Gutiérrez, J.S. (2014). Living in Environments with Contrasting Salinities: A Review of Physiological and Behavioural Responses in Waterbirds. *Ardeola: Revista Ibérica de Ornitología,* 61(2), 233-256

Published version: dx.doi.org/10.13157/arla.61.2.2014.233

Link NIOZ Repository: www.vliz.be/nl/imis?module=ref&refid=244619

LIVING IN ENVIRONMENTS WITH CONTRASTING SALINITIES: A REVIEW OF PHYSIOLOGICAL AND BEHAVIOURAL RESPONSES IN WATERBIRDS

Jorge S. GUTIÉRREZ[1, 2, *]

[1]Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands. [2]Conservation Biology Research Group, Department of Anatomy, Cell Biology and Zoology, Faculty of Sciences, University of Extremadura, Avenida de Elvas, 06006 Badajoz, Spain. [*]E-mail: jorgesgutierrez@unex.es

SUMMARY.— *Living in environments with contrasting salinities: a review of physiological and behavioural responses in waterbirds*

During the course of their lives many vertebrates live and forage in environments characterized by different salinities and must therefore respond to changes in salt intake. This is particularly true for numerous species of migratory waterbirds, especially those that routinely commute between saltwater and freshwater wetlands throughout their annual cycle and/or within a season. These birds have evolved a suite of morphological, physiological and behavioural mechanisms to successfully maintain osmoregulatory balance. However, relatively little is known about the impacts of salinity on the distribution, physiological performance and reproductive success of waterbirds. Here I review the current knowledge of the physiological and behavioural mechanisms through which waterbirds cope with contrasting salinities and how some of the adjustments undertaken might interfere with other relevant aspects of their performance. I argue that, because of their strong reliance on wetland ecosystems for foraging and breeding, waterbirds may be particularly vulnerable to climate-induced changes in salinity, especially in arid or semiarid tropical areas where increases in both temperature and salinity may affect their body condition and, ultimately, survival prospects. I conclude by offering some suggestions for future research that could take us beyond our current level of understanding of avian osmoregulation.

Key words: ecophysiology, energetic costs, habitat selection, immunocompetence, global change, migration, osmoregulation, phenotypic flexibility, salinity, trade-offs, waterbirds, wetlands

RESUMEN.—*Viviendo en ambientes con distintas salinidades: una revisión de respuestas fisiológicas y comportamentales en aves acuáticas*

Durante el transcurso de sus vidas muchos vertebrados viven y se alimentan en ambientes caracterizados por tener distintas salinidades y por tanto deben responder a cambios en la ingestión de sal. Esto ocurre particularmente en numerosas especies de aves acuáticas migratorias, especialmente aquellas que se mueven rutinariamente, a lo largo de su ciclo anual, entre humedales de agua salada y agua dulce. Estas aves han desarrollado un conjunto de mecanismos morfológicos, fisiológicos y comportamentales para mantener el balance osmorregulatorio exitosamente. Sin embargo, todavía se conoce relativamente poco sobre los impactos de la salinidad en la distribución, rendimiento fisiológico y éxito reproductor de las aves acuáticas. Aquí describo el conocimiento actual sobre los mecanismos fisiológicos y comportamentales por los cuales ciertas aves acuáticas son capaces de hacer frente a distintas salinidades y cómo algunos de los ajustes llevados a cabo podrían interferir con otros aspectos relevantes de su rendimiento. Argumento que, debido a su fuerte dependencia a los ecosistemas húmedos para la alimentación y reproducción, las aves acuáticas son particularmente vulnerables a cambios en salinidad inducidos por el clima, especialmente en áreas áridas o semiáridas donde los incrementos en tanto temperatura como salinidad podrían afectar a la condición corporal y, finalmente, a las expectativas de supervivencia. Concluyo ofreciendo algunas sugerencias para futuras investigaciones que podrían permitir avanzar en el conocimiento de la osmorregulación en aves.

Palabras clave: ecofisiología, costes energéticos, selección de hábitat, inmunocompetencia, cambio global, migración, osmorregulación, flexibilidad fenotípica, salinidad, compromisos, aves acuáticas, humedales

INTRODUCTION

It is has long been assumed that the sea constitutes a major physiological barrier to vertebrate distributions (Darwin 1939; Darlington 1957). One of the main reasons proposed is its high salt content (Bentley 2002). Indeed, maintenance of constant intra- and extracellular ionic and osmotic conditions — *i.e.*, osmoregulation — is considered a fundamental challenge for vertebrates living in saline environments, including birds (Skadhauge 1981; Sabat 2000; Goldstein 2002; Gutiérrez *et al.* 2011a). Birds, as with other vertebrates, have blood concentrations of around 250-300 mOsm, which is essential for the proper functioning of cells (Bradley 2009). However, when these organisms ingest water or food with a high salt concentration and lose water through both respiration and skin, the concentration of salts in their body increases. Under such circumstances, they must excrete excess salt and conserve body water to maintain their ionic and osmotic homeostasis. Despite the fact that avian kidneys have a limited concentrating ability (Goldstein & Skadhauge 2000; Goldstein 2002), many birds live in saline environments during at least part of their life cycles, and some — *e.g.*, shorebirds, petrels and penguins — typically feed on marine invertebrates that are in osmotic and ionic equilibrium with seawater without regular access to freshwater. How can birds endure such osmotically challenging environments? In the struggle to maintain osmotic and ionic balance, birds living in saline environments have evolved a suite of physiological, behavioural and morphological mechanisms.

The supraorbital nasal saltglands — hereafter, “saltglands” — are the most powerful extra-renal salt-secreting structures used by waterbirds to ensure survival under saline conditions (Schmidt-Nielsen 1959; Peaker & Linzell 1975). Saltglands are typically located above the orbit of the eye and extract salt ions from the bloodstream producing a concentrated salt solution that is discarded through the nostrils (Fig. 1). This retains osmotically-free water to sustain other physiological processes. Although the presence of the saltglands in marine and non-marine birds was observed by Comelin in 1667 (see Technau 1936), and their anatomy described by Jacobson (1813) and Nitzsch (1820), it was not until the second half of the 20th century that their excretory function was discovered by Knut Schmidt-Nielsen and colleagues (1957, 1958). After salt-loading double-crested cormorants *Phalacrocorax auritus*, they found a highly hypertonic liquid that dripped out from the internal nares and accumulated at the tip of the beak, from which the birds shook the drops with a sudden jerk of the head. It was in this way that they first discovered that birds — and some reptilian relatives (Schmidt-Nielsen & Fange 1958) — living in saline environments had an extrarenal mechanism to eliminate excess salt (reviewed in Schmidt-Nielsen 1959, 1960, 1997). Since the publication of these seminal articles, osmoregulation has become an important part of avian physiology.

Further investigations have made clear that the saltgland secretion is the result of a set of highly integrated interactions among the gut, kidneys, hindgut, saltglands, and supporting organs (reviewed in Goldstein & Skadhauge 2000; Goldstein 2002; Hughes 2003; see Fig. 2). Therefore, the functioning of this osmoregulatory machinery in an integrative manner is exceedingly important to tolerating and exploiting saline habitats. Additionally, it has been demonstrated that the ingestion of salts initiates large compensatory responses in the osmoregulatory physiology and behaviour of birds.

Marine birds and domesticated waterfowl have been primary targets of osmoregulation studies (Peaker & Linzell 1975; Goldstein 2002). Whilst marine birds are normally exposed to constant salinity levels throughout the year — *osmotic specialists* —, many waterbirds live and forage in environments where they experience large fluctuations in salinity and/or periodically alternate between freshwater and saline habitats — *osmotic generalists* — and could be subjected to greater physiological stresses than those confronting marine species (Blakey *et al.* 2006). This could especially be the case for migratory shorebirds that shift seasonally from freshwater environments during the breeding season to marine environments during migration and the wintering period (Gutiérrez *et al.* 2013). Such seasonal changes inevitably lead to substantial increases in salt intake that must be counteracted by flexible osmoregulatory organs. However, we do not know to what extent these species are able to overcome the challenges posed by increases in salt intake. The aim of this review is to establish the ecophysiological significance of the adaptations and adjustments (see Box 1 for terminology) that enable waterbirds to cope with environments with contrasting salinities. Various aspects of the anatomy, morphology and hormonal control of the avian osmoregulatory system are not addressed as they have been extensively reviewed elsewhere (Schmidt-Nielsen 1960; Peaker 1971; Phillips & Ensor 1972; Peaker & Linzell 1975; Holmes 1975; Sturkie 1976; Skadhauge 1981; Simon 1982; Holmes & Phillips 1985; Butler *et al.* 1989; Braun 1999; Shuttleworth & Hildebrandt 1999; Goldstein & Skadhauge 2000; Sabat 2000; Hildebrandt 2001; Goldstein 2002; Bentley 2002; McNab 2002; Hughes 2003). Although marine birds (Sphenisciformes, Procellariiformes, Pelecaniformes, Charadriiformes), long-legged wading birds (Ciconiiformes) and waterfowl (Anseriformes) are covered in this paper, I concentrate largely on migratory shorebirds (Charadriiformes: suborder Charadrii) as they have proven to be a robust model system for the study of avian osmoregulation.

MIGRATORY SHOREBIRDS AT A GLANCE

Migratory shorebirds offer a particularly interesting opportunity for studying physiological and behavioural adaptations/adjustments to salinity because they differ in habitat preferences, diet and saline tolerance (Staaland 1967; Blakey *et al.* 2006; Gutiérrez *et al.* 2012a,b, 2013). Many species spend a large portion of their annual cycle in marine habitats: for instance, red-necked *Phalaropus lobatus* and red phalaropes *P. fulicarius* spend up to 9 and11 months of the year, respectively, on the open ocean (Piersma *et al.* 1996; Tracy *et al.* 2002), while others, such as American *Scolopax minor* and Eurasian woodcocks *S. rusticola*, spend the entire year in freshwater habitats (Piersma *et al.* 1996). According to their nonbreeding habitat occupancy, most shorebirds can be classified as either 'coastal' or 'inland' species (Piersma 2003, 2007; Gutiérrez *et al.* 2012a,b); however, other species — or populations— fall in between these extremes, occurring in both coastal and inland habitats, and can be classified as 'mixed' species (Piersma 1997, 2007; Gutiérrez *et al.* 2012a,b). Habitat occupancy is generally linked with migration strategy, with High Arctic breeders wintering in coastal saline wetlands, and more southerly breeding congeners wintering in inland freshwater wetlands (Piersma 1997, 2003, 2007). Coastal shorebirds generally feed on marine invertebrates found in intertidal substrates, which are in osmotic and ionic balance with seawater and thus have a high salt content, meaning that they regularly face an osmotic challenge.

