AVOIDANCE OF SALT-LOADING BY A DIVING BIRD AT A HYPERSALINE AND ALKALINE LAKE: EARED GREBE

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ABSTRACT.—Data from captive Eared Grebes (*Podiceps nigricollis*) suggest that the birds do not like the taste of Mono Lake (California) water, which is highly alkaline and saline (pH ~ 10.0, osmolality ~ 2,400 mOsm/kg). Nevertheless, Eared Grebes are present continuously at Mono Lake for several months, reaching peak numbes of 750,000 in late fall, when they feed primarily by diving for brine shrimp (*Artemia* sp.). The birds do not drink fresh water during their stay at Mono Lake. Yet, data on blood chemistry, osmolality of food and gut contents, and salt gland weights and their hypertrophy show that the ingestion of salt is not a major physiological problem for Eared Grebes in hypersaline environments. They evidently meet their water requirements from the body fluids of their prey, which are more dilute than the lake water, and minimize salt intake by minimizing the amount of water that they ingest during feeding. Their large tongue, which fills the oral cavity, is important in achieving this result.

Many of the lakes of the Great Basin of the western United States are ephemeral and are characterized by strong alkalinity and salinity; those lacking fishes often contain a few invertebrate species that occur in great abundance. Many species of migratory birds visit alkaline lakes, yet only a few occur in large numbers. Among the most numerous are Eared Grebes (*Podiceps nigricollis*), Northern Shovelers (*Anas clypeata*), Snowy Plovers (*Charadrius alexandrinus*), American Avocets (*Recurvirostra americana*), Red-necked Phalaropes (*Phalaropus lobatus*), Wilson's Phalaropes (*P. tricolor*), and California Gulls (*Larus californicus*).

Mono Lake, California, a large and permanent alkaline salt lake at the eastern base of the Sierra Nevada, is an important breeding or stop-over place for several of these species. The birds are attracted by the seasonally superabundant food—brine shrimp (*Artemia* sp.) and brine flies (*Ephydra hians*). While feeding upon these aquatic invertebrates, the birds inevitably ingest some of the highly alkaline and saline lake water. Marine birds have supraorbital salt glands, which provide an extrarenal means of eliminating monovalent ions, mainly sodium chloride. But the salinity of many saline lakes far exceeds that of the sea. Mono Lake's salinity, 90 ppt (2,700 mOsm/kg) in 1982, is about 2.5 times that of sea water, and the chemical composition of the water is different than sea water. Mono Lake is a "triple lake": high in chloride, sulfate, and carbonate (Table 1). Birds feeding at Mono Lake must cope with the high sodium chloride load, as well as with other ions that contribute to the alkaline pH of 10.

Mono Lake is fed by fresh water creeks and springs. The California Gulls that breed at the lake visit fresh water several times each day to drink and bathe (Mahoney and Jehl 1985). In this way, they maintain adequate fresh water intake, despite feeding in the alkaline waters.

The most abundant of the migratory birds at Mono Lake are the Eared Grebes. A few individuals may be found any time of the year, and by late summer, populations increase dramatically, reaching an estimated 750,000 by late October. Individual grebes remain at the lake for 2–5 months or more (Jehl, unpubl.). During this time, many undergo a complete body molt, and all accumulate large amounts of fat before migrating to the wintering grounds in southern California and the Gulf of California.

For most of the fall, the grebes feed largely on tiny brine shrimp, mostly captured by diving. To feed underwater, the grebes must ingest some alkaline water along with the prey. Detailed observations over four years (Jehl, unpubl.), however, have found that during their extended sojourn at Mono Lake, Eared Grebes, unlike California Gulls, do not visit fresh water sources, and we have never seen them drink.

To determine how Eared Grebes cope with the harsh osmotic environment of hypersaline, alkaline lakes and to investigate whether or not they have any special adaptations for inhabiting these lakes and exploiting these rich food resources, we conducted experiments with wild as well as captive grebes that had fed in

TABLE 1. A comparison of selected Mono Lake water and sea water constituents.

