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# SALT GLAND DEVELOPMENT IN MIGRATORY REDHEADS (*AYTHYA AMERICANA*) IN SALINE ENVIRONMENTS ON THE WINTER RANGE, GULF OF MEXICO, USA

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Redheads (*Aythya americana*) migrate annually from their breeding range in the interior of North America to winter along the coasts of the United States and Mexico. Two of the most important areas where redheads traditionally concentrate in winter are the Laguna Madre and nearby bays in southern Texas and the Chandeleur Sound in southeastern Louisiana. Redheads experience saline-to-hypersaline (>35 ppt) conditions in southern Texas, where they have ready access to numerous coastal ponds for drinking water. Redheads in the Chandeleur Sound experience reduced salinity (<30 ppt), and they seldom use supplemental fresh water. We weighed and analyzed supraorbital salt glands from redheads wintering in Texas and Louisiana. Mean mass of salt glands was lowest in November and became stabilized in size by January. Mean mass of salt glands in Texas did not differ between the two winters. The mass of salt glands of redheads from Texas (winters combined) was intermediate to, and significantly different from, the mean masses of salt glands of redheads from two different winters in Louisiana. Females exhibited smaller salt glands than did males in both Texas and Louisiana, suggesting that they were under less osmotic loading than males. Young birds during the second winter in Louisiana exhibited the heaviest salt glands, and therefore the most osmotic loading, of all birds in both states. Water balance concerns and osmoregulatory costs should be integrated more fully into future foraging and energetics studies of water birds in marine, coastal, and estuarine systems.

Key words: *Aythya americana*, Louisiana, redhead, salinity, salt gland, Texas

## INTRODUCTION

### *Avian salt glands and osmoregulation*

Osmoregulation can be an important consideration for habitat use, water balance, and bioenergetics in both terrestrial and aquatic species of birds. While most terrestrial birds physiologically accommodate salt loading by excreting concentrated salt in urine (SCHMIDT-NIELSEN 1975, POULSON 1969), a few terrestrial bird groups (e.g., Falconiformes and Galliformes) apparently secrete concentrated saline solutions from supraorbital salt glands via their external nares (CADE & GREENWALD 1966). Supraorbital salt glands have been found to be especially pronounced in marine bird species (SCHMIDT-NIELSEN 1960, TECHNAU 1936, SCHILD-

MACHER 1932) and in water birds that are exposed periodically to saline (NaCl) conditions (HOLMES & STEWART 1968, STAALAND 1967, SCHMIDT-NIELSEN & KIM 1964).

According to TECHNAU (1936), avian salt glands were described as early as the seventeenth century, and their anatomy and morphological traits were known by the first half of the nineteenth century (NITZSCH 1820, JACOBSON 1813). Their function, however, was not identified correctly until much later, in such classic papers as SCHMIDT-NIELSEN *et al.* (1958) and SCHMIDT-NIELSEN and FÄNGE (1958). Soon thereafter, surveys of avian taxa revealed the occurrence of functional salt glands in multiple bird orders, including Gaviiformes, Podicipediformes, Procellariiformes, Pelecaniformes, Sphenisciformes, Anseriformes, Gruiformes, Charadriiformes, and Cuculiformes (CARPENTER & STAFFORD 1970, OHMART *et al.* 1970, SCHMIDT-NIELSEN 1960, MCFARLAND 1959). Since then, enormous strides have been made in clarifying the control, histology, biochemistry, and physiology of avian salt glands. A profusion of investigations has led to dramatic advances in understanding neural and hormonal control of avian salt glands, their functional response to variable concentrations of NaCl solutions (ingested by drinking or administered intravenously or by stomach tube), the relative importance of extra-renal salt gland secretions and renal excretion of concentrated urine in removal of salts, and to comparative investigations of osmoregulation and water balance (e.g., BENNETT *et al.* 1997, BØKENES & MERCER 1995, SIMON 1982, HANWELL & PEAKER 1975).

