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# Birds in marine and saline environments: living in dry habitats

## Aves en ambientes marinos y salinos: viviendo en hábitats secos

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## ABSTRACT

For birds, saline environments such as maritime and salt marsh habitats are essentially dry habitats. When birds drink saline water or consume salt-loaded preys, the osmolarity of their body fluids increases. In order to maintain the osmotic equilibrium, they have to eliminate the excess of electrolytes ingested with preys or water. Marine birds use salt glands, which produce excretion solutions more concentrated than seawater to eliminate excess salt. The physiology and phenotypic plasticity of nasal glands appears to be correlated with the ecological features of species. Birds can also minimize osmotic stress by choosing hypo-osmotic preys, preys with reduced water content, and/or by decreasing salt intake. Although the kidney of birds is clearly less efficiently in its capacity to concentrate the urine than that of mammals, there are interspecific differences in renal structure and physiology that may be correlated with the birds ecological habits, and hence to represent adaptive mechanism to prevent water loss. The kidney may be especially important in taxa that lack active salt gland, such as passerines. Passerines, which are supposed to have limited ability to use saline habitats, include several marine and salt-marsh species. In this review I show that the interaction of the kidney and rectum in osmoregulatory physiology, coupled with selective feeding behavior play a major role in the maintenance of water and salt balance of passerines living in salty environments.

**Key words**: salt gland, renal function, food selection, osmoregulation, passerines.

## RESUMEN

Para las aves, ambientes salobres como los marinos y los salares, son en la práctica hábitats secos. Cuando las aves beben agua o consumen presas saladas, sus fluidos corporales aumentan la osmolaridad. Para mantener el equilibrio osmótico, las aves tienen que eliminar el exceso de electrolitos ingerido en los alimentos y el agua. Las estrategias adaptativas utilizadas por las aves marinas incluyen la utilización de la glándula de la sal, la cual produce soluciones de excreción más concentradas que el agua de mar. Tanto la fisiología y la plasticidad de la glándula nasal se correlaciona con las características ecológicas de las especies. Además, las aves pueden minimizar el estrés osmótico escogiendo presas hipo-osmóticas, o con menor contenido de agua, disminuyendo de este modo la ingestión de sales. Aun cuando la capacidad de concentración de la orina del riñón de aves es limitada, existen diferencias interespecíficas en su estructura y fisiología, lo que representa un mecanismo adaptativo para evitar la pérdida de agua. Este órgano es particularmente importante en aquellos taxa que no poseen la glándula de la sal, como paseriformes. Sin embargo, estas aves que aparentemente poseerían una restricción fisiológica para explotar ambientes salobres, incluyen algunas especies que habitan costas oceánicas y de salares. En esta revisión muestro que la interacción funcional del riñón y el intestino grueso en la fisiología osmoregulatoria, junto con la conducta de alimentación juegan un papel crucial en la mantención del balance hídrico y en la adaptación de estas especies a ambientes salobres.

**Palabras clave**: glándula de la sal, función renal, selección de dieta, osmoregulacion, paseriformes.

## INTRODUCTION

A major physiological constraints limiting the distribution of birds is the maintenance of osmotic homeostasis in environments where fresh water is scarce or unavailable (Johnston & Bildstein 1990). For most birds and other air-breathing vertebrates, marine and other saline environments are essentially dry. This is so because birds generally have only saline water to drink, and almost all available prey (specially invertebrates) are in osmotic equilibrium with this water. Eating and drinking imposes a significant salt load (e.g., Janes 1997). The concentration of the different salts in those environment (e.g., $K^+$, $Cl^-$, $Na^+$, $SO_4^{-2}$) is far from constant, but it is always highly

(Managed by F. Bozinovic)

concentrated, in comprison to fresh water. For example sea water has sodium and chloride concentrations of approximately 470 mmol·L$^{-1}$ and 548 mmol·L$^{-1}$ respectively, whilst the river water has sodium concentrations of 7 mmol·L$^{-1}$ and chloride concentration of 14 mmol·L$^{-1}$. Physiological stress associated with life in marine and other saline habitats does not result from the absence of water but from the necessity of eliminating excess electrolytes. When birds drink sea water or consume food with high osmolarity, salts are absorbed by the small intestine, and the concentration in the body fluids increases (Purdue & Haines 1977, Simon 1982, Holmes & Phillips 1985). Unless birds can excrete fluids that are more concentrated than ingested water, the body becomes dehydrated. Birds do not have a unique way to handle or avoid the high osmotic burden imposed by the intake of highly saline fluids. The objective of this review is to discuss the physiological and behavioral strategies that allows birds to live in and exploit extreme salt stressing habitats. In the last section, I provide an example of interspecific physiological differences in the salt tolerance of a group of species in the genus *Cinclodes* that inhabits central and northern Chile.