Constituent	Mono Lake[a]		Sea water[b]	
	(ppt)	(mmol/l)	(ppt)	(mmol/l)
Sodium (Na)	37.0	1,609	10.81	470.2
Chloride (Cl)	18.80	529.6	19.44	548.2
Total alkalinity	21.23	366	0.14	2.34
Sulfate (SO₄)	10.60	110.4	2.71	28.25
Potassium (K)	1.70	43.6	0.39	9.96
Calcium (Ca)	0.003	0.0001	0.41	10.23
Magnesium (Mg)	0.037	1.5	1.30	53.57
Boron (B)	0.400	37.0	—	—
Arsenic (As)	0.015	0.0002	—	—
Iron (Fe)	0.0005	trace	—	—
Fluoride (F)	0.056	2.9	—	—
Total dissolved solids	89.90		35.21	
Specific gravity	1.0767		1.0281[c]	
pH	9.85		8.1–8.3[d]	

[a] From Los Angeles Department of Water and Power, May 6, 1981.
[b] Recalculated from Potts and Parry 1964.
[c] From Riley and Chester 1971.
[d] From Sverdrup et al. 1942.

habitats of differing salinities. We observed their behavioral responses, measured physiological variables that are indicative of salt-loading, and investigated possible anatomical adaptations that might reduce their intake of hypersaline water.

METHODS

LABORATORY EXPERIMENTS

Approximately 80 live Eared Grebes, found on the beach in San Diego, California, in January, 1983, were brought to Sea World Park, San Diego, for rehabilitation. They were kept in a fresh water pond for at least a month and were fed frozen shrimp and fresh meal worms ad lib. For experimental studies in March, 1983, we used 12 birds, most of which had just begun body molt. After being acclimated to small tanks lacking platforms, all were weighed, and blood samples were taken via cardiac puncture from five birds. Seven birds were placed in a 300-gallon holding tank containing 50 gallons of 100% Mono Lake water (approximately 2,400 mOsm/kg). Five others were placed in a similar tank containing 100 gallons of sea water (approximately 960 mOsm/ kg). We fed both groups a mixture (50:50) of shrimp and fresh meal worms ad lib. After 48 h, when the experiment was terminated, we again weighed and obtained blood samples from all birds. We transferred four of the birds that had been in sea water (one died during blood sampling) to a 300-gallon tank containing 50 gallons of 20% (480 mOsm/kg) Mono Lake water, obtained by mixing one part Mono Lake water with four parts of fresh water. The grebes were fed as before and weighed after 24 h. No blood samples were drawn because of

the danger of losing the birds from repeated cardiac punctures. Blood analysis was carried out as described below.

FIELD EXPERIMENTS

Blood analysis. In June and July, 1982 and 1983, we collected 24 Eared Grebes at Mono Lake. We immediately obtained a 2–5 cc blood sample from each bird by cardiac puncture into ammonium-heparinized syringes. Hematocrits were taken from this sample, and the remaining blood was placed in serum separator tubes. All samples and hematocrits were then centrifuged for 3 min at 5,000 rpm. We measured serum osmolality ($\pm$2%) of cooled samples within 1–3 h after separation with a Wescor 5100B vapor pressure osmometer, using 10 μl samples. Sodium and potassium levels ($\pm$1%) were measured with an IL 443 flame photometer. If enough blood was available, we also measured the pH of whole blood immediately after it was withdrawn from the bird, using a Chemtrix 400 portable pH meter.

Stomach analysis. Mono Lake specimens were weighed, aged, and sexed. We identified prey items and measured the osmolality and sodium and potassium concentration of stomach (gizzard) contents and of major food items, as described above. It was impossible to obtain osmolality of proventricular contents, because food almost instantly moved into the gizzard, leaving the proventriculus empty. This was true even when birds were collected within moments of active feeding.