Such a challenge may be particularly severe prior to migration and at intermittent sites *en route*, since migratory shorebirds undergo major physiological adjustments to enable rapid accumulation of fuel stores (Kvist & Lindström 2003; Lindström 2003). As a consequence of their extraordinary food intake rates, coastally migrating shorebirds can receive high salt loads, and thus, face important osmotic challenges that might interfere with other aspects of their performance (Gutiérrez *et al.* 2011, 2013). Coping with salt may be more challenging for molluscivore shorebirds that ingest hard-shelled bivalves containing a large amount of seawater (Gutiérrez *et al.* 2012a). In contrast, terrestrial and freshwater invertebrates — which contain about 65-75% osmotically-free water (Hadley 1994) — do not pose significant osmotic problems to inland shorebirds or ‘coastal’ shorebirds while breeding inland.

In addition to salt stress, migrating shorebirds may encounter energetic constraints imposed by physically demanding flights and high thermoregulatory or food-processing costs (Piersma & Lindström 1997; Piersma 2002). Energetic constraints and osmoregulatory problems may therefore interact in determining several aspects of migration ecology (Gutiérrez *et al.* 2011a, 2013). Rapid phenotypic adjustments — *e.g.*, changes in body composition, including size and function of osmoregulatory organs — during such periods are of critical importance to many migrating shorebirds.

AN INTEGRATED OSMOREGULATORY SYSTEM

Salts ingested while feeding and drinking in saline environments can induce large responses in the principal osmoregulatory organs, including the kidneys, small intestine, hindgut, saltglands, and supporting organs (Hughes 1991; 2003; Braun 1999). Below, I describe the integrated functioning of such organs and provide some examples of ecological adaptations and adjustments to osmotic challenges.

Water and ions first move across the gut and then into the extracellular fluids. At that point, the osmotic concentration of the extracellular fluids increases and intestinally absorbed sodium chloride must be reabsorbed by the kidneys to restore the proper osmotic concentration. Birds, as do mammals, have the capacity to produce urine that is hyperosmotic relative to plasma. However, the avian kidney can generally only concentrate urine to approximately twice the plasma concentration, while the mammalian kidney can concentrate it up to 17 times the plasma concentration (Schmidt-Nielsen 1963). Avian kidneys contain both loopless (“reptilian”-type) and looped (“mammalian”-type) nephrons. Loopless nephrons lack loops of Henle and do not contribute directly to the formation of hyperosmotic urine, whereas looped nephrons have loops of Henle and actively transport ions maximizing urine concentration (Dantzler 1970; Goldstein & Skadhauge 2000). The urine exiting the kidneys passes into the cloaca, where water can be resorbed and returned to the blood to conserve water in the body even if the kidneys are not producing concentrated urine. When the kidneys are producing concentrated urine, it remains in the cloaca until excreted. The cloaca has the potential to uptake ions and water as necessary and can also be made impermeable to allow concentrated urine to pass through. In species with high salt intakes, however, the renal pathway is not sufficient to remove excess salt. In these cases reabsorbed sodium chloride is secreted as a concentrated solution — *i.e.*, twice the maximal urine osmolality — by the saltglands.

Salt excretion by the saltglands is among the most significant physiological mechanisms used by waterbirds to cope with saline conditions. Although the saltglands are present in at least 10 of the 27 extant orders of birds, functional salt-secreting glands are mostly restricted to orders with species inhabiting saline environments (Cooch 1964; Goldstein & Skadhauge 2000; Sabat 2000). Overall, both the size and excretory capacity of these glands reflects the experience of species and individuals with salt water; that is, saltglands are larger and more efficient in species and individuals that are exposed to higher salt loads (Staaland 1967; Gutiérrez *et al.* 2012a). Recent comparisons among and within shorebird species support the notion that habitat salinity and salt content of the diet largely explain variation in saltgland size (Gutiérrez *et al.* 2012a). Among coastal shorebirds, mollusc-eaters have larger saltglands than species eating non-shelled prey, indicating that seawater contained within the shells increases the salt load of the ingested food (Gutiérrez *et al.* 2012a).

Maintaining and using large, active saltglands can be energetically expensive and a trade-off with other activities has thus been suggested on several occasions (Staaland 1967; Peaker & Linzell 1975; Burger & Gochfeld 1984; Nyström & Pehrsson 1988; Gutiérrez *et al.* 2011a; Gutiérrez *et al.* 2012a, 2013). Indeed, there is growing evidence that developing and maintaining osmoregulatory machinery entails substantial energy costs in birds. This explains why birds exposed to experimentally decreased salinity reduce the size and activity of their saltglands (Peaker & Linzell 1975). This also occurs under natural conditions: Most significantly, red knots *Calidris canutus* reduce the size of their saltglands when in mild climates, probably reflecting low energy demands — *i.e.*, low rates of food and salt intake (Gutiérrez *et al.* 2012a). Likewise, bar-tailed godwits *Limosa lapponica* with smaller intestines — *i.e.*, lower relative food intake rates — have smaller saltglands, indicating that they also reduce their saltglands when osmoregulatory demands are low (Gutiérrez *et al.* 2012a). Together, these studies show that shorebirds, and waterbirds in general, adjust the mass of this small but essential osmoregulatory organ to changing osmoregulatory demands.

In addition, birds with functional saltglands have larger kidneys than those without (Hughes 1970). Among Anseriformes, kidney mass is larger in strictly marine species (Kalisinska *et al.* 1999), which presumably reflects the higher salt loads to which these species are exposed. In line with these observations, Bennett & Hughes (2003) found that glomerular filtration rate is also higher among marine birds. Comparing simultaneous kidney and saltgland function in three duck species occupying habitats with different salinities, marine species (Barrow's goldeneye *Bucephala islandica*) had the highest rates of filtration, fractional reabsorption of water and sodium, and saltgland sodium excretion, followed by estuarine (canvasback *Aythya valisineria*) and then freshwater species (mallard *Anas platyrhynchos*). This demonstrates that variations in kidney and saltgland function are, at least in part, correlated with habitat salinity. They also suggested that the larger kidneys and glomerular filtration rates of marine birds presumably reflect an increased number of glomeruli. Other studies have found that the proportion of kidney mass composed of medullary cones is high in marine species (Goldstein & Braun 1989; Goldstein 1993), reflecting a high proportion of mammalian-type nephrons, which form a countercurrent multiplier system and increase their ability to form hyperosmotic urine. Likewise, in passerine birds of the genus *Cinclodes*, the capacity to conserve urinary water by producing concentrated urine is related to differences in renal medullary development and other kidney features (Sabat *et al.* 2004, 2006a,b). These observations indicate that habitat is also an important factor determining kidney structure in birds. Unlike saltglands whose size and activity show substantial *phenotypic flexibility* (Box 1), both the kidney mass and glomerular filtration rate of waterbirds are generally little affected by salt loading (Holmes *et al.* 1968; Bennett & Hughes 2003; Hughes 2003). Nevertheless, several studies on passerines have shown that birds of some species are capable of modifying their kidney morphology in response to salt *acclimation* (Box 1), which increases their ability to produce more concentrated urine (Sabat *et al.* 2004; Peña-Villalobos *et al.* 2013).

Salt intake can increase the mass of intestines (Hughes *et al.* 2002), increase gut water and sodium uptake rates in mallards (Crocker & Holmes 1971) and decrease the time required for fluid to move through the gut (Roberts & Hughes 1984). The hindgut appears to be particularly important for osmoregulation when saltglands are exposed to high salt loads because the hindgut can maintain high rates of intestinal salt and water reabsorption during salt loading, routing the salt to the saltglands for excretion and thereby retrieving “free water” (Schmidt-Nielsen *et al.* 1963; Laverty & Skadhauge 2008; McWorther *et al.* 2009). However, in other marine species, such as glaucouswinged gulls *Larus glaucescens*, reflux and modification of already hyperosmotic ureteral urine seems relatively unimportant in overall osmoregulation (Goldstein 1989).

Besides renal and extrarenal pathways that enable birds to excrete excess salt and yield sufficient free water, there may be additional mechanisms to balance respiratory cutaneous, faecal, and saltgland water losses (Figs. 1 & 2). Recently, it has been demonstrated in several temperate-zone passerines that the process of water loss through skin is under physiological control (Ro & McWilliams 2010), which suggests that cutaneous water loss is a fundamental component of the avian water economy. Since marine and other saline environments can be considered dry in terms of osmotically-free water (Sabat 2000), it cannot be ruled out that waterbirds adjust the rate of water loss through the skin to help maintain water, salt and heat balance.

BEHAVIOURAL AND MECHANICAL MEANS OF SALT AVOIDANCE

Behavioural responses provide waterbirds with additional flexibility when responding to the potential problems presented by high salt loads. The combination of avoidance of high-salinity habitats, choice of salt-free — or low-salt — prey, and, when possible, use of freshwater are all well documented behaviours employed by waterbirds to avoid salt stress (*e.g.*, Nyström & Pehrsson 1988; Rubega & Robinson 1997). While some waterbirds (*e.g.*, some rails, ducks and geese) are limited to freshwater or low-salinity wetlands for their entire lives and thus do not *a priori* face the problem of salt stress, many others (*e.g.*, marine birds, many shorebirds, and some gulls and ducks) rely on high-salinity environments during at least part of their life cycles. These species often resort to ‘behavioural osmoregulation’ to cope with salinities that cannot be physiologically tolerated. For example, some inhabitants of hypersaline environments depend primarily on terrestrial prey with high free water contents to compensate for their limited physiological ability to tolerate salt or reduce water turnover (Purdue & Haines 1977; Rubega & Robinson 1997). Other studies have shown that birds have the ability to select relatively low-salt prey minimizing their salt intake. Nyström & Pehrsson (1988) and Nyström *et al.* (1991) showed that common eiders *Somateria mollissima* — and especially young birds — select small mussels in areas of high salinity, considerably reducing the amount of salt they ingest. In line with these results, Cervencl & Alvarez Fernandez (2012) recently showed that salinity restricted greater scaup *Aythya marila* wintering in the western Dutch Wadden Sea mainly to brackish areas.

In hypersaline habitats, where dietary salt intake may represent an important osmotic challenge for nestlings, some parents raise their chicks with low-salt diets. For instance, flamingos feed their young semiprocessed food or food produced internally from the epithelial tissue lining the digestive tract, which contains far less salt than freshly caught food (O’Connor 1984). Likewise, Janes (1997) found that Adélie penguins *Pygoscelis adeliae* feed their chicks with nutritive secretions containing significantly less salt than the krill ingested by adults. Other studies have also shown that waterbirds nesting in saline habitats feed their nestlings prey containing dilute body fluids (*e.g.*, Mahoney & Jehl 1975c; Johnston & Bildstein 1990), often flying long distances inland to do so. Although nestlings of species breeding in saline habitats do not have regular access to water, some have been reported eating grass, which may provide them with free water (Ensor & Phillips 1972).

