grebes leave the lake.

This paper summarizes information on the biology and feeding ecology of Black-necked or Eared Grebes *Podiceps nigricollis* at Mono Lake, California, collected during a study (Cooper *et al.* 1984) of the impact of grebe predation on the population of its principal prey *Artemia monica*. Although the feeding ecology of other grebes has been studied (e.g., Markuze 1965, Fjelds  1973, 1981), very little is known of the biology of the Eared Grebe, especially during migration (Munro 1941, Palmer 1962, Cramp & Simmons 1977). Studies of this grebe at Mono Lake are especially interesting, as Mono Lake has been declining rapidly in level and is the focus of an environmental controversy (e.g., Steinhart 1980).

Study site and organisms

Mono Lake is a large (150 km²) deep (mean depth = 19 m) lake located high (elev. 1940 m) in the Great Basin at the eastern base of the Sierra Nevada (38°N, 119°W). Its waters are currently nearly three times as saline as the ocean, are highly alkaline (pH = 10), and have very high concentrations of chlorides, sulphates and carbonates. The lake's extreme water chemistry precludes the survival of fish, and the sole permanent macroscopic inhabitants are an endemic brine shrimp *Artemia monica* and a brine fly *Ephydra hians*. Adult *Artemia* are c. 1 cm in length and have dry weights of about 0.45 mg (D. Herbst, pers. comm.). During the winter and early spring, adult shrimp are essentially absent from the lake, and the population

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overwinters on the lake bottom as environmentally resistant cysts. These cysts hatch in March, and adult *Artemia* are usually abundant from June to September or October.

The fly spends its adult stage on the lake's shore, feeding on algae and shore debris, and the aquatic larvae feed on benthic algae and pupate beneath the water. Representative dry weights of the fly larvae, puparia and adults range from 1.5 to 2.5 mg (D. Herbst, pers. comm.). Other macroinvertebrates occur in Mono Lake only when they are blown or washed in. The most common of these are two shore bugs *Saldula arenicola* and *S. opiparia*, which are often washed into the lake from shore areas. For more information on the ecology of the shrimp and fly see Mason (1967), Winkler (1977), Dana (1981), Lenz (1982), Melack (1983) and Cooper *et al.* (1984).

Mono Lake supports very large populations of California Gulls *Larus californicus*, Red-necked and Wilson's Phalaropes *Phalaropus lobatus* and *P. tricolor*, respectively, and Eared Grebes (Winkler *et al.* 1977). The gulls breed at the lake, but most leave the area by August. The phalaropes stop at the lake during migration, and the peaks of their populations have passed by September. Thus, when the grebes reach their peak numbers in September and October, they are the only abundant secondary consumers on the lake.

Methods

We collected 61 grebes between sunrise and 1315 h in August and October 1980 and in August, September and October 1981 (Table 1). The grebes were collected under permits from the California Department of Fish and Game and U. S. Fish and Wildlife Service at limnological sampling stations spaced regularly throughout the

Table 1. *Summary of proportional representation of prey types and proportional dominance of stomach contents of Black-necked Grebes collected during the day in 1980 and 1981*

	1980		1981		
	29-30 Aug	25-27 Oct	23-24 Aug	22-23 Sept	20-23 Oct
<i>n</i>	5	24	9	11	12
Prey items per stomach:					
\bar{x}	688.4	361.9	773.7	1468.8	2260.3
s.e.	225.0	62.0	126.8	236.7	252.2
% of total prey consisting of:					
<i>Artemia</i>	87.0	94.5	95.3	97.5	95.2
<i>Ephydra</i> larvae	10.4	3.4	3.6	1.4	0.3
<i>Ephydra</i> puparia	1.3	0.9	0.9	0.8	3.3
<i>Ephydra</i> adults	0.5	0.06	0	0	0.5
<i>Saldula</i> adults	0.05	0.4	0	0.1	0.2
Misc. terr. prey	0.6	0.7	0.2	0.2	0.4
% of stomachs dominated by:					
<i>Artemia</i>	80	77	89	100	100
<i>Ephydra</i> larvae	20	9	11	0	0
<i>Ephydra</i> puparia	0	9	0	0	0
Other insects	0	5	0	0	0

lake at least 1.5 km apart (Cooper *et al.* 1984). On any given day, one grebe was collected at each station except early in the season, when low densities sometimes made collecting at each station impossible. Conversely, on two occasions later in the season, grebe densities were so high that two individuals were killed with one shot. On the night of 26–27 October 1980, we collected an additional 12 grebes (three each at 1815, 2130, 0130 and 0700 h) from a station in the centre of the western arm of the lake.