To estimate brine shrimp osmolality, we repeatedly blotted the surface water from a sample weighing several grams until we felt we could get no more water out without crushing the shrimp. The sample was then mashed and
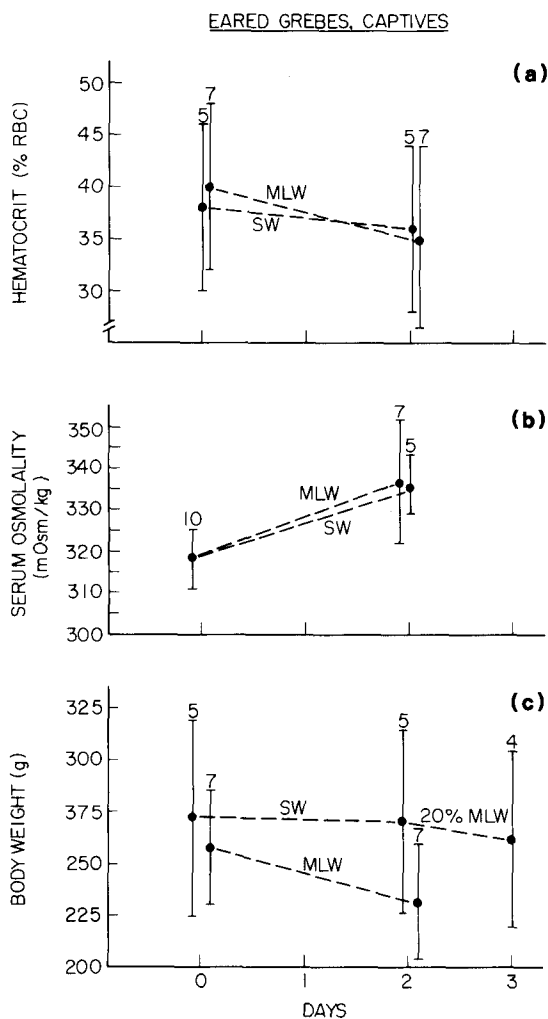
EARED GREBES, CAPTIVES

FIGURE 1. Mean hematocrit, serum osmolality, and body weight of captive Eared Grebes in sea water (SW), Mono Lake water (MLW), and 20% Mono Lake water (20% MLW). Vertical bars are ±1 SD. Sample sizes are on top of vertical bars.

analyzed. To determine brine fly osmolality, we mashed about 1 g of adult flies directly onto the paper sample dish, because too little hemolymph could be obtained from individual flies. The pupal and larval flies were large enough so that hemolymph from several individuals could be squeezed directly onto the paper disks. Only the mashed shrimp were fluid enough to allow us to determine sodium and potassium.

Water analysis. We measured osmolality and pH of lake waters, as described above.

Salt gland weights. Salt glands were dissected from birds collected at Mono Lake through much of the year, and from the Salton Sea in January, 1983, as well as from birds salvaged on the wintering grounds in southern California. They were weighed to the nearest milli-

gram; if both glands could be removed, we used their mean weight in our calculations.

Tongue measurements. The tongue and oral cavity of freshly-dead specimens of three Eared Grebes, a Western Grebe (*Aechmophorus occidentalis*), a Horned Grebe (*Podiceps auritus*), and a Pied-billed Grebe (*Podilymbus podiceps*) were measured with calipers to the nearest millimeter.

Statistical analysis. Statistical comparisons were based on Student t-tests, using a P value less than 0.05 to indicate significant differences.

RESULTS

LABORATORY EXPERIMENTS

Behavior. Grebes that were placed in sea water fed normally and maintained their weight for the 48-h experimental period (Fig. 1c). They pecked food from the water surface or dived for it, and they used diving as an evasive behavior when we approached. Birds in 100% Mono Lake water fed little, and then only from the water surface. We never saw them dive, even when panicked by the approach of humans. A bird might occasionally immerse its head in the water to look for food, but this action seemed unpleasant because the bird immediately stopped and shook its head vigorously for a long time. We ended the experiments after 48 h because only two birds in the Mono Lake water seemed to be eating regularly. The others were hungry and would investigate fresh food as soon as it was introduced; some would mandibulate it briefly but immediately drop it, shaking the head. The bird that ate most regularly took only fresh, floating food and refused to retrieve food from underwater. One bird that would not pick up floating food attempted to rob food from another's bill. Mean food consumption of the seven birds was 40% that of the birds on sea water.

The four birds transferred from sea water to 20% Mono Lake water changed their behavior markedly; they became lethargic, refused to dive unless forced, and ate little. Often they picked up food and then cast it out. They lost a small amount of weight (Fig. 1c). Because they were not eating, we ended the experiment after 1 day and returned them to sea water, where they immediately resumed diving and feeding in a normal manner.

Blood analysis. Serum osmolality can be used as a measure of an animal's state of hydration. If dehydration occurs, water is first lost from extracellular fluids, resulting in increased blood serum concentration (e.g., Arad and Marder 1983) and increased hematocrit (e.g., Koike et al. 1983). After 48 h, the serum osmolality of

TABLE 2. Blood values of Eared Grebes [mean ±1 SD].