## *Birds with salt glands*

Unlike mammalian kidneys that can produce highly concentrated urine, avian kidneys are known to have poor concentrating ability (Sturkie 1976, Dantzler & Braun 1980, Braun 1981, Goldstein & Braun 1989, see below). Some birds are able to cope with salt water with an extrarenal excretory system: the supraorbital or nasal glands that allow some bird species to excrete concentrated electrolyte solutions (Holmes & Phillips 1985). Therefore, marine birds can maintain a positive water balance while drinking hypertonic solutions and while ingesting hypertonic prey, without having to consume fresh water. The nasal glands of the gull *Larus argentatus* can secrete solutions containing 800 mmol·L$^{-1}$ of sodium chloride. Those of the petrel *Oceanodroma leucorhoa* can concentrate their secretions above 1100 mmol·L$^{-1}$ (Schmidt-Nielsen 1990). Considering that normal sodium secretion in blood plasma of marine birds are approximately 150 mmol·L$^{-1}$, the concentrating ability of salt gland can reach from five to eight times.

The nasal glands are paired glandular structures located on top of the skull in or around the dorsal orbit, with ducts that open into the nasal cavity. A typical salt gland consists of several longitudinal lobes composed of secretory tubules radiating from central canals. These, in turn, form secondary and primary ducts running toward the nasal cavity and discharging the hypertonic fluid trough the nares (Sturkie 1976). The capillary blood flow in the nasal gland is counter to that of secreted fluid in a countercurrent exchanger arrangement. This countercurrent flux, which is similar to that found in kidneys, facilitates the exchange and concentration of salts from blood to tubule. Tubule exocrine cells produced the hypertonic secretion of the salt gland. These cells have traits that are characteristic of ion transporting cells, such as basal infoldings and numerous mitochondria (Simon 1982). The cellular mechanism that account for the osmotic work by the exocrine cells is assumed to be produced by an electrogenic, sodium extruding pump (Na-K-adenosine-triphosphatase) and a Na-K-Cl co-transport process (Lowy et al.1989).

The composition of salt secretions varies both within and among species. The concentration of salt gland secretions usually ranges between one and two times that of sea water. Sodium concentrations reported range from 500 to 700 meq·L$^{-1}$, and in some species approach 1000 meq·L$^{-1}$. However, the rate and concentration of salt gland secretions is not constant and depends on the salt load that animals have experienced. In cormorants (*Phalacrocorax auritus*) salt gland secretion of electrolytes occurs only under osmotic load. It does not occur in fasting birds or in birds fed on fish (Schmidt-Nielsen et al. 1958). Even in animals, that had never been exposed to salt water, salt gland secretion can be elicited by salt loading. Mallard ducks, *Anas platyrhynchos*, that have never experienced sea water can produce nasal gland secretions containing 35 mOsmol·Kg$^{-1}$ when challenged with an infusion of saline water. However, this concentration is only 20% of the concentration achieved by ducks that have been chronically adapted to sea water (Simon 1981). As an osmoregulatory organ, the salt gland responds to osmotic loads as well as to salt loads. In addition, non-osmotic stimuli such as physical stresses (e.g., temperature, sounds) can induce salt gland secretions (Sturkie 1976). However, the universal subjacent physiological mechanism of salt gland activation appears to be acetylcholine release from the parasympathetic innervation of the gland (Shuttleworth & Hildebrandt 1999).

There is significant interspecific variation in the function of the salt gland. Conway et al. (1988) reported differences in the rate and concentration of salt gland secretions in newly captured clapper rails *Rallus longirostris* (permanent salt marsh species) and king rails *Rallus elegans* (wintering salt marsh species). *Rallus longirostris* produced more concentrated salt gland secretions at higher rates than *R. elegans*. However, when *R. elegans* individuals were acclimated to sea water, they reached the levels found in *R. longirostris*. Sea water acclimated individuals of this species produced secretions with concentration characteristic of more marine species, although flow rates were slower. The net chloride excretion was about 10 % that of a gull. There is probably a strong correlation between the salinity of a species natural habitat and the concentrating ability of salt glands (see also Staaland 1967, Hughes 1984).

