Living in Environments with Contrasting Salinities: A Review of Physiological and Behavioural Responses in Waterbirds

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Review

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

VIVIENDO EN AMBIENTES CON DISTINTAS SALINIDADES: UNA REVISIÓN DE RESPUESTAS FISIOLÓGICAS Y DE COMPORTAMIENTO EN AVES ACUÁTICAS

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SUMMARY.—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 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.—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

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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 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 tanto en temperatura como en 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: aves acuáticas, cambio global, compromisos, costes energéticos, ecofisiología, flexibilidad fenotípica, humedales, inmunocompetencia, migración, osmorregulación, salinidad, selección de hábitat.

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 and 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 and 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 (i.e. 'pure' 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 and Fange, 1958)– living in saline environments had an extrarenal mechanism to eliminate excess salt (reviewed by Schmidt-Nielsen, 1959, 1960, 1997).

Further investigations have made clear that the saltgland secretion is the result of a set of highly integrated interactions between the gut, kidneys, hindgut, saltglands, and supporting organs (reviewed by Goldstein and Skadhauge, 2000; Goldstein, 2002; Hughes, 2003; see fig. 2). Therefore, the func-

tioning 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 and 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 subject to greater physiological stresses than those confronting marine species (Blakey *et al*., 2006). This
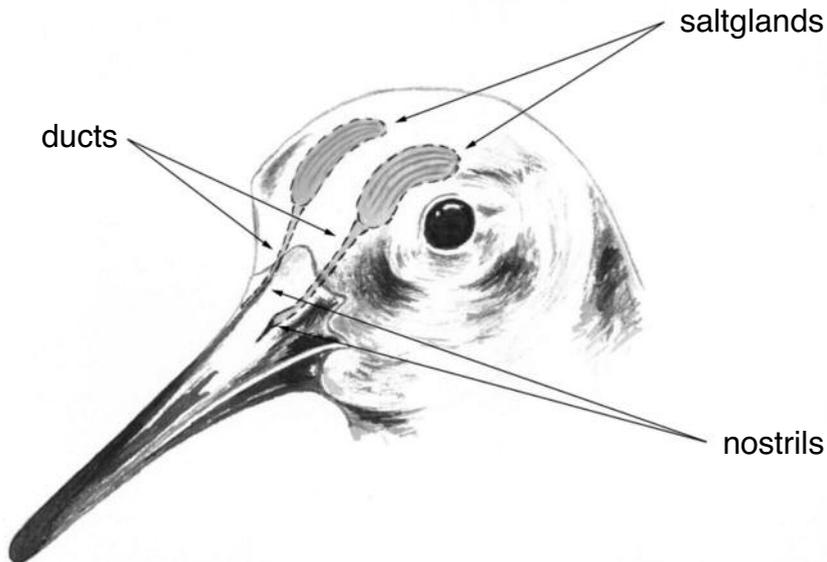
FIG. 1.—Supraorbital saltglands of a shorebird. Note that the ducts (outlined by dashed lines) pass through the beak and empty into the anterior nasal cavity so that the secretion flows out through the nares. *[Glándulas de la sal supraorbitales de un limícola. Nótese que los conductos (indicados por líneas discontinuas) recorren el interior del pico y desembocan en la cavidad nasal anterior, de tal manera que la secreción sale a través de las narinas.]*
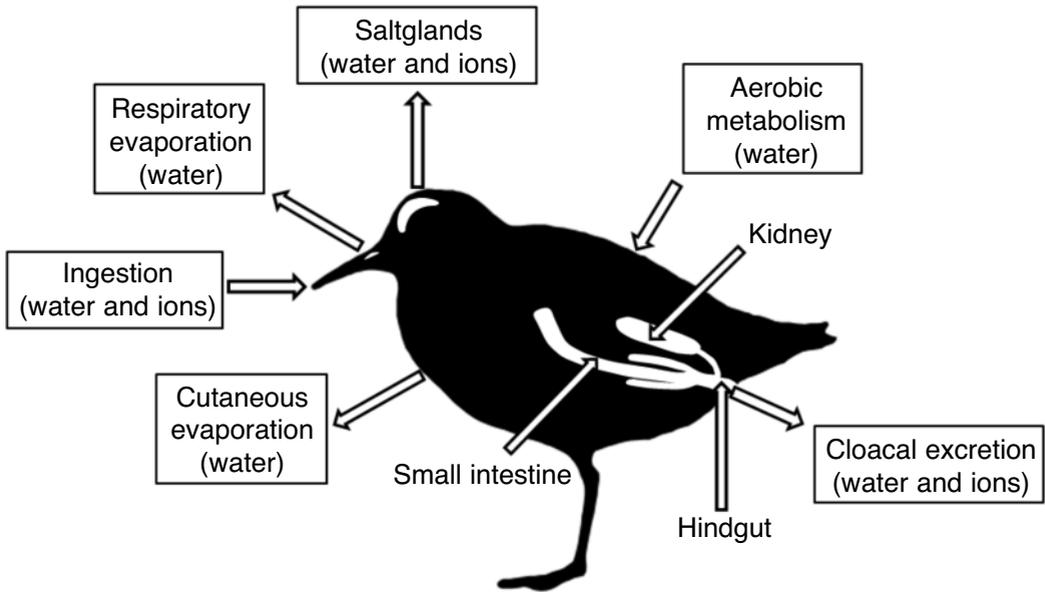
FIG. 2.—Pathways of water and ion influx and efflux, and principal osmoregulatory organs in water-birds (adapted from Goldstein, 2002 and Hughes, 2003).
[Rutas de entrada y salida de agua e iones, y los órganos de osmorregulación principales en aves acuá-ticas (adaptado de Goldstein, 2002 y Hughes, 2003)]