	Mono Lake[b] (body weight 248–465 g)[a] (n)	Fresh/sea water (body weight 196–312 g)[a] (n)
Serum osmolality (mOsm/kg)	316 ± 13 (18)	318 ± 7 (10)
Hematocrit (% RBC)	44 ± 6 (19)	40 ± 6 (7)
Serum Na+ (meq/l)	140 ± 0.5 (12)	140 ± 0.3 (12)
Serum K+ (meq/l)	5.4 ± 1.7 (8)	5.0 ± 2.0 (11)
Blood pH	7.52 ± 0.9 (2)	7.59 ± 0.7 (2)

[a] Weight differences between Mono Lake and captive birds reflect seasonal changes in fat deposits and not a difference in the health of the birds.
[b] 1982 and 1983 data were not significantly different and are pooled.

controls in sea water and experimentals in Mono Lake water each rose 5% ($P < 0.05$) to 336 mOsm/kg (Fig. 1b), showing that some dehydration had occurred. By contrast, hematocrits dropped from 40% to 35% in the Mono Lake group and from 38% to 36% in the sea water controls, but the difference was not significant and all values remained within the general range for healthy birds (Sturkie 1976).

FIELD EXPERIMENTS

Behavior. Eared Grebes use Mono Lake as a staging area in late summer and fall, and remain there for several months before moving to wintering areas farther south. Early in their sojourn, they obtain much food by pecking brine flies (adults and larvae) and brine shrimp from the water surface. Some water that adheres to the prey can be seen dripping from the tip of the bill and some is removed by a quick and almost imperceptible lateral head shake. As fall progresses and the birds add heavy fat deposits, they devote nearly all of their foraging effort to diving for brine shrimp (Jehl, unpubl.).

Blood analysis. Hematocrits, serum osmolality, sodium, potassium, and pH for wild grebes at Mono Lake did not differ from those of the captive grebes feeding in either fresh or sea water (Table 2) and easily fell within the range typical of birds (see Sturkie 1976, Skadhauge 1981).

Stomach analysis. The above findings suggest that salt-loading does not occur. There are two possible explanations: either (i) grebes ingest high salt loads and have the physiological ability to eliminate the salt quickly, or (ii) grebes do not ingest high salt loads. We examined stomach contents to distinguish between these alternatives.

Brine shrimp and brine flies are essentially the only prey available to grebes at Mono Lake. The proportion of these prey items varies seasonally, but in the period of our observations, shrimp typically comprised 60–70% of the diet. Both invertebrate species are hypo-osmotic regulators that maintain their body fluids well below the lake's concentration (Table 3): Mono Lake osmolality was 2,395 mOsm/kg in 1982 and the pH was 9.63; in 1983, osmolality was 2,314 mOsm/kg, and pH was 10.83. Osmolalities listed in Table 3 represent minimum concentrations that the birds ingest while feeding upon a particular item; they do not include adhering lake water, except possibly for the brine shrimp (see Methods). Fly larvae and pupae were more dilute than shrimp, but fly values are for hemolymph only and would be higher if some adhering lake water were ingested with them. Percent body water of shrimp and flies are within the range typical of invertebrates, ca. 80% (Prosser 1973).

The osmolalities of grebe stomach contents did not differ in the two years (ca. 340 mOsm/kg) and were lower than that of the main prey item, brine shrimp (Fig. 2, upper panel). Stomach osmolalities were similar to the hemolymph of aquatic fly larvae and pupae, although these usually constituted a small fraction of the diet.

TABLE 3. Body fluid values of Mono Lake invertebrates.