The osmolarity and secretion rate of salt glands are acutely regulated by dehydration and salt loading. However, chronically, salt loading and dehydration influence salt gland function by determining their size (Knight & Peaker 1979). In some species, salt gland exhibits reversible phenotypic plasticity. Several studies had demonstrated changes in mass and function of salt gland in birds exposed to hypertonic salt solutions both in the field and laboratory (e.g., Holmes & Phillips 1985, Conway et al. 1988, Hammons et al. 1988). In ducks (*A. platyrhynchos*), the size of nasal glands becomes maximal 1-2 weeks after salt water acclimation (Holmes & Stewart 1968). When ducks that are fully acclimated to saline water are returned to fresh water, the weight of the salt gland declines to levels similar to those found in birds that have never been exposed to drinking salt water. Because of phenotypic plasticity, seasonal and population differences in salt gland size and function can be found (Peaker and Linzer 1975). For example, Staaland (1967) documented a great variation in the size of salt glands in charadriform birds from different environments, according to the salinity of habitats. Although it is clear that salt gland morphology and function are phenotypically plastic, comparative data are needed to state if this environmentally induced variation are related to the ecology of species. Also, acclimation studies are needed to disentangle if all population differences in size and function of salt gland are due to phenotypic plasticity, or to an micro-evolutionary change.

Some studies have demonstrated the existence of interspecific variation in the levels of phenotypic plasticity in salt gland function. For example, two anatide species, *A. rubripres* and *A. platyrhyinchos* exhibit significant differences in the magnitude and velocity of response of salt gland when they are exposed to saline loads (Barnes & Nudds 1991). The response of salt gland to osmotic load was always greatest and faster in *A. rubripres* who inhabits environments that are more saline. This results suggest that the variation in the plastic response of bird's salt glands may be related to the ecology, and probably, to the ecological flexibility of species (see also Cornelius 1982).

The function of salt gland also depends of the ontogenetic stage of birds. Hughes (1984) reported that the percent of sodium load secreted by nesting gulls (*Larus glaucescens*) was correlated with age and with the size of salt gland. Hughes & Winkler (1990) reported similar results in *L. californicus* at two developmental stages. However, this pattern does not seem to be shared by all species. Janes (1997) found that the Adelie penguin (*Pigoscelis adeliae*) exhibited no significant ontogenetic changes in their physiological osmoregulatory capacities. Curiously, Hughes (1968) reported that older individuals of Common terns (*Sterna hirundo*), were less efficient at excreting salt loads than younger individuals. Apparently the chicks of marine and salt marsh species have a well-developed extrarenal system at birth. Such feature is very important for young chicks, because they have no opportunity to obtain fluids other than from materials secreted or regurgitated by their parents, which are generally as concentrated as sea water. However, as we shall see, there are another mechanisms that can diminish the salt loads of nestlings. These mechanisms may be of great importance in early developmental stages when the salt gland is not completely developed.

Active nasal glands have been reported in several avian orders (Sphenicíformes, Precelariformes, Charadriformes, Pelecaniformes, Anseriformes, Phoenicopteriformes among others, see Shoemaker 1972). Even though most studies related to osmoregulation in birds have been done mainly on marine taxa, nasal secretions appear not to be restricted to these species. The presence of functional salt gland has been documented in several terrestrial orders. For example, the Roadrunner (*Geococcyx californianus*), a desert species, and the Savanah hawk (*Heterospizias meridionalis*), have active salt glands and can produce hypertonic secretions in response to their protein rich diets (Cade & Greenwald 1966, Ohmart 1972). Although these species are not stressed by high saline load, the active secretions of salt gland allows birds to minimize water losses (Hughes 1970). Other desert birds, such as the Patridge *Ammoperdix heji* and the Ostrich (*Struthio camelus*), have functional salt glands, which are stimulated in response to high temperature (Schmidt-Nielsen et al. 1963). Thus, salt glands are not restricted to birds that live in saline or maritime habitats, and are also present in some terrestrial forms that consume little water.