Virtually all of these studies have been conducted within the tightly controlled experimental environments afforded by laboratories, and only a few species have been used as experimental animals. Domesticated fowl, especially the Pekin duck (*Anas platyrhynchos*) and the goose (*Anser anser*), have been used most commonly in experiments designed to investigate salt gland physiology, control, and function. In contrast, research on ecological aspects related to salt gland function and salt loading in wild birds has been less frequent.

More than forty years ago, BARTHOLOMEW and CADE (1963) noted a persistent imbalance in avian field research, whereby the quantity of scientific papers on avian food habits greatly exceeded the few publications on water balance in birds. This uneven emphasis has continued to this day, although the contrast between topics has metamorphosed. Now, a multitude of investigations related to nutrient dynamics, bioenergetics, body condition, and fat reserves have become prominent in many ornithological journals. In contrast, papers on salinity regimes in wetlands, water balance, osmoregulation, and osmotic dehydration in birds remain relatively low in number. Recent comprehensive species accounts of birds in North America (POOLE & GILL 2002) and in Europe (KEAR 2005) continue to reflect this imbalance, as virtually any species account shows the strong historical emphasis placed on investigations such as food habits, diet, energetics, and nutrient dynamics, as opposed to the minimal emphasis placed on studies of wetland salinity, osmoregulation, and water balance.

### *Redheads and the Winter Range*

Redheads (*Aythya americana*) breed widely throughout much of the interior of the United States and Canada, but most migrate annually to winter along the coasts of the Atlantic and Gulf of Mexico of the United States and along both coasts of Mexico (WOODIN & MICHOT 2002, BELLROSE 1980). Most redheads are concentrated in winter in only a few traditionally important parts of the overall winter range, two of which are the Laguna Madre of southern Texas and the Chandeleur Sound of southeastern Louisiana (Fig. 1). Approximately 400,000 redheads may winter annually in the Laguna Madre, and 15,000–20,000 birds typically will spend the winter in the Chandeleur Sound (MICHOT 2000). Both the Laguna Madre of Texas and the Chandeleur Sound of Louisiana support extensive stands of shoalgrass (*Halodule wrightii*), the primary food of redheads in almost all traditionally important coastal wintering areas (WOODIN & MICHOT 2002).

In the process of consuming marine plants, redheads also ingest sodium chloride (NaCl), which causes the birds to experience salt loading. Redheads that spend winters on the Laguna Madre in southern Texas are exposed to salinities approximating that of sea water (sometimes becoming hypersaline), but they have access to numerous coastal ponds (MOORE 1991, ADAIR 1990, MCADAMS 1987), which provide dietary water to offset the NaCl taken in by redheads when foraging on shoalgrass. Redheads wintering in the Chandeleur Sound of Louisiana are exposed to salinities less than that of sea water, but they have very limited access to sources of drinking water, and they seldom use fresh water (MICHOT 2000).

In this study, we examine the change in salt gland size in migratory redheads on two different winter ranges along the western and northern rim of the Gulf of Mexico, the Laguna Madre and the Chandeleur Sound. We have undertaken the following three objectives in this paper: 1) examine the trend over time of mean salt gland mass of redheads wintering along the Gulf of Mexico, 2) compare salt gland development exhibited by redheads wintering in the Laguna Madre of Texas with those wintering in the Chandeleur Sound of Louisiana, and relate salt gland size to the salinity regimes experienced by redheads on these two winter ranges, and 3) determine if salt gland size differs among sex and age classes of redheads. We then use our results and the earlier findings of CORNELIUS (1982) to explore