Invertebrate species	Osmolality (mOsm/kg)	Sodium (meq/l)	Potassium (meq/l)	pH	Body water (% body weight)
Brine shrimp					
Adults	—	—	—	—	85[d]
1982	555[a]	170	20	7.44	—
1983	518[a]	200	26	—	—
Brine fly					
Adults	472[b]	—	—	—	78[d]
Pupae	352	—	—	—	—
Larvae	345	160[c]	—	—	87[d]

[a] Data are from samples that were blotted dry and mashed, and include not only hemolymph, but also perhaps a small amount of adhering lake water.
[b] Very dry sample, which may overestimate osmolality.
[c] Herbst (1981).
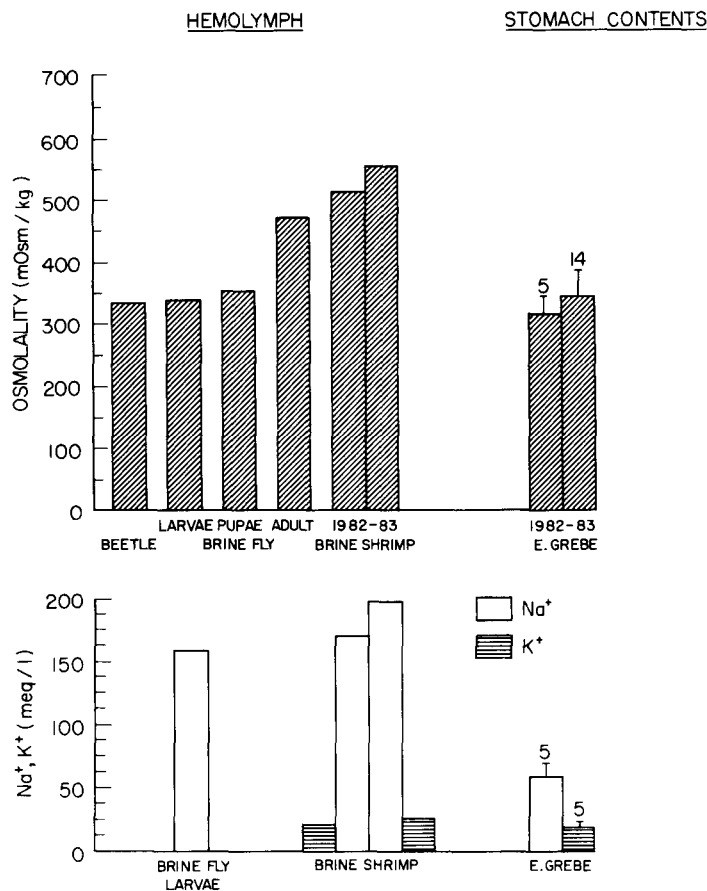[d] D. Herbst, pers. comm.

FIGURE 2.   Osmolality and sodium and potassium concentration of Eared Grebe stomach contents, and hemolymph of several prey species. Vertical bars are ±1 SD. Sample sizes are above bars.

Sodium concentrations, a measure of ionic salt-loading, were lower in grebe stomachs than in brine shrimp or fly larvae hemolymph (Fig. 2, lower panel). Potassium concentrations of shrimp hemolymph and grebe stomach contents were similar.

Salt glands. Weights of salt glands of captive grebes maintained on fresh water or of beached birds from the ocean averaged 50 mg (range 37–67 mg, $n = 3$) in February and were identical to mean weights of glands from grebes found dead on the California coast in January (range 49–55 mg, $n = 6$; Fig. 3). The latter weights included two dead captives and one dead Mono Lake bird. Glands from Mono Lake birds in March were not significantly different from those of captives on fresh water and were approximately half the weight of wintering grebes collected from an inland saline sea, the Salton Sea (1,290 mOsm/kg), in January.

Salt gland weights showed much seasonal variation (Fig. 3), which reflects both the birds' geographic source and the duration of their stay at Mono Lake. The spring samples included newly-arrived migrants as well as grebes

that had been present for longer periods. For example, salt glands of two newly-arrived but similarly-sized grebes collected on 21 April 1983 (body weights 285, 290 g) differed by nearly 100% (41 vs. 81 mg), and possibly were derived from fresh and salt water wintering areas, respectively. Another collected in April, 1982, was even more hypertrophied, 110 mg, a value typical of birds at the Salton Sea.

Mean gland weights of Mono Lake birds in July did not differ from those of birds breeding in a fresh water marsh at Lake Abert, Oregon (757 mOsm/kg) in 1983. On the other hand, salt glands from Mono Lake birds were highly variable and included some of less than 50 mg that were possibly from the unsuccessful breeders that had just returned to Mono Lake.