When possible, birds respond to osmotic stress by visiting freshwater sources close to their feeding grounds. In hypersaline habitats such as the Mono Lake, most — if not all — waterbird species travel regularly to freshwater, where they can be seen vigorously bathing and drinking (Rubega & Robinson 1997). Rubega & Robinson

1997) suggested that birds may avoid hypersaline wetlands even for roosting because increasing water salinity negatively affects the waterproofing of waterbird feathers, which increases thermoregulatory costs under sub-thermoneutral conditions. Even in less osmotically challenging environments, many waterbirds are attracted by the presence of freshwater for drinking and preening (e.g., Woodin 1994; Adair 1996; Ravenscroft & Beardall 2003). It is well established that several species of coastal diving ducks (*Aythya* spp.) commute between saltwater wetlands (feeding grounds) and freshwater wetlands (resting grounds) (Woodin 1994; Adair *et al.* 1996). Ravenscroft & Beardall (2003) observed a similar pattern, noting the importance of freshwater flows over estuarine mudflats for waterbirds wintering in eastern England, UK. They showed that birds were attracted by the presence of freshwater close to intertidal feeding grounds during low tide, which they attributed to the presence of freshwater for drinking and preening.

Beside physiological and behavioural adjustments, variations in morphological traits like bill shape and size — feeding morphology — can influence the ingestion of saltwater. Indeed, it has been suggested that some feeding mechanisms can minimize salt intake. Mahoney & Jehl (1985b), for example, suggested that the large and flat tongue of eared grebes *Podiceps nigricollis* may be used to compress the prey against the smooth palate, flushing saltwater off the prey. Similarly, they reported that Wilson's phalaropes *P. tricolor* and American avocets *Recurvirostra americana* ingest very little saline water while feeding, supporting the idea that these species have some capacity for primitive filter-feeding (see Mahoney & Jehl 1985a for anatomical details). Masero (2002) and Verkuil *et al.* (2003) also suggested that shorebirds feeding on high salinity prey could minimize salt ingestion by using surface tension transport (Rubega 1997), as this includes the disposal of the transported salt water. This feeding mechanism might allow small-sized calidrids to exploit saline habitats dominated by small prey items that are unprofitable and too salty for other shorebird species (Masero 2002; Estrella & Masero 2007). Masero (2002) showed that red knots, in contrast with several other small-sized migrating shorebirds, do not feed extensively on brine shrimps *Artemia* spp. at supratidal salinas. One possible explanation could be the avoidance of salt stress (Masero 2002). It is possible that, although red knots have relatively large saltglands (Staaland 1967; Piersma & van Gils 2011; Gutiérrez *et al.* 2012a), their thick bills do not enable them to ingest *Artemia* without also consuming hypersaline water.

While behavioural and anatomical mechanisms leading to a decrease in salt intake are not as well studied as physiological mechanisms themselves, they may also be crucial to maintaining the osmotic balance in many waterbird species.

ENERGETIC COSTS OF OSMOREGULATION

Unlike the study of osmoregulation in fish and other aquatic animals, where energetics plays a central role (see Tseng & Hwang 2008 and Evans 2009 for reviews), energetics has been largely neglected in the study of avian osmoregulation (but see references in Table 1). Soon after the discovery of the excretory function of saltglands, some authors tried to estimate the energetic costs of salt gland function by measuring oxygen consumption of the tissue *in vitro*, enzyme activity and the levels of metabolic intermediates (reviewed in Peaker & Linzell 1975). Peaker & Linzell (1975) estimated the theoretical energy requirement of saltgland secretory function at *ca.* 7 % the metabolic rate of resting ducks maintained on freshwater. To date, however, there have been only three studies examining the influence of salinity on whole-organism metabolic rate. Nehls (1996) carried out an experiment with salt-acclimated common eiders and found a marked rise in metabolic rate following oral salt administration, estimating salt turnover at 2.0-2.4% of metabolizable energy intake. Although this figure is low compared to those of other costs associated with foraging and food processing (Piersma *et al.* 2003), it reflects the energy expended in salt turnover only and not the total energy devoted to the development, maintenance and use of osmoregulatory machinery. Dunlin *Calidris alpina* experimentally acclimated to different salinities increased their mass-specific basal metabolic rate (BMR) and daily energy consumption by 17 and 20% respectively during saltwater acclimation, demonstrating that the processes of developing and maintaining an active osmoregulatory machinery are indeed energetically expensive (Gutiérrez *et al* 2011a). Although the increased energetic costs under saline conditions appear to be, in part, attributable to short-term adjustments in the saltglands (see Hildebrandt 1997, 2001), substantial energetic costs are not exclusive to birds with functional saltglands. Peña-Villalobos *et al.* (2013) recently assessed the osmoregulatory and metabolic costs of salt excretion in the rufous-collared sparrow *Zonotrichia capensis* — a bird species lacking functional saltglands — and found that salt-acclimated birds increased their BMR by 30%, coupled with an increase in the masses of the kidney and heart, suggesting that the increase in energy expenditure was associated with the elimination of excess salt through the kidney as well as with an increase in the mass of metabolically active tissue.

Several inter- and/or intraspecific comparative studies of avian metabolism have demonstrated that birds in marine habitats have significantly higher basal and field metabolic rates than those in terrestrial ones (Ellis 1984; Rahn & Whittow 1984; Bryant & Furness 1995; Nagy 2005; McNab 2009; Gutiérrez *et al.* 2012b). In a recent study comparing the BMR of coastal and inland migratory shorebirds, Gutiérrez *et al.* (2012b) suggested that the increased osmoregulatory demands of coastal saline habitats may contribute to such a metabolic dichotomy.

Although the studies on the energetics of avian osmoregulation are scarce, they reveal that birds living in saline habitats pay an additional energetic cost for osmoregulation. However, a deeper understanding of how saline environments influence the individual's energy budget would help explain diet and habitat selection patterns in waterbird species and populations.

POTENTIAL TRADE-OFFS WITH OSMOREGULATION

By definition, life history trade-offs result from competition among different organismal functions for limited internal resources (*sensu* Zera & Harshman 2001). Thus, osmoregulation is susceptible to generating resource-based trade-offs with other energetically costly activities, such as growth, thermoregulation, immune function, and moult (see Table 1). For example, the trade-off between osmoregulation and growth is evident in laboratory experiments with chicks (Ellis *et al.* 1963; Schmidt-Nielsen & Kim 1964; Cooch 1964; Harvey & Phillips 1980; Johnston & Bildstein 1990; Barnes & Nudds 1991; Hannam *et al.* 2003; DeVink *et al.* 2005), but also in field studies where dietary salt differs between colonies (Ensor & Phillips 1972; Kushlan 1977a) or is experimentally manipulated (Dosch 1997). Together, these studies demonstrate that birds raised under highly saline conditions often exhibit a decreased growth rate. This may help explain why many waterbirds provide their chicks with low-salt food when in saline habitats (Cantin *et al.* 1974; Mahoney & Jehl 1985c; Johnston & Bildstein 1990; Bildstein *et al.* 1990, 1991; Janes 1997) or breed inland (Nyström & Pehrsson 1988).

Physiological trade-offs with osmoregulation are not exclusive to chicks. For instance, adult white ibis *Eudocimus albus* breeding at coastal colonies had significantly smaller clutches than those breeding at inland colonies (Kushlan 1977a), even though chicks grew at similar rates (Kushlan 1977b). In another field study with scarlet ibis

Eudocimus ruber, Bildstein (1990) found that most adults ceased nesting when freshwater wetlands close to the colony sites became brackish due to freshwater diversion, pointing to a trade-off between osmoregulation and breeding.

Burger & Gochfeld (1984) also suggested that osmoregulation might compete energetically with moult, pre-migratory ‘fattening’ or migration. One would expect such trade-offs to be more pronounced for migratory waterbirds that return to coastal wintering and staging areas from their freshwater breeding grounds and switch from inland to marine foods. This dietary shift inevitably leads to substantial increases in salt load that should be counteracted by the saltglands — and supporting organs —, which may have lost functionality after a long period of inactivity. Despite the fact that many species increase the size of saltglands and volume of secretion within a few days of exposure to salt water (Peaker & Linzell 1975), salt stress may limit food consumption immediately after arrival in saline environments (Burger & Gochfeld 1984). However, Burger & Gochfeld (1984) showed that both captive and wild Franklin’s gulls *Larus pipixcan* exhibited an additional endogenous capacity for saltgland flexibility, independent of the environmental salinity. They proposed that this seasonal — circannual — program of change in saltgland size and activity would have a high selective value in protecting an individual from undue physiological stress when it first arrives at their marine non-breeding sites. In line with these results, Mahoney & Jehl (1985a) noted that the saltglands of Wilson’s phalaropes that had just arrived at the hypersaline Mono Lake in mid-June, presumably after a direct flight from their freshwater breeding grounds, were of similar size to those of birds that had resided at a hypersaline lake for several weeks. These findings provide further evidence that some species exhibit an adaptive syndrome involving a circannual program of change in the mass and composition of digestive machinery (*e.g.*, Piersma *et al.* 1995, 1996; Piersma

& Gill 1998). However, the extent of such endogenous rhythmicity in the size and activity of saltglands — and other osmoregulatory organs —, as well as its underlying mechanism, remain unknown.

As seen in Table 1 immune responses are energetically expensive. In this context, Gutiérrez *et al.* (2013) hypothesized that there is a trade-off between osmoregulation and immune response. Using dunlin experimentally acclimated to fresh- and saltwater conditions, they found that seawater salinity exerted immunosuppressive effects in individuals challenged with phytohaemagglutinin (PHA; a mitogen commonly used to assess the birds' pro-inflammatory potential). A reduced immune response under saline conditions may be associated with the function of essential osmoregulatory hormones, some of which have anti-inflammatory and immunosuppressive effects (Gutiérrez *et al.* 2013). Indeed, essential hormones in extrarenal excretion such as prolactin, melatonin, or corticosterone may be involved in the secretory activity of saltglands (reviewed in Phillips & Ensor 1972). For example, prolactin and corticosterone have been shown to restore saltgland secretion in adenohypophysectomized ducks (Phillips & Ensor 1972; Butler *et al.* 1989), which could facilitate their adjustment to saline environments (Ensor & Phillips 1970). On the other hand, melatonin has been shown to inhibit saltgland secretion rate and its sodium concentration in mallards (Ching *et al.*, 1999; but see Hughes *et al.* 2007). This suggests that melatonin's osmoregulatory function may conflict with its immune function, as there is some evidence that increased exposure to melatonin during long winter nights enhances immune function (Hasselquist 2007). If true, birds wintering in coastal saline environments may be subjected to a hormonally induced trade-off between osmoregulation and immune function — at least in ecosystems where winter is the most demanding time of the year (see Buehler *et al.* 2009). Similarly, it is also possible that exposure to saline conditions could result in an increase in the circulating levels of corticosterone (Phillips & Ensor 1972; Harvey & Phillips 1980), which, in turn, may generate trade-offs with immune response (Martin *et al.* 2005).