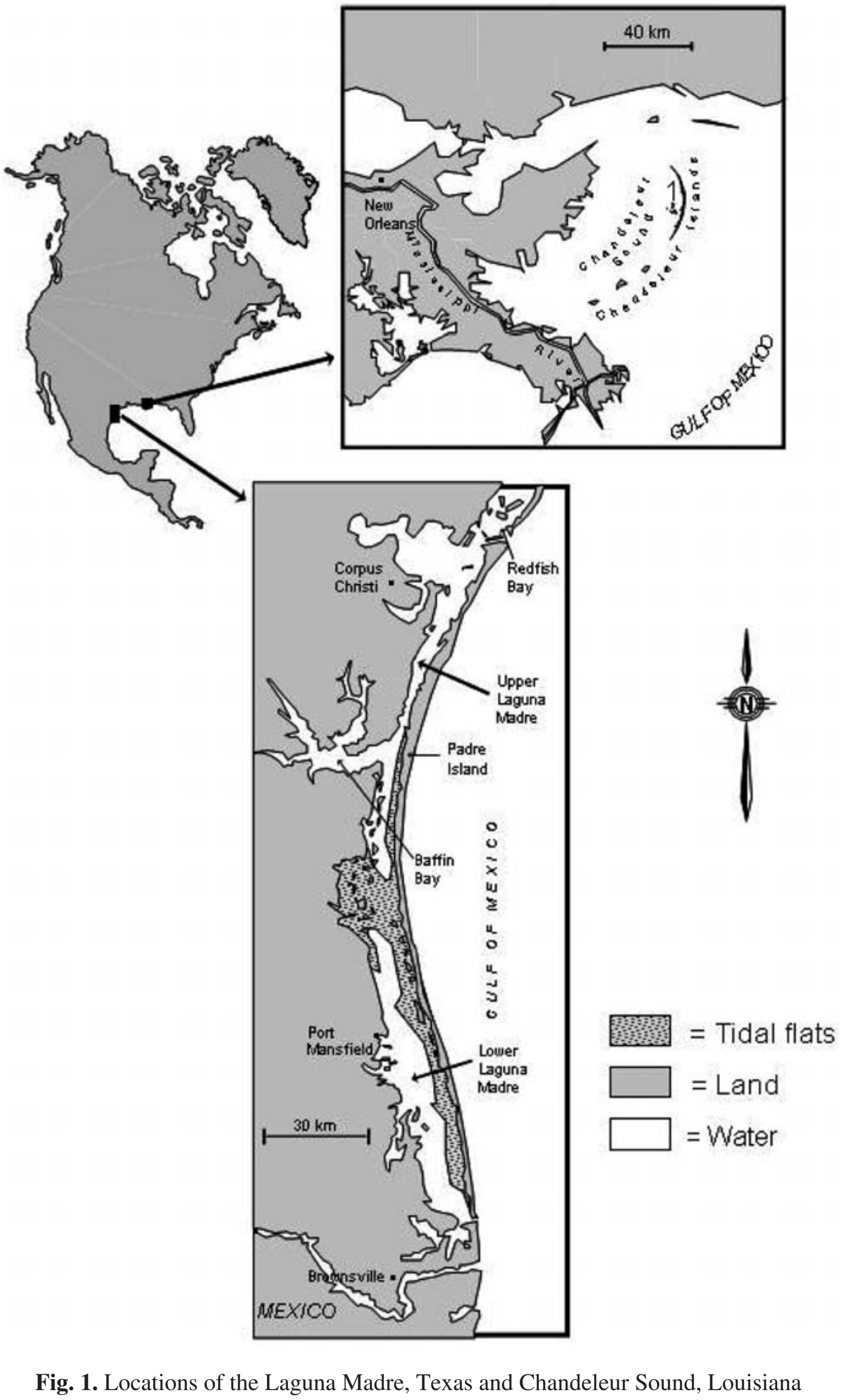

**Fig. 1.** Locations of the Laguna Madre, Texas and Chandeleur Sound, Louisiana

significant implications for diet, foraging behaviour, and energetics studies of waterfowl and other water birds.