When a grebe was shot, the digestive tract was removed immediately, injected with formalin, and placed in a jar of *c.* 7% formalin. Examination of entire digestive tracts revealed that all recognizable food items were limited to the stomach. The grebes were frozen within 6 h of collection and, together with the digestive tracts, returned to the laboratory for analysis. In the laboratory, we sexed and weighed the grebes, weighed their emptied stomachs, recorded their plumage condition and flight feather moult, and measured the thickness of their subcutaneous fat over the keel of the sternum.

Juvenile Eared Grebes cannot be reliably distinguished from basic-plumaged adults in the autumn on the basis of mensural or plumage characters, and we estimated age composition by measuring the bursa of Fabricius in the collected birds (cf. Johnston 1956). The measurements of the bursae in the birds of our sample are bimodally distributed with juveniles possessing a discrete and full-bodied bursa 11 to 28 mm in length. Adults entirely lacked a bursa, and two 'subadults' possessed rudimentary structures 3 and 6 mm in length that were late in stages of resorption.

In analysing stomach contents, we assumed that every *Artemia* fragment that retained at least three pairs of appendages represented one individual; for *Ephydra* larvae and puparia we counted any fragment that consisted of three or more body segments; for *Ephydra* adults, *Saldula*, and miscellaneous terrestrial invertebrates, we counted intact heads. In establishing the counting criteria for *Artemia* and *Ephydra* we considered the overall degradation of prey fragments with increasing digestion. As these prey are digested, not only do they become increasingly fragmented, but their tissue deteriorates as well. *Artemia* fragments bearing only three pairs of appendages were almost invariably the posterior thoracic appendages and the 'tail' of abdominal somites and digestive tract, which were more resistant to disintegration than were the anterior thoracic segments. The heads and large second antennae of males were quite resistant to disintegration, but they were not counted since the corresponding parts of the females were rapidly digested. Thus, a fragment of this minimal countable size would come almost invariably from a shrimp, the remainder of which was thoroughly disintegrated. In *Ephydra* larvae, there are only eight clawed segments, and the chances are small that a larva reduced to a three-segmented fragment would be represented by another of equal or greater size.

We used two different but comparable techniques in the processing of stomach samples. In the first 47 stomachs that we analysed, we placed stomach contents in a series of petri dishes and identified and counted all food items at 6–12 × under a dissecting microscope. This process proved to be exceedingly time-consuming, however, because grebes eat and retain in their stomachs large numbers of their own feathers, which make separation and counting of food items very difficult. We circumvented this problem by boiling the stomach contents in 10% KOH for 10 minutes and staining the remaining material with iodine solution (1.6 g I₂, 10 g KI, 14 ml H₂O) in a concentrated solution of salt. This procedure effectively hydrolyses all protein, converts the chitin in arthropod integument to chitosan, and stains the chitosan brown (Richards 1951). The prey items were then counted under the dissecting scope at 6–12 ×. Comparison of counts obtained from both procedures reveals almost identical results. For example, we counted 328 *Artemia* and 42

Ephydra larvae in a stomach's content with the first method. We recombined these food items with the feathers of the original content and then processed it with the second method. The count from this second treatment yielded 331 *Artemia* and 40 *Ephydra* larvae. As a further check on the persistence of prey items through the second processing technique, we added ten undigested 'reference' *Artemia* of one sex to each of the 26 samples before boiling. In every sample processed, we were able to find all ten reference shrimp, and in all samples these reference shrimp retained all their appendages and an undigested appearance.

Results

Composition of the population

Eared Grebe population size at Mono Lake displays a regular annual pattern, with small numbers in Spring and much larger numbers (up to at least 750,000 birds) in Autumn (Cooper *et al.* 1984, Winkler *et al.* 1977). Grebes on the lake number five thousand or fewer in winter months (Winkler, pers. obs.). The adult:juvenile ratio for our samples varied from 6:2 in August to 5:6 in September and 19:32 in October. The data are few for statistical testing, and a Pitman's permutation test (Bradley 1968: 68–86) revealed a weak effect of month of collection on age (two-tailed $P = c. 0.11$). The sex ratio of adults does not vary significantly from 1:1 in any of our samples. Our sample of juveniles consists of 27 males and 13 females, significantly biased in favour of males ($G = 5.00$, $P < 0.05$).