Although both osmoregulation and moult carry significant energetic costs (Table 1), no study has dealt with the possible trade-off between these two processes. Birds in high saline conditions should likely reduce the amount of energy available for moult (Burger & Gochfeld 1984). Such a potential trade-off could be relevant in saline staging and/or wintering areas where birds normally begin or resume interrupted moult. For example, this could pose a substantial physiological challenge for Wilson's and red-necked phalaropes congregating at hypersaline lakes in western North America who must moult and refuel before migrating to wintering grounds in South America. In 3-6 weeks, these species undergo a rapid replacement of nearly all their body plumage, several primaries, and rectrices (Jehl 1987, 1988). They must simultaneously become hyperphagic by feeding on brine shrimp *Artemia* sp. and brine flies *Ephydra hians*, which may led them to ingest large salt loads (Mahoney & Jehl 1985b). They appear to overcome this problem by frequently flying to nearby freshwater creeks to dilute their salt intake and, perhaps, they are also able to derive appreciable water from their food (Mahoney & Jehl 1985b). In contrast, Jehl (2005) noted that many gadwall *Anas strepera* — which are less saline-tolerant — failed to complete wing moult after breeding at the hypersaline Mono Lake even though food remains abundant in the lake well into the autumn.

SALINITY & PARASITES

Salinity, along with temperature and moisture, is considered a key abiotic factor in shaping parasite and pathogen distribution, thereby influencing the risk of infection and disease. In birds, there is substantial evidence that species restricted to coastal marine and saline habitats have lower prevalence of infection by blood parasites than those relying on inland freshwater habitats (e.g., Piersma 1997; Figuerola 1999; Jovani 2001; Mendes *et al.* 2005; Yohannes *et al.* 2009; Quillfeldt *et al.* 2011). Accordingly, shorebirds restricted to coastal saline habitats during the nonbreeding season may be exposed to fewer parasites and thus invest less in immune defence mechanisms than those using freshwater habitats (Piersma 1997). The relative low parasite prevalence and diversity of blood parasites in saline habitats could be explained by the reduced abundance of invertebrate vectors, but also by other factors such as the immunocompetence of the host and the absence of alternative hosts that could serve as a reservoir for the parasite (Yohannes *et al.* 2009). However, coastal saline habitats are not parasite-free. For instance, trematodes — and other helminths — are extremely common parasites of invertebrates and vertebrates living on mudflats and rocky shores (see Mouritsen & Poulin 2002 and references therein). The life cycle of these parasites typically involves a gastropod or a bivalve as first intermediate host, and is completed when the second intermediate host is eaten by a suitable definitive host, frequently a shorebird. Although the effects of salinity on the replication and transmission of these parasites are still poorly understood, there is evidence that cercarial emergence — and thus its success — generally increases with increasing salinity within a range of values normally occurring in coastal habitats (Mouritsen 2002). Recently, Lei & Poulin (2011) showed that the replication and transmission of the trematode *Philophthalmus* sp., a common parasite of waterbirds, was negatively influenced by salinities below that of normal seawater, suggesting that low salinity would reduce transmission success to waterbirds. Thus the effects of salinity on parasite abundance and distribution will depend on the type of parasite and its life cycle stage. Moreover, although blood parasite vectors are scarce — or absent — in some coastal saline environments, birds may prey on intertidal invertebrates infected by various macroparasites — trematodes, nematodes, polychaetes, cestodes, turbellarians, copepods — that could have dramatic impact on their individual fitness and larger-scale population dynamics (Mouritsen & Poulin 2002). A deeper understanding of how salinity affects the prevalence and intensity of parasitic infection in waterbirds is much needed. Understanding such a link will enhance our ability to predict how birds will respond to changes in salinity — and other factors — predicted by some climate-change scenarios.

CLIMATE-RELATED SALINITY CHANGES AND ITS POTENTIAL IMPACTS

Until now, most climate-related waterbird research has focused on potential shifts in phenology, distribution and abundance driven by changes in temperature, rainfall and sea level (e.g., Austin & Rehfisch 2003; Rehfisch & Crick 2003; Rehfisch *et al.* 2004; Maclean *et al.* 2007; Cox 2010; Senner 2012; Iwamura *et al.* 2013). However, as of yet, there is only a very limited literature dealing with the potential effects of climate-induced salinity changes on the distribution and performance of waterbirds occurring in either coastal or inland wetlands. While such shifts are expected to occur in concert with rising global temperatures, both the direction and magnitude of change vary regionally and may thus affect different waterbird populations differently.

Coastal wetlands are particularly at risk from the predicted effects of global climate change (IPCC 2001a). Global mean sea level is projected to rise between 0.09 and 0.88 m by 2100 (IPCC 2001b), thereby salinizing brackish and freshwater coastal wetlands. Overall, models predict a systematic ‘freshening’ at both poleward ends and increasing salinitities at low latitudes, although most studies suggest that future changes will be regionally variable (e.g., Najjar *et al.* 2000; Gibson & Najjar 2000).

Climate change has been particularly evident in West Africa in the past 30 years. Droughts have led to a significant decrease in freshwater flow, leading to an increased salinity in the region (Cox 2010). These increases could affect the water-salt balance of millions of coastal waterbirds that spend the non-breeding season in the region. In the Banc d'Arguin, Mauritania, more than two million wintering shorebirds cope with relatively high salinities and temperatures without regular access to freshwater (Wolff & Smit 1990). Such conditions may be expected to cause heat (Klaassen 1990) and salt stress (Klaassen & Ens 1990). Indeed, heat and salt stress can potentially limit food consumption in shorebirds, especially in individuals preparing to migrate. Klaassen & Ens (1990) showed that both red knots and sanderlings *Calidris alba* reduced their food intake when they were switched from fresh- to seawater under experimental conditions. Moreover, Klaassen *et al.* (1990) showed that, in captive shorebirds fed with artificial food, digestibility decreased by 2.1% for each degree rise in the air temperature. Assuming this phenomenon also applies to natural food, birds should eat more to compensate for decreased prey digestibility at high temperatures (Zwarts *et al.* 1990) and increased energetic costs at high salinities (Gutiérrez *et al.* 2011a).

Similar problems could be found along the northern coast of Australia, where projections for future climatic changes indicate substantial increases in mean temperatures (Hughes 2003), which in turn will affect salinity regimes. Battley *et al.* (2003) found evidence for heat-load problems in great knots *Calidris tenuirostris* during fuelling at Roebuck Bay, northwest Australia. Although birds might alleviate heat stress through heat-reduction behaviours such as ptiloerection, panting, gular fluttering, belly soaking, or maintaining contact between their feet and relatively cooler seawater (e.g., Klaassen 1990; Battley *et al.* 2003; Amat & Masero 2007), the high temperature and solar radiation levels of tropical coasts elevate water loss through evaporation, *via* respiration or through the skin (see Ro & McWilliams 2010). To compensate for this water loss, birds would need very well-developed osmoregulatory organs that allow them to excrete highly concentrated solutions and obtain salt-free water from prey.

In the near future, changes in seawater salinity are also predicted for European marine ecosystems, although these will be regionally variable and dependent on circulation patterns (Philippart *et al.* 2011). For example, the salinity of the Baltic Sea is expected to decrease as a result of increasing precipitation during winter (Philippart *et al.* 2011). In contrast, modelling studies predict an increase in salinity in the North Atlantic, generated by higher evaporation rates in the tropics (Bethke *et al.* 2006). Such changes are thought to have a major influence on the distribution of waterbird species, as salinity is a major factor affecting the abundance and distribution of food resources for waterbirds and, therefore, waterbird distributions themselves (Ysebaert *et al.* 2000, 2003).

Climate change is not the only component of anthropogenic global change producing changes in salinity. Increasing irrigation, damming, and water diversion either for agricultural or urban uses could result in increased salinization at many of the world's most important waterbird sites. The problem of water salinization in inland wetlands has been addressed by Rubega & Robinson (1997). Focusing on arid lands of western North America, they assessed the direct and indirect effects of salinization, as well as possible management techniques for reducing or eliminating its impacts on shorebird populations. Aside from the direct effects of increased salinity alluded to in previous sections, they also discussed that salinization could also result in severe reductions in biodiversity and abundance of food resources, which may be catastrophic for certain shorebirds (e.g., Rubega & Inouye 1994). Understanding such a relationship is thus essential for predicting future global change scenarios.

CONCLUSIONS AND FUTURE DIRECTIONS

Research on avian osmoregulation makes clear that environmental salinity induces a number of adaptations and adjustments, which critically influence, or even delimit, the distribution of bird species. Phenotypic flexibility in the osmoregulatory system of migratory waterbirds appears to be critically important in allowing birds to successfully overcome osmotic challenges faced during the course of their annual cycles. There is growing evidence that living in saline environments entails significant energetic costs and this could play a significant role in an individual's energy budget, affecting patterns of habitat, diet selection or immunocompetence. Management of freshwater outflows into coastal and inland wetlands is therefore critical for the conservation of many waterbird species (Bildstein 1990; Woodin 1994; Rubega & Robinson 1997; Ravenscroft & Beardall 2003).

As pointed out by Hughes (2003), a comparison of species that seasonally move between freshwater and seawater offers the opportunity to examine adjustments in osmoregulatory features and a comparison of inland and coastal populations of the same species offers a unique opportunity to examine the ecological and genetic basis of osmotic tolerance. Accordingly, more detailed information on the osmoregulatory physiology in different species and populations of waterbirds is needed for empirical tests of hypotheses about the likely consequences of global change and the proper design of conservation strategies.

Despite the considerable effort to examine the effects of salinity *per se* on various life-history traits by experimentally acclimating birds to different salinity levels, we need to design experiments capable of determining the effects of salinity when birds are simultaneously faced with other physiological challenges (e.g., thermoregulation, moult, migratory fuelling). This approach will be useful in identifying potential trade-offs with osmoregulation and could generate more biologically meaningful estimates of environmental tolerance. As has been noted, salinity interacts with other abiotic and biotic factors in complex ways that can critically affect waterbirds and the prey upon which they depend. For example, several authors have shown that osmoregulation and thermoregulation are physiological processes that are intimately linked (e.g., Skadhauge 1981; Verboven & Piersma 1995; Gutiérrez *et al.* 2012a). As a result, climatic-induced increases in both temperature and salinity may have significant impacts on the performance of waterbirds. Such interactive effects of salinity and temperature can be relatively easily quantified by performing laboratory-controlled experiments in which both variables are manipulated but the remainder are held constant. Our understanding of avian ecophysiological responses — and their limits — to saline environments would be greatly improved by combining the effects of different environmental factors.