## MATERIALS AND METHODS

Study areas – The Laguna Madre is shallow; mean water depth is about 1m, whereas the maximum water depth is about 3 m (TUNNELL & JUDD 2002). The Laguna Madre is saline to hypersaline (>35 ppt) (TUNNELL & JUDD 2002) and, based on the classification scheme of VOLLENWEIDER and KEREKES (1980), it is generally eutrophic, although it ranges broadly within a range of mesotrophic to hypertrophic (WHITLEDGE & PULICH 1991). The Chandeleur Sound is also shallow, with water depth about 1 m at mean low water. The salinity of the sound is moderated by fresh water from the nearby mouth of the Mississippi River (see Fig. 1) and, consequently, the range of salinity of its waters is 20–30 ppt (MICHOT *et al.* 1994), less than the prevailing salinity of the Laguna Madre. Chandeleur Sound is oligotrophic, but it may range from ultra-oligotrophic to mesotrophic. Densities of redheads have been estimated to be about 6.1/ha shoalgrass in the Laguna Madre of Texas and about 11.3/ha shoalgrass in the Chandeleur Sound (MICHOT 2000).

Coastal ponds in southern Texas are relatively shallow (<30 cm), and most are slightly brackish (<15 ppt) (ADAIR 1990). These ponds hold water intermittently in their small basins (usually <3 ha), which are recharged with rainfall from tropical storms and hurricanes. Differential use by redheads of saltwater habitats of the Laguna Madre and of brackish and freshwater coastal ponds has been compared frequently, for which an abundant literature has developed (MICHOT *et al.* 2006, SKORUPPA & WOODIN 2000, ADAIR *et al.* 1996, WOODIN 1994, MITCHELL *et al.* 1992, MOORE 1991, ADAIR 1990).

We collected redheads from their ranges (monthly during November–March) during two winters (1987–1989) in southeastern Louisiana and during two winters (1988–1990) in southern Texas as part of a larger study on the winter ecology of redheads. Immediately after collection, birds were placed on ice to delay deterioration. Using wing plumage (CARNEY 1964) and cloacal characteristics (HOCHBAUM 1942), we assigned the birds to mature and immature age classes. The right supraorbital salt gland in each bird was removed, dried by blotting, and then weighed to the nearest 0.01 g. Using month of collection (November–March) and the two winters of collecting in both Louisiana and Texas (Louisiana 1987–1988, Louisiana 1988–1989, Texas 1988–1989, and Texas 1989–1990) as the explanatory variables, salt gland mass was analyzed in a two-way ANOVA (5×4). Mean masses of salt glands during different winters in Texas and Louisiana were plotted by month to compare trends over time. Salt gland mass was analyzed in a three-way ANOVA (2×2×3) to determine if means varied among sex and age classes of redheads in winter in Louisiana (two separate winters) and Texas (two winters combined).

## RESULTS

The main-effect variables of months (November–March) and winter ranges (Louisiana 1987–1988, Louisiana 1988–1989, Texas 1988–1989, Texas 1989–1990) in the two-way ANOVA of mass of salt glands were both significant. Redhead salt gland masses differed among months ($P < 0.0001$; df = 4, 707). Salt glands were lightest in November in all cases, increasing through January. After January, mean mass of salt glands tended to decline slightly or stabilize.

Mean salt gland mass also differed (P < 0.0001; df = 3, 707) among the winters, although the mean salt gland mass of redheads from Texas did not differ between the two winters (P = 0.236). The temporal trends for salt gland mass of redheads in Louisiana in 1987–88 and 1988–89 and in Texas (two winters combined) (Fig. 2) were relatively similar.

ANOVA of salt gland mass of sex and age classes of redheads in Louisiana (two separate winters) and in Texas (two winters combined) indicated that salt glands of redhead males weighed more (0.87 g) than salt glands of females (0.79 g) (P < 0.0005; df = 1, 694). There was also a significant (P < 0.0002); df = 2, 705) effect on salt gland mass due to an interaction among age and winter range. Young birds from Louisiana in 1988–1989 possessed the heaviest salt glands of any age group, while young birds from Texas had the lightest salt glands.