### *Renal Function*

The urinary organs of birds consist of paired kidneys and the ureters, which transport urine to the urodeum of the cloaca. The nephrons of avian kidneys include glomeruli and tubules of two kinds. The reptilian-type, with no loops of Henle are located in the cortex, and the mammalian-type with long or intermediate length loops, are located in the medulla (Braun & Dantzler 1972). The division between avian renal cortex and medulla is different than in mammals, because the loops of Henle and collecting duct, which drain both reptilian-type and mammalian-type nephrons, are bound by a sheath of connective tissue to form medullary cones (Goldstein & Braun 1989). The role of bird kidneys, like the kidneys of other vertebrates is filtration, excretion or secretion, and absorption. They filters water and some substances from blood, as waste products of metabolism and ions, which are voided in the urine. They also conserve water and other needed substances by absorption (Sturkie 1976).

Birds are the only groups of vertebrates other than mammals that have the capacity to produce urine that is hyperosmotic relative to plasma (Braun & Raimer 1988). This capacity resides within the medullary cones, where the operation of countercurrent multiplier system takes place (Poulson 1965). Solutes are actively transported out the ascending limb of Henle´s loop, diffusing into the descending limbs and vasa recta and carried to the tip of the medulla, where they are concentrated (Sturkie 1976). In contrast to mammals where urea play a major role of osmotic gradient, in birds, sodium chloride is the solute that makes up the major portion of the osmotic activity in the medullary cones (Skahudage & Schmidt-Nielsen 1967). When urine passes throughout the osmotic gradient in the medulla, water leaves the tubules and the urine become concentrated. Because only the looped nephrons contribute in a positive manner to the intramedullary osmotic gradient, the presence of loopless nephrons may limit the capability to which the kidneys can produce hyperosmotic urine (Braun & Raimer 1988, Braun 1993). Thus, the concentrating ability of avian kidneys is poorer than that of mammals. Birds generally produce urine that is only 2-3 times more concentrated than plasma (see Skadhauge 1981, Goldstein & Braun 1989).

The renal concentrating ability depends on state of hydration. Several studies have reported the response of birds to dehydration and salt loading (Braun 1978, Goldstein & Braun 1989, Goldstein & Zahedi 1990). The common response to salt load is to exhibit a rise in the urine osmolarity. In some birds, as the Desert quail (*Lophortyx gambelii*) and the Starling (*Sturnus vulgaris*), such a rise in urine concentration is related to a decrease in glomerular filtration rate of reptilian-type nephrons (Braun & Dantzler 1972, Braun & Dantzler 1984, Braun 1978). Nevertheless, not all bird's responses to dehydration and salt load are similar. For example, in the desert quail the rise in urine concentration is not due to a rise in urine/plasma concentration ratio, like in starlings. Indeed, when quails are salt-loaded by intravenous infusion of 1 $mmol \cdot L^{-1}$ NaCl, their urine remains nearly isosmotic relative to the plasma. However, when quails are salt-loaded, plasma osmolarity increases. Such a rise allows birds to excrete urine with increased osmolarity. Braun (1981) suggested that the difference between starling and quail physiological response to salt load reflects their respective powers of flight. The Desert quail is not capable of long distance flight to reach water supplies, whilst the opposite is true for the passerine. Although the physiological responses of renal function in birds appears to be variable, all of them produce a higher amount of salts excreted trough the urine, allowing birds to economize water.

In spite of the limited renal capacity of birds, studies on salt metabolism of avian taxa have demonstrated considerable variation in saline tolerance and in the ability to produce concentrate urine (Johnson & Mugaas 1970a, Goldstein & Brown 1989). Hughes (1970) found that the relative size of kidneys is greater in non-passerine birds that live in saline environments. Moreover, in other taxa which lack salt gland, the capacity to conserve urinary water by producing a concentrated urine is related to differences in renal medullary development and other kidney features (Poulson 1965, Johnson & Ohmart 1973a, Johnson & Ohmart 1973b, Jhonson & Skadhauge 1975, Casotti et al. 1998). Furthermore, Goldstein & Braun (1986) reported that the desert House sparrow (*Passer domesticus*) has more mammalian-type nephrons than the White-crowned sparrow (*Zonotrichia leucophris*). Such relative reduction of reptile-type nephrons may reduce the flow of dilute urine through the collecting ducts permitting a greater concentration of urine along the medullary cones. In the same vein, Skaudhage (1976) reported that the mean length of medullary cones and the proportion of medulla in kidneys were correlated to the concentrating ability in several Australian xerophilic birds. However, the urinary concentrating abilities and some morphological features of kidneys of several species were not correlated with their ecological differences (Golstein & Braun 1989). Indeed, among those studied species, the proportion of reptilian and mammalian-type nephrons varied considerably but were not significantly correlated with urinary concentrating ability (see also Johnson 1972). As pointed out by these authors, there are broad scale influences, such a body size and phylogeny determining the features of the kidney that affect concentrating ability.