Post-breeding adults and juveniles begin to appear in August and continue to arrive into October, or perhaps later. Salt gland weights of some August birds were among the lowest recorded for the entire year (Fig. 3), indicating that they had spent the summer in fresh water habitats.
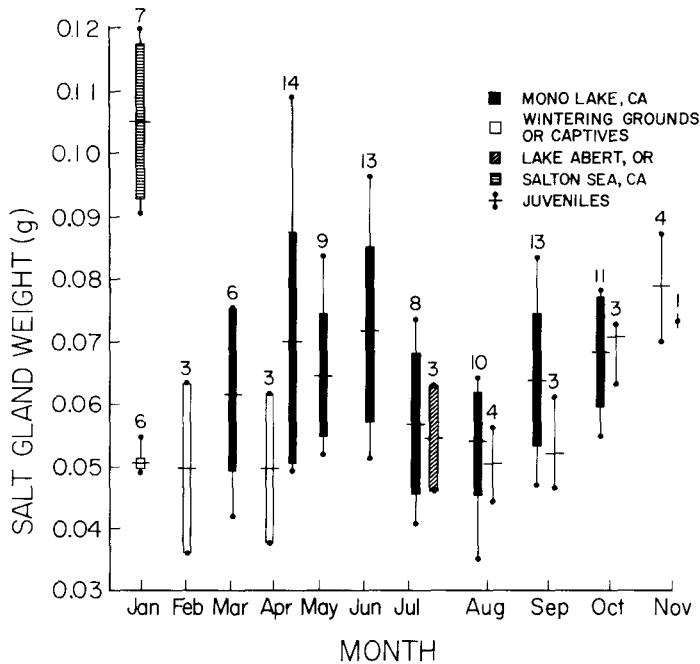
Mean salt gland weights increased through

FIGURE 3. Seasonal change in mean salt gland weights (horizontal bar), range (vertical line), and ±1 SD (box) of Eared Grebes. Numbers above vertical lines are sample sizes.

the fall, reaching a peak of 80 mg in November, still less than the weight of salt glands from Salton Sea grebes ($P < 0.005$, Fig. 3). Although body weights of the Mono Lake birds also increased during this time, salt gland weight showed an apparent linear increase with body weight only for lighter birds (those that had arrived more recently; Fig. 4).

Tongue measurements. The tongue of the Eared Grebe is similar in proportions to those of the Horned and Pied-billed grebes (Table 4). The latter species feed mainly on much larger prey and occur only rarely at hypersaline lakes. The tongue of the Western Grebe is relatively much smaller and occupies only about half of the mouth (Fig. 5). Evidently, tongue size and shape have remained fairly constant in grebe evolution, but the bill of the Western Grebe has become greatly lengthened in association with its piscivorous habits.

DISCUSSION

The most dramatic result of the captive experiments was the striking change in the grebes' behavior as soon as they encountered Mono Lake water or even 20% Mono Lake water; they became lethargic and refused to feed or dive. The accompanying physiological changes—elevated serum osmolality and weight loss—are consequences, because an animal that does not eat or drink loses weight and becomes dehydrated. The slight drop in

hematocrit could have been due to either replacement of plasma volume following blood sampling, or the beginning of molt (Chilgren and deGraw 1977, Rehder et al. 1982). Because the behavioral changes occurred even in 20% Mono Lake water, which is only half the concentration of sea water, we conclude that Eared Grebes respond adversely not to salinity but to the taste of Mono Lake water. Our results thus suggest that wild birds may require a period of taste acclimation before they can take advantage of the food supply at Mono Lake.