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*.

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 and Ensor, 1972; Peaker and Linzell, 1975; Holmes, 1975; Sturkie, 1976; Skadhauge, 1981; Simon, 1982; Holmes and Phillips, 1985; Butler et al., 1989; Braun, 1999; Shuttleworth and Hildebrandt, 1999; Goldstein and 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 proved 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 grey phalaropes P. fulicarius spend up to 9 and 11 months of the year, respectively, on the open ocean (Piersma et al., 1996; Tracy et al., 2002), while others, such as green Tringa ochropus and wood sandpipers T. glareola 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 (e.g. dunlin Calidris alpina) fall in between these extremes, occurring in both coastal and inland habitats, and can be classified as 'mixed' species (Piersma, 1997; 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 intervening sites en route, since migratory shorebirds undergo major physiological adjustments to enable rapid accumulation of fuel stores (Kvist and 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., 2011a, 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 and 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 and 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 and 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 the 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 and Linzell, 1975; Burger and Gochfeld, 1984; Nyström and 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 and Linzell, 1975). This also occurs under natural conditions: Most significantly, red knots *C. canutus* reduce the size of their saltglands when in mild climates, probably reflecting low energy demands –i.e. low rates of food and corresponding salt intake (Gutiérrez *et al.*, 2012a). Likewise, individual 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 these small but essential osmoregulatory organs 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 and Hughes (2003) found that the 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 and 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 and 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 and Holmes, 1971) and decrease the time required for fluid to move through the gut (Roberts and 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 and Skadhauge, 2008; McWhorter *et al*., 2009). However, in other marine species, such as glaucous-winged 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 and 2). Recently, it has been demonstrated in several temperate-zone passerines that the process of water loss through the skin is under physiological control (Ro and 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 use of freshwater when possible, are all well documented behaviours employed by waterbirds to avoid salt stress (e.g. Nyström and Pehrsson, 1988; Rubega and 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 (e.g. the kentish plover *Charadrius alexandrinus*, the killdeer *Ch. vociferus* and the semipalmated sandpiper *C. pusilla*) depend primarily on an insectivorous diet with high free water contents to compensate for their limited physiological ability to tolerate salt or reduce water turnover (Purdue and Haines, 1977; Rubega and Robinson, 1997). Other studies have shown that birds have the ability to select relatively low-salt prey minimizing their salt intake. Nyström and Pehrsson (1988) and Nyström *et al*. (1991) showed that common eiders *Somateria mollissima* –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 and Álvarez Fernández (2012) recently showed that salinity restricted greater scaup *A. 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 and Jehl, 1975c; Johnston and 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 and 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 in California, most –if not all– waterbird species travel regularly to freshwater, where they can be seen vigorously bathing and drinking (Rubega and Robinson, 1997). Rubega and 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 and 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 and Beardall (2003) observed a similar pattern, noting the importance of freshwater flows over estuarine mudflats for waterbirds wintering in eastern England. 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.