Studies in closely related birds would be more instructive to determinate adaptive interspecific differences in renal structure and function in birds with broad ecological differences. Cassoti & Richardson (1992) studied honeyeaters (Melphiphagidae), and found that species from arid zones had a higher percentage of medulla in their kidneys, whereas species from wet zones had a higher percentage of renal cortex. They also found that in one arid zone species, the volume and surface of the brush border in the proximal tubule of the cortex was higher, which may lead to a greater ability to absorb water. Although the authors did not reported physiological variables, as plasma and urine osmolarity, these morphological features may be indicative of urine concentrating ability. McNab (1969) found the same trends in three species of quails inhabiting different habitats. *Callipepla gambelii*, which inhabit xeric areas, excrete the most concentrated urine and have a greatest proportion of medulla in the kidney in comparison to other quails that inhabit wet areas. Moreover, in two races of Savannah sparrow (*Paserculus sandwichensis*) differences in osmoregulatory parameters were found (Goldstein et al. 1990). These authors studied the osmoregulatory strategies of passerine birds inhabiting salt marshes (*P. s. beldingi*) and compared them with a subspecies that inhabits the uplands surrounding the salt marsh. *Paseruculus sandwichensis beldingi* had higher plasma and ureteral urine osmolarities than upland sparrows. Johnson & Mugaas (1970b) reported larger kidneys with higher proportion of medullary tissue in *P. s. beldingi* than other less effective water conservers birds. At the other extreme, the opposite trend in the histological features of kidneys is seen as an adaptation to the high dilute diets and the high needs of processing large volumes of very dilute urine. For example, the Anna's hummingbird (*Calypte anna*) produce very dilute urine ($< 100$ mOsm·Kg$^{-1}$) and have more than 99% of reptilian-type nephrons, and a very small proportion (2%) of medullary tissue (Casotti et al. 1998).

In birds, kidneys do not function as the sole organ of osmoregulation, as they do in mammals. The unique aspect of bird physiology is that the lower intestine is used not only to recapture the fluids and electrolytes not absorbed by the small intestine, but also those excreted by kidneys (Powel 1987). Instead, retrograde flow of urine at a relative low osmotic potential from cloaca to the colon and paired ceca, has been reported elsewhere (see Braun 1999). In this sections of the lower intestine the urine become into contact with epithelia of high transport capacities for sodium and water. Changes in retrograde peristalsis in ceca appear to be a main mechanism that controls the amount of ureteral urine that is brought into contact with the absorptive surfaces (Brummermann & Braun 1994). These changes in the muscle activity of the colon and the cloaca are also associated to changes of urine osmolarity of animals when they are exposed at two levels of hydration. Although the most important function of the avian cecum seems to be their role in the energy balance (see Goldstein 1989), some morphological differences at interspecific level, suggest a osmoregulatory role as well. For example, the above mentioned salt-marsh passerine, *P. s. beldingi*, have a rectum with more smooth apical surface with sparce short microvilii than the subspecies inhabiting more mesic upland habitats (Goldstein et al. 1990). These structural differences in the lower intestinal tract resemble those found in acclimated and non-acclimated chickens to salty diets (Clauss et al. 1988). Moreover, when physiological features of the cloaca were studied in a desert bird, the galah (*Cacatua roseicapilla*), strong differences were found when compared with those exhibit by the Domestic fowl, *Gallus domesticus* (Skadhauge 1976). The galah exhibits lower osmotic permeability and higher solute-linked water flow in the cloaca than the fowl. This physiological feature allows do diminish the water loss even when the urine is highly concentrated.