## DISCUSSION

The increase in size of salt glands after the arrival of redheads on the winter range (Fig. 2) was expected. With the sudden exposure to elevated salinity levels in coastal wetlands, the salt glands of newly arrived redheads and other waterfowl are characterized by extremely rapid growth and development, as TIETJE and TEER

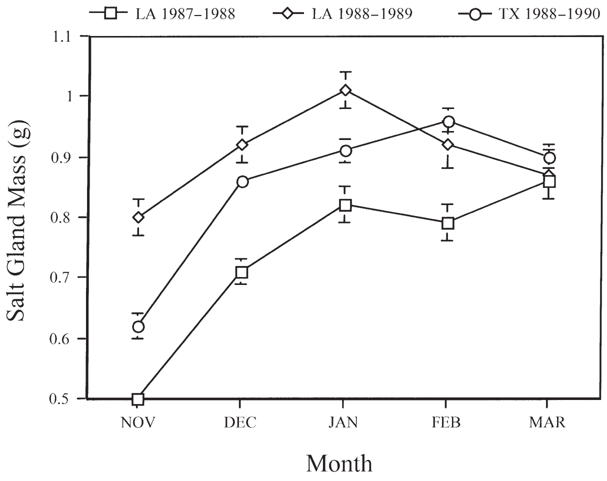

**Fig. 2.** Changes in salt gland masses of redheads wintering (November–March) in Chandeleur Sound, Louisiana during 1987–1988 and 1988–1989 and in Laguna Madre region, Texas during 1988–1990 (winters combined)

(1988) and CORNELIUS (1982) had demonstrated previously. Increased salt gland size from low initial masses in November (this study) and in October (CORNELIUS 1982) indicated that the supraorbital salt glands had become active osmotically and were secreting relatively large volumes of NaCl-rich fluid through the external nares (FLETCHER *et al.* 1967, SCHMIDT-NIELSEN & KIM 1964). The values for salt gland mass in CORNELIUS (1982) were approximately twice what we report, so we assume that both nasal glands were excised in the earlier study, though the methods were not stated explicitly.

Trends in mean salt gland mass of redheads in this study (Fig. 2) were generally similar to data reported by CORNELIUS (1982) for birds wintering in the Laguna Madre during 1972–75. Our data showed that salt glands gradually increased from November to January, after which they stabilized in size. Salt glands measured by CORNELIUS (1982) exhibited a nearly linear increase in mass all winter, beginning in October and extending into March, although late-winter salt gland masses did not differ significantly among months. Of special note in this study and in TIETJE and TEER (1988) was the apparent convergence of mean salt gland mass at winter's end (Fig. 2), which lends substance to the suggestion that salt glands respond to internal annual rhythms, possibly related to migration, as well as to variation in salt loading (BURGER & GOCHFELD 1984).

Lack of a significant difference in redhead salt gland mass between winters in Texas implies that salt loading there remained about the same. The location of the trend line for mean salt gland mass in winter in Texas between the two trend lines for mean salt gland mass for Louisiana birds (Fig. 2) indicates that birds in Louisiana were exposed to greater salt loading during 1988–1989 than in 1987–1988 or in Texas. CORNELIUS (1982) showed that salt gland size in redheads and a number of other waterfowl species was related directly to the salinity of the Texas bays in which they occurred, and TIETJE and TEER (1988) demonstrated a similar phenomenon for northern shovelers (*Anas clypeata*) in estuarine and freshwater wetlands in Texas. Consequently, our findings were somewhat surprising, since the Laguna Madre and nearby bays of southern Texas generally are considered harsh saline environments (TUNNELL & JUDD 2002). The second half of the twentieth century, with the opening of the Gulf Intracoastal Waterway throughout the length of the Laguna Madre, has seen salinity levels in the lagoon frequently stabilized at about 40 ppt (TUNNELL & JUDD 2002). Salinity data from the Chandeleur Sound are limited for the time of this study, but they confirm that the sound is less saline than the Laguna Madre. A few readings from February, 1988, showed a mean of 22 ppt, and several measures in January and March of 1989 yielded a mean salinity of 27 ppt (MICHOT, unpubl. data). Unfortunately, data on discharge rates for the Mississippi River for the period of this study are unavailable below Vicksburg, Mississippi, more than 200 km upriver of the river mouth.