Alongside 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 and 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 and 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 may 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 and Masero, 2007). Masero (2002) showed that red knots, in contrast to several other small 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 and 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 (for reviews see Tseng and Hwang, 2008; Evans, 2009), 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 and Linzell, 1975). Peaker and Linzell (1975) estimated the theoretical energy requirement of salt-gland secretory function at *c*. 7% of 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. Dunlins 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 and Whittow, 1984; Bryant and 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 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 and Harshman, 2001). Thus, osmoregulation is susceptible to generating

TABLE 1

Estimated energetic costs of osmoregulation and other physiological demands in waterbirds as a proportion of BMR.
[Costes energéticos de la osmorregulación y otras demandas fisiológicas en aves acuáticas expresados como proporción de la tasa metabólica basal.]

Demands/species	Details	Change (%)	Source
Osmoregulation			
Ducks *Anas* spp.	Ion transport. Theoretical metabolic change using freshwater-acclimated ducks	+7	Peaker and 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)

TABLE 1 (cont.)

Demands/species	Details	Change (%)	Source
Moult			
Macaroni penguin *Eudyptes chryrsolophus*	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 non moulting periods	+80	Portugal *et al*. (2007)
European shoveller *Anas clypeata*	Pre-nuptial plumage moult	+35	Guozhen and Hongfa (1986)
Common teal *Anas crecca*	Pre-nuptial plumage moult	+25	Guozhen and 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 and Piersma (1998)
Red knot *Calidris canutus islandica*	Cold acclimation. Metabolic change estimated as the difference in metabolic rate between 4º C- and 25º C-acclimated birds	+26	Vézina *et al*. (2006)

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 and Kim, 1964; Cooch, 1964; Harvey and Phillips, 1980; Johnston and Bildstein, 1990; Barnes and Nudds, 1991; Hannam *et al.*, 2003; DeVink *et al.*, 2005), but also in field studies where dietary salt differs between colonies (Ensor and 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 and Jehl, 1985c; Johnston and Bildstein, 1990; Bildstein *et al.*, 1990, 1991; Janes, 1997) or breed inland (Nyström and Pehrsson, 1988).

Physiological trade-offs with osmoregulation are not exclusive to chicks. For instance, adult white ibises *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 ibises *E. 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 and 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 and Linzell, 1975), salt stress may limit food consumption immediately after arrival in saline environments (Burger and Gochfeld, 1984). However, Burger and Gochfeld (1984) showed that both captive and wild Franklin's gulls *L. pipixcan* exhibited an additional endogenous capacity for saltgland flexibility, independent of the environmental salinity. They proposed that this seasonal –circannual– programme of change in saltgland size and activity would have a high selective value in protecting individuals from undue physiological stress when they first arrive at their marine non-breeding sites. In line with these results, Mahoney and 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 and 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, remains 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 experi-

mentally 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 and Ensor, 1972). For example, prolactin and corticosterone have been shown to restore saltgland secretion in adenohypophysectomized ducks (Phillips and Ensor, 1972; Butler et al., 1989), which could facilitate their adjustment to saline environments (Ensor and 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 and Ensor, 1972; Harvey and 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 and 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 which 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 lead them to ingest large salt loads (Mahoney and 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 and Jehl, 1985b). In contrast, Jehl (2005) noted that many gadwall Anas strepera –which are less salt-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 AND 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 a lower prevalence of infection by blood parasites than those relying on inland freshwater habitats (e.g. Piersma, 1997; Figuerola, 1999; Jovani, et al., 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 and 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 and 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 and 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 THEIR 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 and Rehfisch, 2003; Rehfisch and 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, 2014). Global mean sea level is projected to rise above 1 m by 2100 (IPCC, 2014), thereby salinizing brackish and freshwater coastal wetlands. Overall, models predict a systematic 'freshening' at both poleward ends and increasing salinities at low latitudes, although most studies suggest that future changes will be regionally variable (e.g. Najjar *et al*., 2000; Gibson and 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 and Smit, 1990). Such conditions may be expected to cause both heat stress (Klaassen, 1990) and salt stress (Klaassen and Ens, 1990). Indeed, heat and salt stress can potentially limit food consumption in shorebirds, especially in individuals preparing to migrate. Klaassen and Ens (1990) showed that both red knots and sanderlings *C. 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 *C. 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 and 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 and 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 and 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 bio-

diversity and abundance of food resources, which may be catastrophic for certain shorebirds (e.g. Rubega and 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 and Robinson, 1997; Ravenscroft and 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 or 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 and 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 and 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 stimuli could influence the osmoregulatory ability in birds have not been formally addressed. Burger and 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 and 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 behavioural responses to salinity and the relative tolerance of species is critical for understanding community level impacts of salinity changes, whether natural or anthropogenically induced.

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