The urine of birds not only possess electrolytes in soluble state. Uric acid, the principal product of protein metabolism (Braun 1993), has a very low aqueous solubility and therefore does not contribute to the osmotic activity of the urine (Braun 1981). In the urine, uric acid is excreted packaged in small lipophilic spheres, forming a stable colloid suspension in the liquid phase. These spheres contain ions, and although spheres are osmotically inactive, ions are in excess of equimolar ratios (Braun et al 1987). For example, the proportion of excreted $Na^+$ associated to uric acid reach 50%

when Starlings (*S. vulgaris*) are salt loaded, and can rise the proportion when animals are well hydrated (Braun 1978). Thus, throughout this mechanism birds can excrete additional amount of ions and hence can overpass the limited ability of kidneys to concentrate the urine.

Hence, although the morphology of avian kidney apparently represents a constraint to the ability to concentrate efficiently the urine, some morphological adaptive differences are correlated to environmental differences. In addition, the uricotelic mode of nitrogen excretion and the physical arrangement in which uric acid is excreted do augment the capacity to economize water. Moreover, the functional relationships between low intestine and kidneys which results in the post renal modification of urine, may play a significant role in water conservation of birds that lack salt glands.

### *Behavioral strategies*

The exploitation of maritime and saline habitats seems to be inevitably coupled with the physiological stress produced by the intake of highly salty fluids. However, salt stress may be avoided or minimized by feeding in habitats with lower salinity, such as estuaries, by drinking fresh water and by feeding on less salty food. It has been documented that some species of birds are capable to choose preys having less content of saline water, or even on osmoregulator hiposmotic preys (Nihstrom & Pearson 1988, Mahoney & Jehl 1985b). For example, the gull *Larus californicus* an habitant of salt marshes, predates almost exclusively on brine shrimps (*Artemia sp.)* and brine flies (*Ephydra hians*) which has a salt concentration of one-tenth that of saline water where they live (Hughes & Winkler 1990). Mahoney & Jehl (1985a) found that in two charadride species, *Phalaropus tricolor* and *Recuvirostra americana*, the relative size of salt gland were not correlated with the salinity of water in different habitats. These authors reported that the stomach content of birds had a lower osmolarity than the water where they feed, determined by a behavioral mechanism and a morphological adaptation in the oral cavity. This behavior, allowed birds to avoid an excess of salt ingestion whilst feeding in saline lakes. Similar phenomenon has been documented in the colimbide *Podiceps nigricolis* (Mahoney & Jehl 1985c) and the gull, *L. californicus* (Mahoney & Jehl 1985b). Therefore, is possible that birds with a limited extrarenal excretion capacity may be capable to obtain most of their water need only from preys, avoiding a high osmotic burden.

Even in birds with functional salt gland, prey selection may be a behavioral strategy to prevent salt-related dehydration. Because considerable ATP is required to excrete the excess of salt, prey selection may contribute to save energy and to maintain a positive energy balance. Accordingly, two marine species, the Long tailed Duck (*Clangula hyemalis*) and the Common scoter (*Melanitta nigra*) prefers feeding on mussels smaller than the maximum size possible to swallow (see Nystrom & Pehrson 1987). Because the proportion of sea water increases with increasing mussel size, the preference for smaller prey is related to a salt stress avoidance. Furthermore, prey preference depends on the salinity of the environment. Madsen (1954) documented that *C. hyemalis* include 47 % of bivalves (which have high content of salt in relation to other preys) in their diet, when feeding in localities of moderate salinity, but reach near to 65% of total preys when feeding in low-salinity localities.

Prey selection is not the unique mechanism that birds exhibit in order to diminish the osmotic load imposed by high saline foods. Particularly important is the modification of food when parent feed their chicks by regurgitation. Several studies had demonstrated that the parents can diminish the salt content of food by drinking fresh water and/or by actively absorbing chloride (e.g., Hughes & Robert 1988). Janes (1997) reported that if the food resides for sufficient time in the stomach of the penguin, *Pigoscelies adeliae*, it could be desalinated before being given to the chicks. Because larger chicks reside nearer to the coast, and hence they are fed first than smaller, they receive food that is drier compared to that eaten by smaller chicks. This mechanism may be of great importance in birds with salt gland not completely developed in initial life-cycle stages and when the environments are additionally stressing (for example due to high temperatures) and the need for water are comparatively high. (Hughes & Winkler 1990). Thus, behavioral mechanisms and their interactions with some physiological features of birds would be the first responses to avoid salt stress. Indeed, this strategy may be the main adaptive response to saline habitats in birds with limited extrarenal salt excretion capacity.