Unravelling how salinity influences the links within- and between-host disease processes remains another important challenge, especially in the face of global climate change. Changes in salinity have the potential to affect parasite development and survival rates, disease transmission, and host susceptibility (e.g., Mouritsen 2002; Lei & Poulin 2011). Moreover, salinity itself can have immunosuppressive effects (Gutiérrez *et al.* 2013), which may have significant consequences for waterbirds that periodically alternate between fresh- and saltwater habitats. Hence, further work is necessary to investigate the effect of salinity on the different components of the immune system — innate, humoral, and cell-mediated.

While several experimental studies have investigated the short-term effects of salinity on different osmoregulatory traits, the possibility that other environmental factors or exogenous stimulus could influence the osmoregulatory ability in birds have has not been formally addressed. Burger & Gochfeld (1984) suggested that endogenous control of saltglands would be advantageous for birds seasonally moving between saline and freshwater habitats. Indeed, the ability to adjust the size and activity of saltglands in absence of salt loading might mitigate both short-term physiological costs when arriving in saline environments and potentially deleterious carry-over effects from one season to the next. The underlying mechanisms behind this endogenous control, however, remain unknown. As previously pointed by Burger & Gochfeld (1984) and Gutiérrez *et al.* (2013), the relationships between the size and activity of osmoregulatory organs, endocrine factors, and other aspects of migration physiology should be another important avenue for future work.

An integration of knowledge on physiological and behavioral responses to salinity and the relative tolerance of species is critical for understanding community level impacts of salinity changes, whether natural or anthropogenically induced.

AKNOWLEGMENTS.— Foremost I would like to acknowledge the major role played by José A. Masero, Juan M. Sánchez-Guzmán and Theunis Piersma in developing this project. I thank Jordi Figuerola and Juan A. Amat for encouraging me to write this article and commenting most helpfully upon it. JAM, TP, Nathan R. Senner, Pablo Sabat and two anonymous reviewers gave helpful comments on the manuscript. NRS kindly improved the English. Manuel Parejo provided the schematic drawing represented in Fig. 1. Much of the thinking behind this paper was carried out for a doctoral thesis funded by the Government of Extremadura (PRE07034).

BIBLIOGRAPHY

ABAD-GÓMEZ, J. M., GUTIÉRREZ, J. S., VILLEGAS, A., SÁNCHEZ-GUZMÁN, J. M., NAVEDO, J. G. & MASERO, J. A. 2013. Time course and metabolic costs of a humoral immune response in the little ringed plover *Charadrius dubius*. *Physiological and Biochemical Zoology*, 86: 354-60

ADAIR, S. E., MOORE, J. L. & KIEL, W. H., JR 1996. Wintering diving duck use of coastal ponds: an analysis of alternative hypotheses. *Journal of Wildlife Management*, 60: 83-93.

AMAT, J. A. & MASERO, J. A. 2007. The functions of belly-soaking in Kentish Plovers *Charadrius alexandrinus*. *Ibis*, 149: 91–97.

AUSTIN, G. E & REHFISCH, M. M. 2006. The likely impact of sea level rise on waders (Charadrii) wintering on estuaries. *Journal for Nature Conservation*, 11: 43–58.

BATTLEY, P. F., ROGERS, D. I., PIERSMA, T. & KOOLHAAS, A. 2003. Behavioural evidence for heat-load problems in great knots in tropical Australia fuelling for long-distance flight. *Emu*, 103: 97–103.

BARNES, G. G. & NUDDS, T. D.1991. Salt tolerance in American Black ducks, Mallards, and their F-l hybrids. *Auk*, 108: 89-98.

BENNETT, D. C & HUGHES, M. R. 2003. Comparison of renal and salt gland function in three species of wild ducks. *Journal of Experimental Biology*, 206, 3273 - 3284.

BETHKE I., FUREVIK, T. & DRANGE, H. 2006. Towards a more saline North Atlantic and a fresher Arctic under global warming. *Geophysical Research Letters*, 33: L21712.

BENTLEY, P. J. 2002. *Endocrines and osmoregulation: A comparative account in vertebrates*, 2nd edn. Springer-Verlag, Berlin.

BILDSTEIN, K. L. 1990. Status, conservation and management of the Scarlet Ibis (*Eudocimus ruber*) in the Caroni Swamp, Trinidad, West Indies. *Biological Conservation*, 54: 61–78.

BLAKEY, R., ZHARIKOV, Y. & SKILLETER, G. A. 2006. Lack of an osmotic constraint on intake rate of the eastern curlew (*Numenius madagascariensis*). *Journal of Avian Biology*, 37: 299–305.

BRADLEY, T. J. *Animal osmoregulation*. Oxford University Press Inc., New York.

BRAUN, E. J. 1999. Integration of organ system in avian osmoregulation. *Journal of Experimental Zoology*, 238: 702–707.

BRUINZEL, L. W. & PIERSMA, T., 1998. Cost reduction in the cold: heat generated by terrestrial locomotion partly substitutes for thermoregulation costs in Knot *Calidris canutus*. *Ibis*, 140: 323-328.

BRYANT, D. M. & FURNESS, R. W. 1995. Basal metabolic rates of North-Atlantic seabirds. *Ibis,* 137: 219–226.

BURGER, J. & GOCHFELD, M. 1984. Seasonal variation in size and function of the nasal salt gland of the Franklin's Gull (*Larus pipixcan*). *Comparative and Biochemical Physiology*, 77: 103–110.

BUEHLER, D. M., KOOLHAAS, A., VAN'T HOF, T. J., SCHWABL, I., DEKINGA, A., PIERSMA, T. & TIELEMAN, B. I. 2009. No evidence for melatonin-linked immunoenhancement over the annual cycle of an avian species. *Journal of Comparative Physiology* A, 195: 445–451.

BUTLER, D. G., SIWANOWICZ, H. & PUSKAS, D. 1989. A re-evaluation of experimental evidence for the hormonal control of avian nasal salt glands. In:

Hughes, M. R., Chadwick, A. (eds) *Progress in avian osmoregulation*. Leeds Philosophical and Literary Society, Leeds, UK, pp. 127-141.

CANTIN, M., BEDARD, J. & MILNE, H. 1974. The food and feeding of common eiders in the St. Lawrence estuary in summer. *Canadian Journal of Zoology*, 52: 319-334.

CERVENCL, A., ALVAREZ FERNANDEZ, A. 2012. Winter distribution of Greater Scaup *Aythya marila* in relation to available food resources. *Journal of Sea Research*, 73: 41-48.

CHING, A. C. T., HUGHES, M. R., POON, A. M. S. & PANG, S. F. 1999. Melatonin receptors and melatonin inhibition of duck salt gland secretion. *General Comparative Endocrinology*, 116: 229–240.

COOCH, F. G. 1964. A preliminary study of the survival value of a functional salt gland in prairie Anatidae. *Auk*, 81: 380-93.

COX, G. W. 2010. *Bird Migration and Global Change*. Island Press, Washington, D.C.

CROCKER, A.D. & HOLMES, W.N. 1971. Intestinal absorption in ducklings (*Anas platyrhynchos*) maintained on fresh water and hypertonic saline. *Comparative and Biochemical Physiology A* 40: 203–211.

DANTZLER, W. H. 1970. Kidney function in desert vertebrates. *In* G. K. Benson and J. G. Phillips (eds.), *Hormones and the Environment,* pp. 157–189, Cambridge University Press, Cambridge,.

DARLINGTON, P. J. 1957. *Zoogeography: The geographical distribution of animals*. John Wiley & Sons, Inc., New York.

DARWIN, C. R. 1839. *Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world*. George Routledge, London.

DEVINK, J.-M. A., GILCHRIST, H. G. & DIAMOND, A. W. 2005. Effects of water salinity on growth and survival of common eider (*Somateria mollissima*) ducklings. *Auk*, 122: 523-529.

DOSCH, J. J. 1997. Salt tolerance of nestling Laughing Gulls: An experimental field investigation. *Colonial Waterbirds*, 20: 449–457.

ELLIS, H.I. 1984. Energetics of free-ranging seabirds. In: Whittow, G. C, Rahn H. eds. *Seabird energetics*. New York: Plenum Press. 203–234.

ELLIS, R. A., GOERTEMILLER, C. C., DELELLIS, R. A. AND KABLOTSKY, Y. H. 1963. The effect of a saltwater regimen on the salt glands of domestic ducklings. *Developmental Biology*, 8: 286-308.

ENSOR, D. M. & PHILLIPS J. G. 1970. The effect of salt loading on the pituitary prolactin levels of the domestic duck (*Anas platyrhynchos*) and juvenile herring or lesser black-backed gulls (*Larus argentatus* or *Larus fuscus*). *Journal of Endocrinology*, 48: 167-172.

ENSOR, D. M., & PHILLIPS, J. G. 1972. The effect of age and environment on extrarenal excretion in juvenile gulls (*Larus argentatus* and *L. fuscus*). *Journal of Zoology*, 168: 119-126.

ESTRELLA, S. M., MASERO, J. A. & PÉREZ-HURTADO, A. 2007. Small prey profitability: field analysis of shorebirds' use of surface tension of water to transport prey. *Auk* 124, 1244–1253.

EVANS, D. H. 2009. *Osmotic and Ionic Regulation: Cells and Animals*. CRC Press, Boca Raton, FL.

FIGUEROLA, J. 1999. Effects of salinity on rates of infestation of waterbirds by haematozoa. *Ecography*, 22: 681–685.

GIBSON, J. R. & NAJJAR, R. G. 2000. The response of Chesapeake Bay salinity to climate-induced changes in streamflow. *Limnol. Oceanogr.*, 45(8): 1764–1772.

GOLDSTEIN, D. L. 1993. Renal response to saline infusion in chicks of Leach's storm petrels (*Oceanodroma leucorhoa*). *Journal of Comparative Physiology* B 163, 167-173.

GOLDSTEIN, D. L. 1999. Patterns of variation in avian osmoregulatory physiology and their application to questions in ecology. In: Adams, N.J. & Slotow, R.H. (eds) Proc. 22 Int. Ornithol. Congr., Durban: 1417-1426. Johannesburg: BirdLife South Africa.

GOLDSTEIN, D. L. 2002. Water and salt balance in seabirds. In *Biology of Marine Birds* (ed. E. A. Schreiber and J. Burger), pp. 467–483. CRC Press, New York.