If grebes at Mono Lake ingest much lake water while feeding, they would be expected to incur a salt load, resulting in elevated serum sodium levels and subsequent increased excretion of sodium. This would result in increased urinary water loss followed by dehydration, as evidenced by elevated serum osmolality and hematocrit. Furthermore, because Mono Lake has high levels of carbonates, ingestion of much lake water might cause blood pH to become more alkaline. Our results of blood chemistry indicate that if the Mono Lake birds do ingest a salt or ion load, the amount is within their regulatory capacity, because they did not show the predicted elevation in serum osmolality, pH, sodium concentration, or hematocrit that would accompany these conditions. The lack of evidence of dehydration from blood chemistry is further sup-
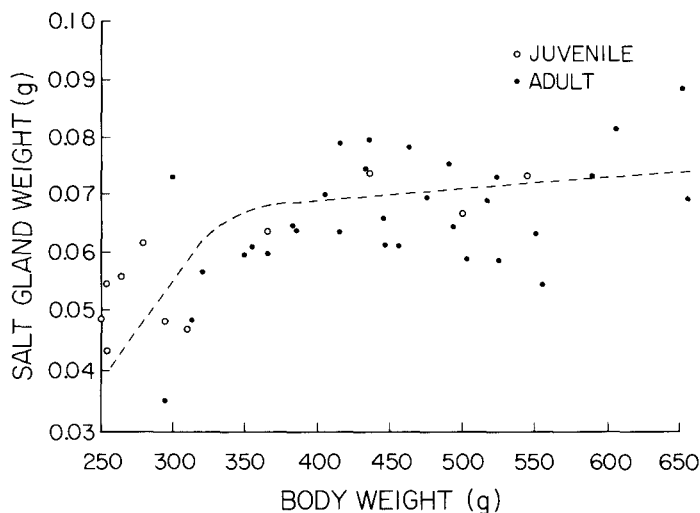
FIGURE 4. Mean weight of salt glands of Eared Grebes vs. mean body weight at Mono Lake, California. Dashed line is drawn by eye.

ported by our earlier finding that Eared Grebes from Mono Lake have "normal" total body water of ca. 65% (Mahoney and Jehl 1984).

Our data from stomach analyses further show that even though the birds feed on aquatic prey, they do not ingest large amounts of lake water. Stomach contents were actually more dilute, and the sodium concentrations were lower, than the body fluids of the major prey item, brine shrimp. The *simultaneous* decrease in osmolality and sodium suggests that dilute body fluids from the proventriculus, which is very large in grebes, are added to the food as it rapidly passes to the gizzard. Potassium does not become diluted (Fig. 2, lower figure) and may be secreted, along with hydrogen ions, into the proventriculus and gizzard. Dilution of stomach contents, followed by reabsorption of water in the small intestine, has been shown to occur in several avian species that have been examined thus far (for review, see Thomas 1982).

Salt glands provide the major means of sodium chloride excretion in marine birds. These organs undergo rapid (hours to several days) hypertrophy when birds move to saline waters, and the degree of hypertrophy is related to the degree of salt-loading (for review, see Peaker and Linzell 1975). Because of the high salinity of Mono Lake, we expected the grebes' salt glands to show great hypertrophy. Salt glands of the Canada Goose (*Branta canadensis*) may become so enlarged when they move to saline lakes that they affect the shape of the entire head (Hanson and Jones 1976: Figs. 253, 254). Those of the Redhead (*Aythya americana*) may undergo a four-fold increase when birds move to wintering areas on the Texas coast, where "salinities normally range from 5 to 35 ppt chlorides" (Cornelius 1983: 776). Mono Lake grebes undergo only a 40% increase in salt gland size (fall mean of 70 mg vs. winter minimum of 50 mg) while feeding in water that approaches 90 ppt. This occurs during a 2- to

TABLE 4. Dimensions of tongues of grebes.

|	Eared Grebe (3)[a]	Western Grebe (1)[a]	Horned Grebe (1)[a]	Pied-billed Grebe (1)[a]
Exposed culmen	19.9–23.2 (21.8) mm	68.5 mm	24.5 mm	18.7 mm
Length of tongue from basal notch	18.4–21.0 (19.8) mm	28.5 mm	22.3 mm	19.6 mm
Ratio: length of tongue/ exposed culmen	0.83–1.05 (0.91)	0.42	0.91	1.05
Width of tongue at base	4.0–4.2 (4.2) mm	5.8 mm	4.1 mm	5.4 mm
Ratio: width of tongue/ length	0.19–0.23 (0.21)	0.20	0.18	0.28
Thickness of tongue at base	2.5–3.7 (2.9) mm	3.7 mm	2.7 mm	3.5 mm
Ratio: thickness of tongue/ width	0.60–0.92 (0.70)	0.64	0.66	0.65

[a] Sample size.
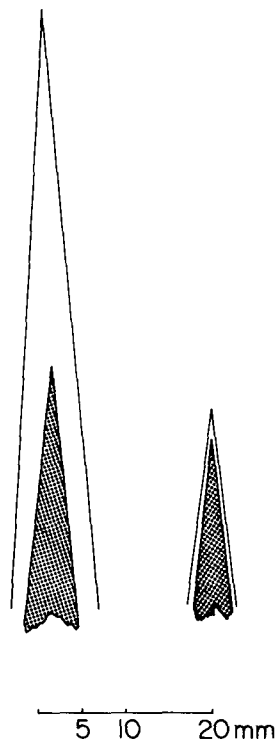
FIGURE 5. Relative size of tongue and bill in the Western Grebe (left) and Eared Grebe (right). Drawn to scale.