### *Passerines in marine habitats*

Passerine birds living in saline environment face particular stressful conditions relative to water economy, because they lack functional salt glands. However, several species have become adapted to such habitats (see Goldstein et al. 1990). Among passerines, the genus *Cinclodes*, (Furnaridae) represents an well-suited group to the study behavioral and physiological adaptations to maritime habitats because it includes several species with broad ecological differences. Because those species are closely related, the influence of phylogenetic factors can be minimized and hence variation among species would be related to ecological differences. Among theses, Sea-side cinclodes (*Cinclodes nigrofumosus*) live at intertidal zones (Goodall et al. 1946, Hockey et al. 1987) and forages on almost exclusively marine invertebrates (Paynter 1971). Darck-bellied cinclodes (*Cinclodes patagonicus* ) and Gray-flanked cinclodes (*Cinclodes oustaleti*) possess a broader ecological niche, living both in marine coastal and riverine habitats (House 1945, Goodall et al. 1946). Studying those birds in different localities from central and northern Chile, Sabat (unpublished results) found several differences in their field ecological physiology. I had found that the osmotic load those animals experienced varied considerably between species and localities. Thus, *C. nigrofumosus* (from both localities) had higher stomach content osmolarity than *C. patagonicus* and *C. oustaleti* from El Quisco, a coastal locality from central Chile. Although the marine populations from El Quisco do predate at intertidal zones on marine invertebrates, their stomach content osmolarity is lower than expected, and never reaches the osmolarity of the sea water. Such differences between stomach content osmolarity and sea water osmolarity, strongly suggest that birds are capable of choosing preys with lower osmolarity, and/or to drink more dilute water. Effectively in a beach at El Quisco locality, birds occasionally drink in temporary pounds formed by a mix of sea water and human-settlement discharges. However, where no fresh or dilute water is available, as in the coastal desert locality of Taltal, *C. nigrofumosus* had a higher stomach content osmolarity, and it was similar to that of sea water (Table 1).

In *Cinclodes*, feeding behavior was different among species (Sabat et al. umpublished results). Cinclodes nigrofumosus from El Quisco and Taltal incorporated a greater proportion of crustaceans and lower proportion of insects (including "dilute" brine flies and larvae, see Hughes & Winkler 1990) in their diet than *C. oustaleti* and *C. patagonicus*. Thus, individuals that predate on marine invertebrates, particularly on crustaceans, acquire more salty food than those that predated on other invertebrates, such as insects. According to this, the proportion of crustaceans eaten by *Cinclodes* was positively correlated to the stomach content osmolarity. Nevertheless, although the amount of crustacean and insects incorporated to diet of *C. nigrofumos*us did not vary considerably between populations (more than 70% of crustaceans), the stomach content osmolarity differed considerably. This fact also suggests that *C. nigrofumosus* from El Quisco possibly decreased the osmotic load by drinking water that is more dilute. Moreover, the stomach content osmolarity of *C. patagonicus* and *C. oustaleti*

TABLE 1

Resume of osmoregulatory physiological features of three species of *Cinclodes* in two coastal localities from Chile. Values and ranges are approximated

Resúmen de las características fisiológicas de la osmorregulación en *Cinclodes* en dos localidades costeras de Chile. Los valores y los rangos son aproximados

| | Osmolarity (mOsm· Kg$^{-1}$) | | | Kidney features | |
|---|---|---|---|---|---|
| | Diet | Urine | Plasma | Size (% body mass) | Medulla (% kidney tissue) |
| Taltal | | | | | |
| *Cinclodes nigrofumosus* | >1000 | >1000 | 370-465 | 2.5-3.0 | 25-30 |
| El Quisco | | | | | |
| *Cinclodes nigrofumosus* | < 850 | < 850 | 365-420 | 2.0-2.7 | 25-30 |
| *Cinclodes patagonicus* | < 650 | < 600 | 400-440 | 1.8-2.0 | 12-15 |
| *Cinclodes oustaleti* | < 650 | < 700 | 340-380 | 1.8-2.5 | 13-15 |

from El Quisco may be influenced both by the dilute water they drink and by the higher proportion of insect they eat.