GOLDSTEIN, D. L. 1989. Transport of water and electrolytes by the lower intestine and its contribution to avian osmoregulation. In *Avian Osmoregulation* (ed. M. R. Hughes and A. Chadwick), pp. 271–294. Leeds Philosophical and Literary Society, Leeds.

GOLDSTEIN, D. L. & BRAUN, E. J. 1989. Structure and concentrating ability in the avian kidney. *American Journal of Physiology*, 256: R501-R509.

GOLDSTEIN, D. L. & SKADHAUGE, E. 2000. Renal and extrarenal regulation of body fluid composition. *Sturkey's Avian Physiology* (ed. G.C. Whittow), pp. 265–297, Academic Press, New York.

GREEN, J. A., BUTLER, P. J., WOAKES, A. J. & BOYD, I. L. 2004. Energetics of the moult fast in macaroni penguins *Eudyptes chrysolophus*. *Journal of Avian Biology*, 35: 153-161.

GUILLEMETTE, M., PELLETIER, D., GRANDBOIS, J. M., BUTLER, P. J. 2007. Flightlessness and the energetic cost of wing moult in a large sea duck. *Ecology*, 88: 2936–2945.

GUOZHEN, Q. & HONGFA, X. 1986. Molt and resting metabolic rate in the common teal *Anas crecca* and the shoveller *Anas clypeata*. *Acta Zoologica Sinica*, 32: 73-84.

GUTIÉRREZ, J. S., MASERO, J. A., ABAD-GÓMEZ, J. M., VILLEGAS, A. & SÁNCHEZ-GUZMÁN, J. M. 2011a. Understanding the energetic costs of living in saline environments: effects of salinity on basal metabolic rate, body mass and daily energy consumption of a long-distance migratory shorebird. *Journal of Experimental Biology*, 214: 829–835

GUTIÉRREZ J. S., MASERO, J. A., ABAD-GÓMEZ, J. M., VILLEGAS, A. & SÁNCHEZ-GUZMÁN, J. M. 2011b. Metabolic consequences of overlapping food restriction and cell-mediated immune response in a long-distance migratory shorebird, the little ringed plover *Charadrius dubius*. *Journal of Avian Biology*, 42: 259-265.

GUTIÉRREZ, J. S., DIETZ, M. W., MASERO, J. A., GILL, R. E. JR., DEKINGA, A., BATTLEY, P. F., SÁNCHEZ-GUZMÁN, J. M. & PIERSMA, T. 2012a. Functional ecology of saltglands in shorebirds: flexible responses to variable environmental conditions. *Functional Ecology*, 26: 236–244.

GUTIÉRREZ, J.S., ABAD-GÓMEZ, J.M., SÁNCHEZ-GUZMÁN, J.M., NAVEDO, J.G. & MASERO, J.A. 2012b. Avian BMR in marine and non-marine habitats: a test using shorebirds. *PLoS ONE*, 7(7): e42206.

GUTIÉRREZ, J. S., ABAD-GÓMEZ, J. M., VILLEGAS, A. & SÁNCHEZ-GUZMÁN, J. M. & MASERO, J. A. 2013. Effects of salinity on the immune response of an ‘osmotic generalist’ bird. *Oecologia*, 171: 61–69.

HADLEY, N. F. 1994. *Water relations of terrestrial arthropods*. Academic Press, London.

HANNAM, M. K., ORING, L.W. & HERZOG, M. P. 2003. Impacts of salinity on growth and behavior of American Avocet chicks. *Waterbirds*, 26: 119–125.

HARVEY, S. & PHILLIPS, J. G. 1980. Growth, growth hormone and corticosterone secretion in freshwater and saline-adapted ducklings (*Anas platyrhynchos*). *General Comparative Endocrinology*, 42: 334–344.

HASSELQUIST, D. 2007. Comparative immunoecology in birds: hypotheses and tests. *Journal of Ornithology*, 148: S571–S582.

HILDEBRANDT, J. P. 1997. Changes in Na^+/K^+-ATPase expression during adaptive cell differentiation in avian nasal salt gland. *Journal of Experimental Biology*, 200: 1895–1904.

HILDEBRANDT, J. P. 2001. Coping with excess salt: adaptive functions of extrarenal osmoregulatory organs in vertebrates. *Zoology*, 104: 209-220.

HOLMES, W. N. 1975. Hormones and osmoregulation in marine birds. *General and Comparative Endocrinology*, 25, 249-258.

HOLMES, W. N. & PHILLIPS, J. G. 1985. The avian salt gland. *Biological Reviews*, 60: 213 256.

HOLMES, W. N., FLETCHER, G. L. & STEWART, D. J. 1968. The patterns of renal electrolyte excretion in the duck (*Anas platyrhynchos*) maintained on freshwater and on hypertonic saline. *Journal of Experimental Biology* 45: 487-508.

HUGHES, L. 2003. Climate change and Australia: trends, projections and impacts. *Austral Ecology*, 28: 423–443.

HUGHES, M. R., 1991. Integrative aspects of osmoregulation in birds. *Acta Congressus Internationalis Ornithologici*, 20: 2138–2146.

HUGHES, M. R. 2003. Regulation of salt gland, gut and kidney interactions. *Comparative Biochemistry and Physiology* A, 136: 507–524.

HUGHES, M.R., BENNETT, D.C. & SULLIVAN, T.M. 2002. Effect of saline drinking water on the size and water content of the gut and other organs of male and female mallards. *Canadian Journal of Zoology* 80, 70–76.

IPCC 2001a. *Special report on the regional impacts of climate change*. Intergovernmental Panel on Climate Change. Available at: http://www.ipcc.ch

IPCC 2001b. *Third report of the working group of the intergovernmental panel on climate change*. Intergovernmental Panel on Climate Change. Available at: http:/www.ipcc.ch

IWAMURA, T, POSSINGHAM, H. P., CHADÈS, I., MINTON, C., MURRAY, N. J., ROGERS, D. I., TREML, E. A. & FULLER, R. A. 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proceedings of the Royal Society of London B*, 280: 20130325.

JACOBSON, L. L. 1813. Sur une glande conglomérée appartenant à la cavité nasale. *Bulletin de la Société Philomatique de Paris*, 3: 267.

JANES, D. N. 1997. Osmoregulation by Adelie penguin chicks on the Antarctic Peninsula. *Auk*, 114: 488-495

JOHNSTON, J. W. & BILDSTEIN, K. L. 1990. Dietary salt as a physiological constraint in white ibis breeding in an estuary. *Physiological Zoology,* 63: 190–207.

JOVANI, R., TELLA, J. L., FORERO, M. G., BERTELLOTTI, M., BLANCO, G., CEBALLOS, O. & DONAZAR, J. A. 2001. Apparent absence of blood parasites in the patagonian seabird community: is it related to the marine environment? *Waterbirds*, 24:430–433.

KALISIŃSKA, E., DAŃCZAK, A., PIERKO, M. & WYSOCKI, D. 1999. Relationships between kidney mass and body size in some Anseriformes. *Anatomia, Histologia, Embryologia*, 28: 55-59.

KLAASSEN, M. & ENS, B. J. 1990. Is salt stress a problem for waders wintering on the Banc d'Arguin, Mauritania? *Ardea*, 78: 67–74.

KLAASSEN, M., KERSTEN, M. & ENS, B. J. 1990. Energetic requirements for maintenance and premigratory body mass gain of waders wintering in Africa. *Ardea*, 78: 209-220.

KUSHLAN, J. A. 1977a. Population energetics of the American White Ibis. *Auk*, 94: 114-122.

KUSHLAN, J. A. 1977b. Growth energetics of the White Ibis. *Condor*, 79: 31-36.

KVIST, A. & LINDSTRÖM, Å. 2003. Gluttony in migratory waders – unprecedented energy assimilation rates in vertebrates. *Oikos*, 103: 397–402.

LAVERTY, G. & SKADHAUGE, E. 2008. Adaptive strategies for post-renal handling of urine in birds. *Comparative and Biochemical Physiology A*, 149A: 246-254

LEI, F. & POULIN, R. 2011. Effects of salinity on multiplication and transmission of an intertidal trematode parasite. *Marine Biology*, 158: 995–1003.

LINDSTRÖM, Å. 2003. Fuel deposition rates in migrating birds: causes, constraints and consequences. In *Avian migration* (eds P. Berthold, E. Gwinner & E. Sonnenschein), pp. 307–320. Berlin, Germany: Springer.

MACLEAN, I. M. D, REHFISCH, M. M, DELANY, S. & ROBINSON, R. A. 2007. *The Effects of Climate Change on Migratory Waterbirds within the African-Eurasian Flyway*. British Trust for Ornithology.

MAHONEY, S. & JEHL, J. R. JR. (1985a) Adaptations of migratory shorebirds to highly saline and alkaline lakes: Wilson’s Phalarope and American Avocet. *Condor*, 87: 520-527.

MAHONEY, S. & JEHL, J. R. JR. (1985b) Avoidance of salt loading by a diving bird at a hypersaline and alkaline lake: Eared Grebe. *Condor*, 87: 389-397.

MAHONEY, S. & JEHL, J. R. JR. (1985c) Physiological ecology and salt loading of California Gulls at an alkaline, hypersaline lake. *Physiological Zoology*, 58: 553-563.

MARTIN, L. B., GILLIAM, J., HAN, P., LEE, K. A. & WIKELSKI, M. 2005. Corticosterone suppresses immune function in temperate but not tropical house sparrows, *Passer domesticus*. *General and Comparative Endocrinology*, 140: 126-135.

MASERO, J.A. 2002. Why don't Red Knots *Calidris canutus* feed extensively on the crustacean *Artemia*? *Bird Study*, 49: 304–306.

McNAB, B. K. 2002. *The physiological ecology of vertebrates. A view from energetics*. Cornell University Press, Ithaca.

McNAB, B. K. 2009. Ecological factors affect the level and scaling of avian BMR. *Comparative Biochemistry and Physiology* A 152: 22–45.

McWHORTER, T. J., CAVIEDES-VIDAL, E. & KARASOV, W. H. 2009. The integration of digestion and osmoregulation in the avian gut. *Biological Reviews*, 84: 533-565.

MENDES, L., PIERSMA, T., LECOQ, M., SPAANS, B., RICKLEFS, R. E. 2005. Disease-limited distributions? Contrasts in the prevalence of avian malaria in shorebird species using marine and freshwater habitats. *Oikos*, 109: 396–404.

MOORMAN, A. M., MOORMAN, T. E., BALDASSARRE, G. A. & RICHARD, D. M. 1991. Effects of saline water on growth and survival of Mottled Duck ducklings in Louisiana. *Journal of Wildlife Management*, 55: 471-476.

NAGY, K. A. 2005. Field metabolic rate and body size. *Journal of Experimental Biology* 208: 1621–1625.

NAJJAR, R. G. *et al.* 2000. The potential impacts of climate change on the mid-Atlantic coastal region. *Climate Research*, 14: 219–233.