Moult

Juvenile Eared Grebes retain their initial wing feathers through their first autumn, whereas the adults moult both their wing and contour feathers. Of six adults collected on 22–23 August 1981, one had already completed its wing moult and five had not yet begun. On 22–23 September one of five adults had completed wing moult and three of the four others were in late stages of moult completion. These three adults had their distal five primaries two-thirds to three-quarters emerged from their sheaths, and their proximal primaries were three-quarters to fully emerged. In one of these birds the distal two secondaries were three-quarters emerged. In the remaining moulting adult, all the primaries were one-third to one-half emerged and all secondaries were two-thirds emerged. Four of the five adults collected on 20–23 October 1981 had recently completed wing moult, and the fifth had not yet begun. These data suggest that Eared Grebes at Mono Lake undergo a simultaneous moult of at least the primaries and perhaps the secondaries as well. Most birds appear to moult in the period between late August and late September. In any event, moult is post-breeding in this species, as suspected by Cramp *et al.* (1977), and is not pre-nuptial as suspected by Stresemann & Stresemann (1966).

Fat and weight

The data on depth of ventral subcutaneous fat and total body-weight (including alimentary tract with feathers removed) indicate that our simple measure of fat gives a representative indication of variation in total fat stores: weight and fat are strongly correlated for both the 1980 ($r = 0.81$, $P < 0.001$) and 1981 samples ($r = 0.86$, $P < 0.001$) as well as for both samples taken together ($r = 0.74$, $P < 0.001$). Grebes increased in both fat and weight during their stay at Mono Lake in 1981 (Fig. 1), and

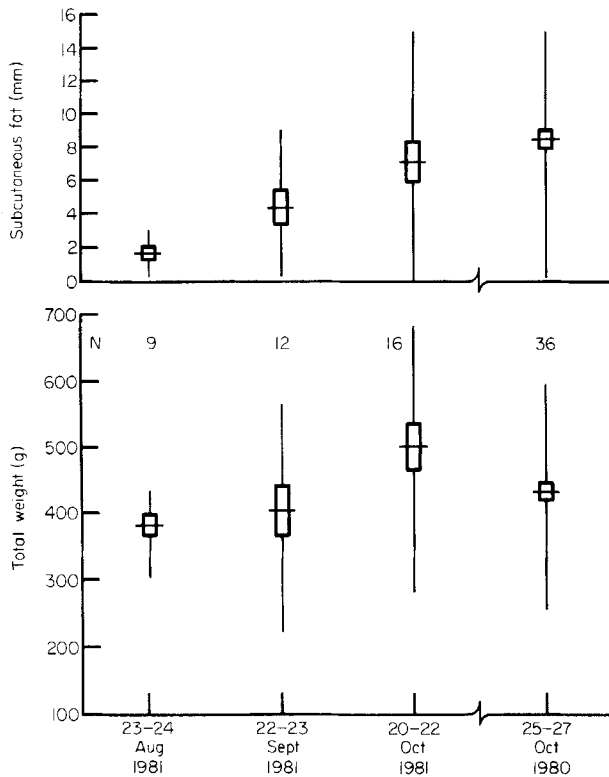


Figure 1. Trends in total weight (below) and depth of ventral subcutaneous fat deposits (above) in Black-necked Grebes at Mono Lake. Means (horizontal lines), 95% confidence intervals of the means (rectangles) and ranges (vertical lines) are graphed.

the major period of fat accumulation appears to be between late September and October. A multiple analysis of covariance (ANCOVA) indicates that season has a significant effect on fat ($P < 0.05$), whereas annual, age- and sex-related differences have no significant effect. A similar analysis for weight revealed significant effects of annual, seasonal and age-related effects but no significant effect of sex.

Diet and feeding behaviour

Artemia is the predominant component of Eared Grebes' diets at Mono Lake. The average proportion of the diet composed of shrimp is over 75% by numbers in all periods sampled (Fig. 2). Shrimp comprise over 85% of all pooled prey items in all sample periods (Table 1), and most grebes in all periods have diets dominated by shrimp (Table 1). Next in decreasing order of importance as prey are *Ephydra* larvae, puparia and adults; *Saldula* adults; and miscellaneous terrestrial arthropods (mostly Hemiptera and Diptera).