Our results on salt gland size confirm that redheads in southern Texas and in the Chandeleur Sound of Louisiana respond differently, both physiologically and behaviourally, to osmoregulatory demands. The availability and use by redheads of shallow, coastal ponds in southern Texas for drinking water (MICHOT *et al.* 2006, ADAIR *et al*. 1996, WOODIN 1994), which assists the work of salt glands, apparently results in reduced salt loading experienced by redheads. In contrast, redheads wintering in Louisiana experienced more variable salt loading conditions than those in Texas, even though the salinity of the Gulf of Mexico waters near the Chandeleur Sound is not considered exceptionally harsh. Redheads wintering in the Chandeleur Sound rely on their salt glands and renal excretion, apparently without supplementary fresh water on a regular basis, for removal of excess NaCl. They may opportunistically consume fresh water from the few freshwater pools on the Chandeleur Islands or from the sea surface, whenever it is available from rainfall or spring seeps. Young ducklings reared on saline prairie wetlands of North America (SWANSON *et al*. 1984) and mountain duck (*Tadorna tadornoides*) ducklings on saline lakes in Australia (RIGGERT 1977) rely on a thin spring-fed surface layer of fresh water for drinking, which overlies denser saline water.

Redheads in winter subsist largely on shoalgrass rhizomes throughout almost all of their coastal winter range (WOODIN 1996, MICHOT & NAULT 1993, PERRY & UHLER 1982, CORNELIUS 1977, MCMAHAN 1970, STIEGLITZ 1966), but small molluscs, especially gastropods, are also consumed (MICHOT *et al.* 2008, WOODIN 1996, CORNELIUS 1977). We suggest that the consumption of very small gastropods by redheads in winter, especially pronounced in Louisiana, may be a foraging adaptation in part for meeting water balance needs. Very small marine gastropods, unlike filter-feeding marine bivalves, do not contain sea water reservoirs within their shells. Eiders in the Baltic Sea region are known to alter foraging on mussels, gastropods, and crustaceans in relation to salinity gradients in sea water and osmotic concentrations within the invertebrate prey (NYSTRÖM *et al.* 1991, NYSTRÖM & PEHRSSON 1988). Consumption of invertebrates with hypo-osmotic body fluid in order to obtain fresh water and maintain water balance has been noted for white ibis (*Eudocimus albus*) breeding in South Carolina (JOHNSTON & BILDSTEIN 1990); for snowy plovers (*Charadrius alexandrinus*), Wilson's phalaropes (*Phalaropus tricolor*), and American avocets (*Recurvirostra americana*) (MAHONEY & JEHL 1985*a*, PURDUE & HAINES 1977) at hypersaline and alkaline lakes in the western United States; and for eared grebes (*Podiceps nigricollis*) and California gulls (*Larus californicus*) on hypersaline, alkaline Mono Lake in California (MAHONEY & JEHL 1985*b*, *c*).

Our data on mean salt gland masses of male and female redheads agreed with those of CORNELIUS (1982), who also reported that mean mass of salt glands was greater in males than in females of redheads and three other species of waterfowl. This difference could be attributed to the fact that males typically weigh more than female Anatidae, and body mass often is correlated with size of other body parts and internal organs. However, salt gland mass and body mass in birds usually are difficult to correlate in non-marine birds (BURGER & GOCHFELD 1984, PEAKER & LINZELL 1975, ANDERSON & WARNER 1969). In this study, whilst there was a significant correlation ($P < 0.0001$) between salt gland mass and body mass, we did not begin collecting birds until November, after the most dramatic increase in size of salt glands had already occurred in recently arrived redheads (CORNELIUS 1982). The rapid increase in size and secretion rate of salt glands is primarily a function of the salt loading to which birds are subjected (GRAY & ERASMUS 1989) in their wetland habitats, although in some species there apparently also occurs an annual cycle of change in size of salt glands, independent of salt loading (BURGER & GOCHFELD 1984).