NELHS, G. 1996. Low costs of salt turnover in common eiders *Somateria mollissima*. *Ardea*, 84: 23-30.

NITZSCH, C. L. 1820. Ueber die Nasendrüse der Vögel. *Deutsches Archiv für die Physiologie (Meckel's Archiv)* 6: 234-269.

NYSTRÖM, K. G. K. & PEHRSSON, O. 1988. Salinity as a constraint affecting food and habitat choice of mussel-feeding diving ducks. *Ibis*, 130: 94–110.

NYSTRÖM, K. G. K., PEHRSSON, O. & BROMAN, D. 1991. Food of juvenile common eiders (*Somateria mollissima*) in areas of high and low salinity. *Auk*, 108: 250–256.

O'CONNOR, R. J. 1984. *The growth and development of birds*. Wiley, New York.

PEAKER, M. 1971. Avian salt gland. *Philosophical Transactions of the Royal Society of London* B, 262: 289–300.

PEAKER, M., LINZELL, J. L. 1975. *Salt glands in birds and reptiles*. Cambridge University Press, Cambridge.

PEÑA-VILLALOBOS, I., VALDÉS-FERRANTY, F. & SABAT, P. 2013. Osmoregulatory and metabolic costs of salt excretion in the Rufous-collared sparrow *Zonotrichia capensis*. *Comparative Biochemistry and Physiology Part A*, 164 (2), 314–318.

PHILIPPART, C.J.M., ANADÓN, R., DANOVARO, R., DIPPNER, J. W., DRINKWATER, K. F., HAWKINS, S. J., OGUZ, T., O'SULLIVAN, G. & REID, P. C. 2011. Impacts of climate change on European marine ecosystems: Observations, expectations and indicators. *Journal of Experimental Marine Biology and Ecology*, 400: 52–69.

PHILLIPS, J. G. & ENSOR, D. M. (1972) The significance of environmental factors in the hormone mediated changes of nasal (salt) gland activity in birds. *General and Comparative Endocrinology Supplement,* 3: 393-404.

PIERSMA, T. 1997. Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? *Oikos* 80: 623–631.

PIERSMA, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. *Integrative and Comparative Biology*, 42: 51–67

PIERSMA, T. 2003. ‘Coastal’ versus ‘inland’ shorebird species: interlinked fundamental dichotomies between their life- and demographic histories? *Wader Study Group Bulletin*, 100: 5-9.

PIERSMA, T. & LINDSTRÖM, Å. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends in Ecology and Evolution*, 12: 134–138.

PIERSMA, T. & GILL, R. E. JR .1998. Guts don’t fly: small digestive organs in obese bar-tailed godwits. *Auk*, 115: 196–203.

PIERSMA, T. & VAN GILS, J.A. 2011. *The Flexible Phenotype. A Body-Centred Integration of Ecology, Physiology, and Behaviour*. Oxford University Press, Oxford.

PIERSMA, T., CADEE, N. & DAAN, S. 1995. Seasonality in basal metabolic rate and conductance in a long-distance migrant shorebird, the knot. *Journal of Comparative Physiology*, 165:37-45

PIERSMA, T., VAN GILS, J. & WIERSMA, P. 1996. Family Scolopacidae (sandpipers, snipes and phalaropes). In: del Hoyo, J., Elliott, A, & Sargatal. J. (eds) *Handbook of the Birds of the World*, *Vol. 3: Hoatzin to Auks*. Lynx Edicions, Barcelona, pp. 444–533.

PIERSMA, T., DEKINGA, A., VAN GILS, J. A., ACHTERKAMP, B., VISSER, G. H. 2003. Cost-benefit analysis of mollusc-eating in a shorebird I. Foraging and processing costs estimated by the doubly labelled water method. *Journal of Experimental Biology* 206: 3361–3368.

PIERSMA T., BRUINZEEL, L., DRENT, R., KERSTEN, M., VAN DER MEER, J., & WIERSMA, P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (red knots, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology* 69:191–217.

PORTUGAL, S. J., GREEN, J. A. & BUTLER, P. J. 2007. Annual changes in body mass and resting metabolism in captive barnacle geese (*Branta leucopsis*): the importance of wing moult. *Journal of Experimental Biology*, 210: 1391–1397.

PURDUE, J. R. & HAINES, H. 1977. Salt water tolerance and water turnover in the Snowy Plover. *Auk*, 94: 248–255

QUILLFELDT, P., ARRIERO, E., MARTÍNEZ, J., MASELLO, J. F. & MERINO, S. 2011. Prevalence of blood parasites in seabirds – a review. *Frontiers in Zoology* 8: 26.

RAHN, H. & WHITTOW, G. C. 1984. Comparison of embryonic development in birds and mammals: birth weight, time and cost. In: Taylor C.R., Johanssen, K. & Bollis L, eds. *A Comparison to Animal Physiology*. Cambridge: Cambridge University Press. 124–137.

RAVENSCROFT, N. O. M. & BEARDALL, C. H. 2003. The importance of freshwater flows over estuarine mudflats for wintering waders and wildfowl. *Biological Conservation*, 113: 89–97.

REHFISCH M. M., & CRICK, H. Q. P. 2003. Predicting the impact of climatic change on Arctic-breeding waders. *Wader Study Group Bulletin*, 100: 86-95.

REHFISCH, M. M., AUSTIN, G. E., FREEMAN, S. N., ARMITAGE, M. J. S. & BURTON, NHK. 2004. The possible impact of climate change on the future distributions and numbers of waders on Britain's non-estuarine coast. *Ibis*, 146: 70–81.

RO, J. & WILLIAMS, J. B. 2010. Respiratory and cutaneous water loss of temperate-zone passerine birds. *Comparative Biochemistry and Physiology*, 156: 237-246.

BERTS, J. R., HUGHES, M. R., 1984. Saline acclimation and water and sodium transport across avian small intestine. *American Journal of Physiology*, 247: R246–R249.

RUBEGA, M. A. 1997. Surface tension prey transport in shorebirds: How widespread is it? *Ibis*, 139:488–493.

RUBEGA, M.A. & ROBINSON, J.A. 1997. Water salinization and shorebirds: emerging issues. *International Wader Studies*, 9: 45–54.

RUBEGA, M. A. & INOUYE, C. 1994. Prey switching in red-necked phalaropes *Phalaropus lobatus*: Feeding limitations, the functional response and water Management at Mono Lake, California, USA. *Biological Conservation*, 70: 205–210.

SABAT, P. 2000. Birds in marine and saline environments: living in dry habitats. *Revista Chilena de Historia Natural*, 73: 401–410.

SABAT, P., MALDONADO, K., RIVERA-HUTINEL, A. & FARFAN, G., 2004. Coping with salt without salt glands: osmoregulatory plasticity in three species of coastal songbirds (ovenbirds) of the genus Cinclodes (Passeriformes: Furnariidae). *Comparative and Biochemical Physiology* B, 174: 415–420.

SABAT, P., MALDONADO, K., CANALS, M. & RIO, C. M. D. 2006a. Osmoregulation and adaptive radiation in the ovenbird genus *Cinclodes* (Passeriformes: Furnariidae). *Functional Ecology*, 20: 799–805.

SABAT, P., MALDONADO, K., FARIÑA, J. M. & RIO, C. M. D. 2006b Osmoregulatory capacity and the ability to use marine food sources in two coastal songbirds (*Cinclodes*: Furnariidae) along a latitudinal gradient. *Oecologia*, 148: 250–257.

SCHMIDT-NIELSEN, K. 1959. Salt glands. *Scientific American*, 200: 109-116.

SCHMIDT-NIELSEN, K. 1960. The salt-secreting gland of marine birds. *Circulation*, 21: 955–967.

SCHMIDT-NIELSEN, K. 1997. *Animal physiology: Adaptation and environment*. Cambridge University Press, New York.

SCHMIDT-NIELSEN, K & FANGE, R. 1958. Salt glands in marine reptiles. *Nature*, 182: 783-785.

SCHMIDT-NIELSEN, K. & KIM, Y. T. 1964. The effect of salt intake on the size and function of the salt gland of ducks. *Auk*, 81: 60–172.

SCHMIDT-NIELSEN, K., JÖRGENSEN, C. B. & OSAKI, H. 1957. Secretion of hypertonic solutions in marine birds. *Federation Proceedings*, 16: 113.

SCHMIDT-NIELSEN, K., JÖRGENSEN, C. B. & OSAKI, H. 1958. Extrarenal salt excretion in birds. *American Journal of Physiology*, 193: 101–107.

SCHMIDT-NIELSEN, K., BORUT, A., LEE, P. & CRAWFORD, E. C. 1963. Nasal salt excretion and the possible function of the cloaca in water conservation. *Science*, 142: 1300–1301.

SHUTTLEWORTH, T. J. & HILDEBRANDT, J. P. 1999. Vertebrate salt glands: short- and long-term regulation of function. *Journal of Experimental Zoology*, 283: 689-701.

SENNER N. R. 2012. One species but two patterns: populations of the Hudsonian godwit (*Limosa haemastica*) differ in spring migration timing. *Auk*, 129: 670-682.

SIMON, E. 1982. The osmoregulatory system of birds with salt glands. *Comparative and Biochemical Physiology*, 71A: 547-556.

SKADHAUGE, E. 1981. *Osmoregulation in birds*. Springer-Verlag, Berlin.

STAALAND, H. 1967. Anatomical and physiological adaptations of the nasal glands in Charadriiformes birds. *Comparative Biochemistry and Physiology*, 23: 933–944.

STURKIE, P. D. 1976. Kidneys, extrarenal salt excretion, and urine. In: *Avian Physiology*, pp. 264-285. Springer-Verlag, New York.

TECHNAU, G. 1936. Die Nasendrüse der Vögel. *Journal für Ornithologie*, 84: 511.

TIETJE, W. D. & TEER, J. G. (1996) Winter feeding ecology of northern shovelers on freshwater and saline wetlands in south Texas. *Journal of Wildlife Management*, 60: 843–855.

TSENG, Y. & HWANG, P. 2008. Some insights into energy metabolism for osmoregulation in fish. *Comparative Biochemistry and Physiology*, 148C: 419-429.

VERKUIL, Y., VAN DER HAVE, T. M., VAN DER WINDEN, J. & CHERNICHKO, I. I. 2003. Habitat use and diet selection of northward migrating waders in the Sivash (Ukraine): the use of Brine Shrimp *Artemia salina* in a variably saline lagoon complex. *Ardea,* 91(1): 71-83.

VÉZINA, F., JALVINGH, K. M., DEKINGA, A. & PIERSMA, T. 2006. Acclimation to different thermal conditions in a northerly wintering shorebird is driven by body mass-related changes in organ size. *Journal of Experimental Biology*. 209, 3141-3154.