In 1980, when autumnal shrimp densities were relatively low (Cooper *et al.* 1984), grebes took many more non-shrimp prey than in 1981 (Fig. 2). A multiple ANCOVA evaluating the effects of year, month, time of day, *Artemia* density at the collection site, water transparency, grebe density around the collection site, grebe weight, sex, age, fat, length of bill plus head and distance from shore on the square-

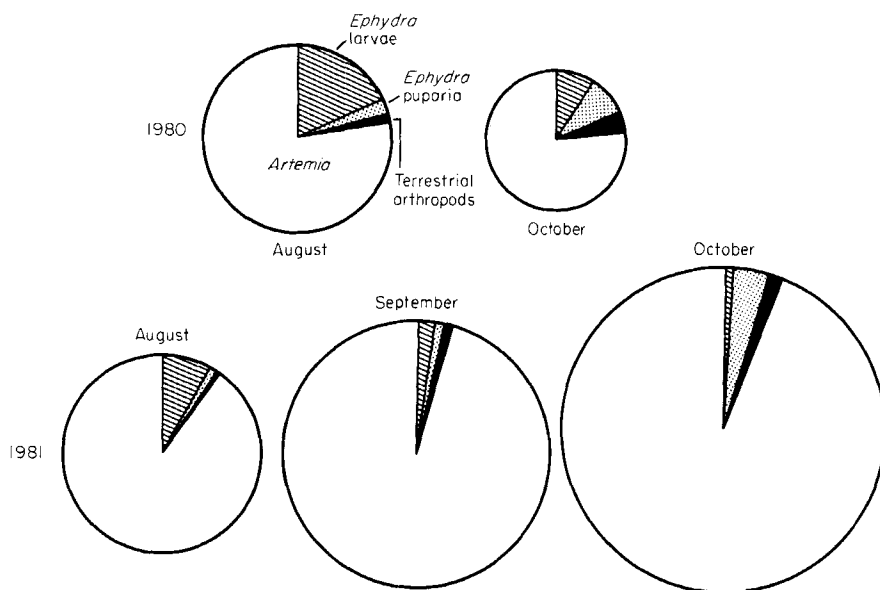


Figure 2. Mean proportional composition of Black-necked Grebe diets at Mono Lake in 1980 and 1981. Areas of circles are proportional to total mean number of prey items in stomachs (see also Table 1).

root-transformed numbers of shrimp in the diet revealed that only year ($P < 0.001$), month of collection ($P = 0.04$) and the density of grebes ($P = 0.01$) have significant effects on the numbers of shrimp eaten. The correlations between grebe density and the number of shrimp eaten are negative in August 1980 and 1981, positive in September 1981 and positive in October 1980 and 1981. These correlations are not significant, however, when taken individually.

Although we did not sample grebe foraging behaviour systematically, in the course of our sampling on the lake we gained a general picture of the grebes' daily activity cycle in late fall. The majority of the grebes spend the night in large rafts over deep water at least several km from shore. At first light, the birds begin swimming away from these nocturnal roosts, and by sunrise they have begun foraging in areas throughout the lake. The grebes seldom forage in water less than 2 m deep, and they feed actively throughout the morning hours. On calm days, grebes forage until dusk, but it is not known whether they forage during the frequent periods of afternoon wind on the lake, as it has not been possible to collect grebes at this time, and repeated observations on a given individual are next to impossible in the wind-generated chop. Our impression of the daily cycle of foraging behaviour, with all feeding limited to the daylight hours, is reinforced by the stomach contents of a series of grebes collected through a 24-h period on 26–27 October 1980. Grebes collected from 0845 h DST (75 minutes after sunrise) to 1315 h contained an average of 351.7 *Artemia* ($n = 12$, s.e. = 82.6), whereas those collected from c. 1815 (30–60 minutes after sunset) to 0715 h (15 minutes before sunrise) of the following day contained an average of 0.17 shrimp ($n = 12$, s.e. = 0.17). Eleven of the 12 nocturnal samples lacked shrimp entirely, while one sample contained two shrimp. By contrast, only one of the 12 diurnal samples lacked shrimp, and this stomach also lacked prey of any other kind.