The difference in mean salt gland mass between males and females may suggest that redhead females experienced less salt loading and osmotic stress than did males. Evidence has accumulated to indicate that a difference in water balance and hydration indeed exists between males and females (LANDYS *et al.* 2000, HUGHES *et al*. 1992, HUGHES *et al*. 1991). Wild female mallards (*Anas platyrhynchos*) had more total body water than did males, and female Pekin ducks had lower plasma osmolality and plasma sodium than did males (HUGHES *et al*. 1991, HUGHES 1983). Therefore, they physiologically were preconditioned to deal with salt loading more effectively than were males. More total body water in female waterfowl makes them less susceptible to osmotic dehydration, which may explain the smaller salt glands in females than those possessed by males of some species of waterfowl (HUGHES *et al*. 1995, CORNELIUS 1982). Total body water of some marine species may approach 80%, presumably as an adaptation to buffer body fluids against salt loading of sea water (WALTER & HUGHES 1978, RUCH & HUGHES 1975). However, these extremely high values for total body water in marine birds have been contested (MAHONEY & JEHL 1984) as a product of the methodology used to measure them.

Since the largest salt glands in this study were possessed by young birds wintering in Louisiana in 1988–1989 (the winter of greater salinity in the Chandeleur Sound), this indicates that these birds experienced the greatest salt load during the study. Very young ducklings are known to be susceptible to salt stress (BARNES & NUDDS 1991), but our results indicate that the period of time during which young birds can experience enhanced osmotic stress may persist for months after they have departed the breeding range.

Diet and foraging ecology of waterfowl and other water birds are functions of the need to maintain water balance and hydration, in addition to meeting caloric demands. Sex and age differences in hydration, osmotic regulation, and water balance (HUGHES *et al*. 1991) suggest that these physiological needs may be playing a much larger role in nutrient dynamics of waterfowl and other water birds than has been realized previously. Birds exposed to excessive salinity can experience osmotic dehydration (GRAY & ERASMUS 1989) and may lose mass and reduce food consumption (HUGHES *et al*. 1995, FLETCHER & HOLMES 1968), thereby mimicking characteristics of birds on a diet containing insufficient nutrients. In extreme cases, high salt loading can create such excessive osmoregulatory demands that birds perish (FLETCHER & HOLMES 1968, POULSON & BARTHOLOMEW 1962). Ducklings, in particular, seem to be sensitive to the demands imposed by osmoregulating in saline wetlands, especially if fresh water is limited. These conditions are known to retard duckling growth rates and increase duckling mortality (MOORMAN *et al.* 1991, SWANSON *et al.* 1984).

Water balance, osmoregulation, and hydration generally are not considered in studies of avian energy budgets, nutrient dynamics, or in construction of energetics models. This represents a potentially significant oversight. For example, in marine systems, foraging ecology and water balance of sea birds, sea ducks, and scaup (*Aythya* spp.) probably are closely intertwined. For waterfowl wintering in coastal lagoons, high salinities could impose energetically expensive osmoregulatory costs on such species as redheads, red-crested pochards (*Netta rufina*), and northern pintails (*Anas acuta*). For birds that breed in coastal brackish wetlands and estuaries, such as mottled ducks (*Anas fulvigula*) and rails (*Rallus* spp.), energy costs of osmoregulation could alter habitat use, growth rates, and mortality of young birds. We suggest that in these types of aquatic environments, the salinity regime could be a major constraint commonly influencing diet composition, foraging behavior, habitat use, and survival.

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