The first most immediate response of *Cinclodes* species in the intertidal habitat seems to be behavioral. The ability to choose more hyposmotic preys and/or drinking dilute water decreasing the osmotic load, allow birds to exploit such a prey-rich environment. The rise of plasma osmolarity is probably the second response, a physiological one, to the high osmotic load imposed by the marine diet. Plasma osmolarity in *Cinclodes* exhibits high values in maritime populations, compared to those found in species living in dry and saline habitats and in dehydrated birds (see Mahoney & Jehl 1985, Goldstein & Braun 1989, Goldstein & Zahedi 1990, Goldstein et al. 1990). Also, plasma osmolarity showed a high variability (from near 340-465 mOsm·Kg$^{-1}$), and was positively correlated with the osmolarity of the stomach content. Such a rise in plasma osmolarity is similar to that found in salt-loaded quails (*Lophortyx gambelii*). As pointed out by Braun (1981), this kind of response may be related to the restricted access to fresh water sources. However, animals have to eliminate the excess of electrolytes "stored" in the plasma, and without nasal glands, the kidneys must play an active role.

The urine osmolarity was higher in maritime species *C. nigrofumosus*. Moreover *C. nigrofumosus* population from Taltal exhibits higher urine osmolarity than the El Quisco population, reaching osmolarity values above 1000 mOsm·Kg$^{-1}$. Such a difference was correlated to differences of the osmotic load. In addition, the urine osmolarity differences were correlated to kidney morphology, specifically the kidney mass and the proportion of medullary tissue (Sabat, unpublished data). *Cinclodes nigrofumos*us which has heaviest kidneys with more medullary tissue (comparable to that found in the kidneys of the salt-marsh passerine [Johnson & Ohmart 1973a, Johnson & Mugaas 1970b]) appears to be able to concentrate more efficiently the urine than their congeners. This extraordinary ability to concentrate urine above sea water values, probably is related to the capacity of these birds to live and exploit successfully marine coast environments. The higher urine osmolarity found in *C. nigrofumosus* from Taltal compared to their conspecific from El Quisco may reflect the great differences in fresh water availability that these two populations experience. Hence, we cannot answer if these differences are immediate physiological adjustments due to differences in the osmotic load, or due to a more chronic exposition to this condition (physiological plasticity). Indeed, it is not possible to assume that the above described physiological features of *Cinclodes*, particularly those related to renal function, are their maximal capabilities. Only acclimation and osmotic load experiments would help to disentangle this questions. Nevertheless, it is probably that *C. patagonicus* and *C. oustaleti* have more physiological-osmoregulatory constraints than *C. nigrofumosus*. This is suggested by the dietary habits of the formers, which includes more "dilute" insects than *C. nigrofumosus* and by the apparent lower ability to concentrate the urine. In fact, if their feeding behavior is effectively constrained by osmoregulatory capacities, and not by other physiological capacities (see Sabat 2000 for digestive-biochemical features of *Cinclodes*), then, this pattern of feeding behavior is expected.

Furthermore, it has been reported that several *Cinclodes* species (including *C. patagonicus* and *C. oustaleti*) have seasonal migratory patterns, from the coast to inland in summer. Such behavior, which is not exhibited by *C. nigrofumosus* (see Jorge et al. 1998, Sielfeld et al. 1996) may be related to seasonal differences in the ability of birds to maintain their electrolyte and water balance. Because in summer the sources of fresh water probably decay in the coastal regions (e.g., rain pounds, morning dew drops), and the water loss rise due to higher temperatures, these species may not satisfy their minimal water requirements when they feed on marine invertebrates. Such constraint may lead to birds being forced to migrate toward regions where the availability of fresh water would not be limiting. Although other ecological factors may be acting (as the competitive exclusion by migratory shorebirds), congruence between the migratory behavior and osmoregulatory physiology suggest that this phenomena may be related. Thus, physiological features of *Cinclodes* species may account for their ecological differences, as habitat and resource use, and may reflect the unusual circumstance of passerines living in marine coast.

In summary, although birds without salt gland confront serious problem relative to water conservation in marine and other dry environments, they have several mechanisms to avoid dehydration. First, they can diminish the salt intake throughout the selection of preys with lower salt content. In addition, some birds can rise their body fluids concentration in response to high salt intake. This physiological response allows birds to storage salts, delaying their elimination before fresh water is available and/or to excrete more concentrate urine without any augmentation of their concentrating ability. In spite of the conservative features of kidney morphology and physiology among related species, some exceptional cases account for an extraordinary concentrating ability. This unusual ability for birds, coupled with the functional relationship between kidney and the lower intestine may also contribute to explain the success of some birds species without salt gland to living and exploiting marine habitats.

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