This diel sample series also provides evidence that the persistence times of non-shrimp prey in grebe stomachs are substantially longer than for shrimp. Stomachs

collected after dark and before midnight contained up to 1588 *Ephydra* larvae, nine *Ephydra* puparia, 44 *Ephydra* adults and 385 adult *Saldula*. Although it is possible that these birds had been foraging at night, it seems more reasonable to attribute the later presence of non-shrimp prey in the stomachs to longer persistence times. Furthermore, nearly all grebes collected during the day or night contained large numbers of shrimp cysts. Because grebes undoubtedly ingest shrimp cysts with mature female shrimp, the presence of shrimp cysts indicates grebe feeding on shrimp in the recent past. After midnight, only shrimp cysts and the highly-chitinized parts of *Ephydra* puparia and terrestrial insects were found in grebe stomachs. There was no tendency for the number of shrimp cysts per grebe stomach to decline through the night, and as many as 6000 intact cysts were found in grebe stomachs just before daybreak. Our estimate of the average persistence time of shrimp through grebe stomachs is 25 minutes (Cooper *et al.* 1984). (Note that our average persistence times represent the mean length of time between ingestion and the point of digestion at which the prey no longer meets our counting criterion, and total digestion times are likely to be substantially longer. Also, these are mean times, and some prey items last a good deal longer in grebe stomachs than others of their kind.) The mean persistence times of *Ephydra* larvae are probably in the vicinity of 1–3 h, while hard parts of other prey persist much longer. Data from Markuze (1965) suggest mean persistence times of approximately 8–10 h for 'invertebrates' (mostly beetles) and approximately 2–3 h for carp *Cyprinus carpio* in the stomachs of captive Red-necked Grebes *Podiceps grisegena*.

Discussion

There are several sources of bias which should be considered in evaluating our results. The age-structure of our sample may be biased by age-specific differences in the propensity of grebes to avoid our approach, but it is not evident a priori whether juveniles would be more or less tolerant of human approach than would adults. Our estimates of dietary composition are based on numbers of prey rather than their biomass. Shrimp weigh less than flies, and this might, therefore, lead to an underestimation of the importance of non-shrimp prey. The longer gut passage times of the flies, however, probably counteract this potential overestimation of shrimp's importance.

The available data suggest a regular pattern in the grebe's autumnal use of Mono Lake. Grebes begin arriving in large numbers at Mono Lake in August. Adults probably arrive before most juveniles. The grebes do not forage at night and they feed intensively during the day, predominantly on brine shrimp. As grebes continue to accumulate at the lake throughout the following months, fat stores and total body-weight increase, even during the period of wing feather moult in August and September. In late autumn, when shrimp densities decline (Cooper *et al.* 1984), the grebes leave the lake, apparently for wintering areas on the Pacific Coast (Jehl & Bond 1983) and the fresh water areas of the southwest (Palmer 1962).

At first sight, it may appear strange that such enormous populations of aquatic birds could be supported by feeding on a small crustacean. However, California Gulls survive on much the same diet at Mono Lake in the early summer months (Winkler 1983), and chicks of Oldsquaw or Long-tailed Duck *Clangula hyemalis* and perhaps other tundra-nesting waterfowl rely on closely-related phyllopod crustaceans for most of their food up to independence (Andersson 1973, Pehrsson 1974). In both systems, the critical condition appears to be the lack of fish predators and consequent large standing crops of available prey. Such high concentrations of

invertebrates, often typical of hypersaline lakes, also probably explain the enormous aggregations of related grebe species on saline lakes in South America (Wetmore 1926, Fjelds  1981), of the European race of *P. nigricollis* on saline Lake Tunis (J. Fjelds  pers. comm.) in central Asia and of the Eared Grebe on Great Salt Lake, Utah (D. Paul, pers. comm.).

Our research highlights the importance of Mono Lake to the aquatic bird populations of North America. Along with Great Salt Lake, Utah, Mono Lake appears to be one of the two principal staging areas for the Eared Grebe on this continent. While at the lake the grebes consume astronomical numbers of their brine shrimp prey, but despite the fact that they may consume up to 83% of the shrimp standing crop, their predation is not apparently responsible for the autumnal decline in shrimp densities (Cooper *et al.* 1984). Thus, removal of the grebes would not appear to have a large affect on the populations of shrimp in the lake. By contrast, the grebes depend critically on the continued productivity of the shrimp population, and recent fluctuations in the population dynamics of the shrimp (Lenz 1982) have raised the possibility that this grebe may soon be deprived of one of its two most important migratory stop-overs in North America.

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