3-month period in fall when the birds are hyperphagic and nearly doubling their weight. Therefore, we conclude that salt-loading is not a physiological problem for Eared Grebes under the hypersaline conditions of Mono Lake. Indeed, salt-loading is evidently not a problem for Eared Grebes under far more saline conditions, as evidenced by large numbers of grebes which stage at Great Salt Lake, Utah (>4,500 mOsm/kg) and their occurrence at highly saline ponds associated with commercial salt works (Schenk 1970).

The Eared Grebes at Mono Lake do, however, have salt glands that are capable of excreting more salt than they take in when they are salt-loaded in the laboratory with NaCl solutions approaching the concentrations of Mono Lake water: grebes adapted to Mono Lake conditions and infused with 1,900 mOsm/kg NaCl at a rate of 0.13 mOsm/min kg were able to secrete a concentration of 2,200 mOsm/kg at the rate of 0.14 mOsm/min kg from their salt glands (H. T. Hammel, pers. comm.). Despite possessing the physiological capability to ingest large salt loads, however, all evidence indicates that the Mono Lake grebes do not do so. It would seem impossible for a diving bird that has no obvious adaptations for filter-feeding to avoid taking in great quantities of lake water along with the prey. How, then, do the grebes cope?

The structure of the mouth offers a possible explanation. The tongue of an Eared Grebe is large and fleshy and occupies virtually the entire oral cavity (cf. Fig. 5). When a grebe that is feeding underwater closes its mouth, most of the water is presumably extruded. We surmise that the large, flat tongue may then be used to compress the prey against the smooth palate, removing more water. If some brine shrimp rupture in the process, the pressing action may even generate additional fluid to flush lake water off the prey, because shrimp are largely (ca. 80%) composed of water. The feeding mechanics of the closely-related Silver Grebe (*Podiceps occipitalis*) of South America have been interpreted in a similar fashion by Fjeldså (1981: 224), who believed that after prey are captured, the tongue "rapidly takes over manipulation of the prey ... moves it backwards, pressed against the roof of the mouth cavity." (See also Fjeldså 1981, Fig. 38, for an illustration of the process.) The similarity of the tongue and mouth size of Horned and Pied-billed grebes to those of Eared Grebes, however, suggests that the large, fleshy tongue is not, in itself, an anatomical adaptation for feeding in hypersaline habitats, because the former two species are only rarely found there.

We conclude that the Eared Grebe is functionally a filter-feeder for much of the year, even though it lacks any special anatomical adaptations for filtering. Its relatively large tongue is apparently used to provide a major behavioral line of defense against osmotic stress and is sufficient to prevent the bird from swallowing much water, even when it is feeding underwater.

The hypothesis that Eared Grebes act as filter-feeders while eating soft-bodied prey is supported by data from the Salton Sea, where salinity is only half that at Mono Lake. Nevertheless, salt glands of grebes taken there averaged 35% heavier than the maximum weights of those from birds at Mono Lake ($P < 0.005$, cf. Fig. 3). At the Salton Sea, the grebes forage by diving for small invertebrates and probably fishes, whose bodies are less compressible than the brine shrimp and brine flies at Mono Lake. We infer that the birds consequently ingest more adhering water, which is accommodated by greater enlargement of the salt glands compared to those of Mono Lake grebes. The size of the salt glands, therefore, is not necessarily proportional to environmental salinity (cf. Cornelius 1983), but may also be affected by the physical structure of the prey. These observations confirm the finding that high salinities at Mono Lake do not pose an osmoregu-

latory problem for Eared Grebes, inasmuch as greater hypertrophy of the salt glands is possible, and anatomical and behavioral features protect against salt-loading.

ACKNOWLEDGMENTS

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