VÉZINA, F., GUSTOWSKA, A., JALVINGH, K. M., CHASTEL, O. & PIERSMA, T. 2009. Hormonal correlates and thermoregulatory consequences of molting on metabolic rate in a northerly wintering shorebird. *Physiological and Biochemical Zoology,* 82: 129–142.

WOODIN, M. C. 1994. Use of saltwater and freshwater habitats by wintering redheads in southern Texas. *Hydrobiologia*, 279-280: 279-287.

YOHANNES, E., KRIŽANAUSKIENÈ, A., VALCU, M., BENSCH, S. & KEMPENAERS, B. 2009. Prevalence of malaria and related haemosporidian parasites in two shorebird species with different winter habitat distribution. *Journal of Ornithology*, 150: 287–291.

YSEBAERT, T., MEININGER, P. L., MEIRE, P., DEVOS, K., BERREVOETS, C. M., STRUCKER, R. C. W. & KUIJKEN, E. 2000. Waterbird communities along the estuarine salinity gradient of the Schelde estuary, NW- Europe. *Biodiversity Conservation*, 9: 1275–1296.

YSEBAERT, T, HERMAN, P.M.J., MEIRE, CRAEYMEERSCH, P., J., VERBEEK, H., HEIP, C.H.R. Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. *Estuarine, Coastal and Shelf Science*, 57: 335–355

ZERA, A. J. & HARSHMAN, L. G. 2001. The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics*, 32: 95–126.

ZWARTS, L., BLOMERT, A. M. & HUPKES, R. 1990. Increase of feeding time in waders preparing for spring migration from the Banc d’Arguin, Mauritania. *Ardea*, 78: 237-256.

Box 1. Terminology:

Adaptation, *acclimatization*, *acclimation*, and *phenotypic flexibility*

The terms *adaptation* and *acclimatization* are often used interchangeably in ecological and physiological studies, but — in evolutionary terms — they have different connotations. *Adaptation* usually refers to a long, slow process occurring over generations — and not in an individual organism — and is rarely reversible. For example, the presence of cephalic saltglands in secondarily marine vertebrates serves as an example of adaptation to marine environments. In contrast, *acclimatization* is a more rapid phenomenon, whereby a physiological or biochemical change occurs within the life of an individual animal, resulting from exposure to new conditions in the animal's environment. For example, short-term changes in the size of saltglands as a function of salt intake could be interpreted as acclimatization. *Acclimation* is normally used for similar processes occurring in the laboratory, in response to experimentally-imposed changes in conditions. An example of acclimation reviewed in this paper is the metabolic adjustments made by some captive waterbirds to different salinity levels. Overall, reversible changes as a result of acclimation or acclimatization in adult individuals are examples of *phenotypic flexibility*.

Table 1. Estimated energetic costs of osmoregulation and other physiological demands in waterbirds as a proportion of BMR.

demands/species	Details	change (%)	source
Osmoregulation			
ducks *Anas spp*.	Ion transport. Theoretical metabolic change using freshwater-acclimated ducks	+7	Peaker & Linzell (1975)
common eider *Somateria mollissima*	Ion transport in salt-acclimated (20‰) individuals receiving oral salt administrations (1.25, 2.5 or 5 g salt in 50 ml water	up to +100	Nehls (1996)
dunlin *Calidris alpina*	Birds maintained consecutively under freshwater (0‰), brackish water (10‰) and saltwater (33‰) regimes. Metabolic change refers to the difference between the freshwater and saltwater regimes	+17	Gutiérrez *et al.* (2011a)
Immune responsiveness			
little ringed plover *Charadrius dubius*	Birds challenged with sheep red blood cells to induce a humoral (primary and secondary) immune response. Metabolic change refers to the secondary response	+21	Abad-Gómez *et al.* (2013)
red knot *Calidris canutus canutus*	Birds injected with a vaccine containing diphtheria and tetanus toxoid to induce a primary and a secondary antibody response. Increment in BMR corresponds to the secondary response	+15	Mendes *et al.* (2006)

dunlin *Calidris alpina*	Birds injected with phytohaemagglutinin to induce inflammatory and metabolic responses	+16	Gutiérrez *et al.* (2011b)
ruff *Philomachus pugnax*	Birds injected with a vaccine containing diphtheria and tetanus toxoid to induce a primary and a secondary antibody response. Increment in BMR corresponds to the secondary antibody response	-13	Mendes *et al.* (2006)
Moult			
macaroni penguin *Eudyptes chyrsolophus*	Body plumage and primary feather moult. Metabolic change estimated as the difference between the average metabolic rate of female individuals during the moult and the breeding season	+40	Green *et al.* (2004)
barnacle goose *Branta leucopsis*	Wing moult in captive individuals. Metabolic change calculated as the difference of the rate of oxygen consumption between moulting and nonmoulting periods	+80	Portugal *et al.* (2007)
European shoveller *Anas clypeata*	Pre-nuptial plumage moult	+35	Guozhen & Hongfa (1986)
common teal *Anas crecca*	Pre-nuptial plumage moult	+25	Guozhen & Hongfa (1986)

common eider *Somateria mollissima*	Wing moult. Metabolic change estimated as the difference between the average metabolic rate (derived from heart rate data) during the pre-moult period and during the flightless period in the same individuals	+12	Guillemette *et al*. (2007)
red knot *Calidris canutus islandica*	Body moult and primary feather moult. Individuals measured while in full summer and winter plumage as well as during peak of moult	+10	Vézina *et al*. (2009)
Thermoregulation			
red knot *Calidris canutus islandica*	Cold acclimation. Same individuals measured at 10 and 25ºC while walking on a linear treadmill	+55	Bruinzeel & Piersma (1998)
red knot *Calidris canutus islandica*	Cold acclimation. Metabolic change estimated as the difference in metabolic rate between 4ºC- and 25ºC-acclimated birds	+26	Vézina *et al*. (2006)

1076

Fig. 1. Supraorbital saltglands of a shorebird. Note that the ducts (outlined by dashed lines) pass through the beak and empty into the anterior nasal cavity so that the secretion flows out through the nares.

Fig. 2. Pathways of water and ion influx and efflux and principal osmoregulatory organs in waterbirds (adapted from Goldstein 2002 and Hughes 2003).

Figure 1.

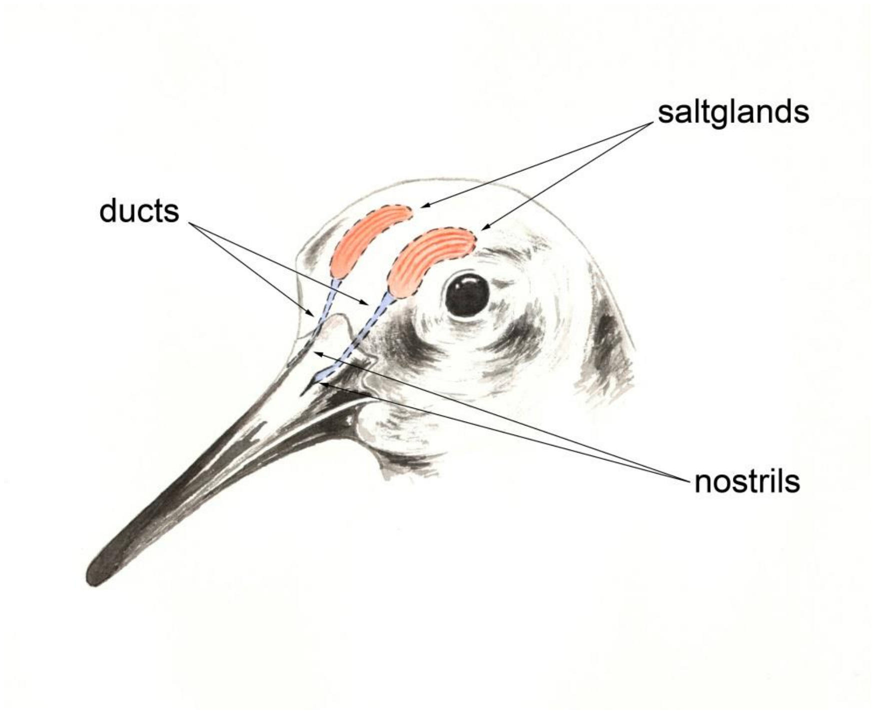
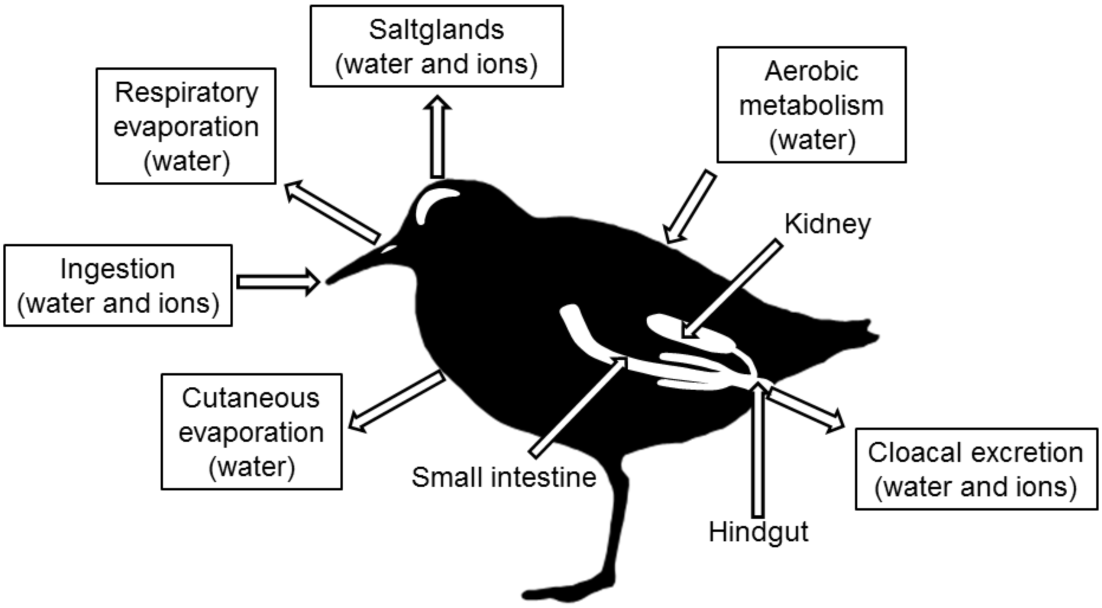


Figure 2.


Saltglands
(water and ions)
Respiratory evaporation (water)
Aerobic metabolism (water)
Kidney
Ingestion (water and ions)
Cutaneous evaporation (water)
Small intestine
Cloacal excretion (water and ions)
Hindgut