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ROLE OF THE LOWER INTESTINE IN THE ADAPTATION OF GULLS (*LARUS GLAUCESCENS*) TO SEA WATER

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SUMMARY

We used *in vivo* perfusion of the lower intestine (colon plus coprodeum) to examine the osmoregulatory role of that organ in glaucous-winged gulls (*Larus glaucescens* Naum.) drinking sea water and fresh water. The area of the lower intestine was small, $0{\cdot}59\,cm^2\,100\,g^{-1}$ body mass. Its electrolyte and water transport rates were unaffected by salt water acclimation. Sodium and chloride were always reabsorbed from the intestinal lumen to the plasma. The maximum sodium transport rate we measured was $37\,\mu equiv\,cm^{-2}\,h^{-1}$, from a sodium concentration of $200\,mequiv\,l^{-1}$. Potassium transport from the different perfusion fluids differed, and was generally negatively correlated with sodium transport, suggesting some form of sodium–potassium exchange. Solute-linked water was reabsorbed at a rate of $3{\cdot}5\,\mu l\,\mu equiv^{-1}$ Na^+, permitting the lower intestinal epithelium to maintain a luminal fluid up to $130\,mosmol\,kg^{-1}$ hyperosmotic to plasma. The serosal-to-mucosal osmotic permeability coefficient of the lower intestinal epithelium was $0{\cdot}21\,\mu l\,cm^{-2}\,h^{-1}\,(mosmol\,kg^{-1})^{-1}$. Ureteral urine from birds in both groups was usually strongly (up to $250\,mosmol\,kg^{-1}$) hypertonic to plasma, but sodium, potassium and chloride concentrations were low and constituted less than 25 % of total osmolytes. We suggest that the lower intestine of *L. glaucescens* does not play a major role in reclaiming urinary water and electrolytes for recycling to the salt glands.

INTRODUCTION

Because the lower intestine (colon plus coprodeum) of birds receives fluids both from the kidneys and from the small intestine, this region is considered to function in an integrative role in avian osmoregulation (see Thomas, 1982; Skadhauge, 1981 for reviews). The absorption of NaCl in the lower intestine, and the accompanying reabsorption of water, may be particularly important for terrestrial birds exposed to conditions of dehydration or NaCl depletion. Indeed, in these circumstances NaCl and water reabsorption are significantly enhanced compared with control or salt-loaded states (Bindslev & Skadhauge, 1971; Rice & Skadhauge, 1982).

Key words: avian osmoregulation, cloacal function, marine bird.

A different situation might be expected in marine birds. In these species, NaCl is more efficiently excreted (with less water) *via* the supra-orbital salt glands than by the kidneys, and after ingestion of salt water most NaCl is excreted by the salt-secreting glands. It has been suggested that NaCl absorption from the lower intestine of marine birds remains high or even increases in response to salt ingestion so that urinary water may be reclaimed and salt recycled to the salt glands for excretion (Schmidt-Nielsen, Borut, Lee & Crawford, 1963). In domestic ducks (*Anas platyrhynchos*), this prediction appears to be unsubstantiated: as in the chicken, rates of NaCl absorption by the lower intestine are significantly reduced after adaptation to saline drinking water (Skadhauge, Munck & Rice, 1984). However, these ducks are not truly marine birds, and they are unable to maintain body mass or plasma sodium levels even when their saline drinking solutions are substantially less concentrated than the salt-gland secretions (Roberts & Hughes, 1984*a*). In contrast, glaucous-winged gulls (*Larus glaucescens*) are able to tolerate much higher concentrations of dietary NaCl (Hughes, 1970), and we presume that these coastal marine birds routinely ingest hypertonic water (and perhaps food). In the present study, we examined the transport capacities of the lower intestine of this marine bird, and we also compared these capacities in gulls drinking fresh water and sea water.

MATERIALS AND METHODS

Animals

Glaucous-winged gulls (*Larus glaucescens*) were captured as nestlings on Christie Islet off the west coast of British Columbia (49° 30′ N; 123° 18′ W), and were raised in captivity at the University of British Columbia. The gulls were given fresh water to drink during this period in captivity. Birds used for the present experiments were 1–3 years old, and were matched for age between the two experimental groups. All birds were fed frozen herring ($[Na^+] = 82\,mequiv\,kg^{-1}$, $[K^+] = 124\,mequiv\,kg^{-1}$, $[Cl^-] = 69\,mequiv\,kg^{-1}$) supplemented with a liquid vitamin mixture (Paramette, Ayerst Laboratories, Montreal). Gulls acclimated to fresh water (FW) were provided with tap water *ad libitum*. To acclimate gulls to salt water (SW), simulated sea water was prepared (Instant Ocean, Aquarium Systems, Mentor, OH). The concentration of the sea water given to the gulls was increased over a period of 2 weeks to equal two-thirds sea water ($[Cl^-] = 320\,mequiv\,l^{-1}$). This acclimation regime is more than sufficient to stimulate both maximal salt gland secretion (Holmes & Stewart, 1968) and changes in transport characteristics of the small intestine (Roberts & Hughes, 1984*b*). Eighteen hours before the experiments, food was removed from the birds; gulls acclimated to FW retained access to tap water, whereas those acclimated to SW were switched to full strength sea water.

Perfusion of the lower intestine

At the start of each experiment the gull was weighed to the nearest 10 g using an Ohaus spring balance. A stylet-supported catheter (I-cath, Delmed, Canton, MA)

Table 1. *Composition of perfusion solutions*

	Na^+ (mequiv l^{-1})	K^+ (mequiv l^{-1})	Cl^- (mequiv l^{-1})	Osmolality (mosmol kg^{-1})
Hyposmotic	25	40	37	135
Isosmotic	112	40	124	297,325*
Hyperosmotic	249	40	261	550
Raffinose	—	32	10	630

* Osmolality was 297 mosmol kg^{-1} for FW gulls; to compensate for increased plasma osmolality of SW-adapted gulls, osmolality of SW isosmotic perfusion solution was increased to 325 mosmol kg^{-1} by addition of raffinose.

was inserted into a brachial vein and the bird was anaesthetized with sodium pentobarbital (25 mg kg^{-1}, Somnotol, MTC Pharmaceuticals, Mississauga, Canada). A cannula was inserted at the junction of the small and large intestines (marked by a pair of small caeca) and a flow-through perfusion was used (as described by Skadhauge, 1974; Goldstein & Braun, 1986). Four different perfusion solutions (hypo-, iso- and hyperosmotic saline and sodium-free hyperosmotic raffinose) were used for each bird (only the three saline solutions for two of the FW-acclimated birds). The three saline solutions were made from a stock solution which was prepared fresh weekly. The composition of the stock solution was (in mmol l^{-1}): KCl, 34; $MgSO_4$, 2; $CaCl_2$, 1·5; $NaHCO_3$, 25; KH_2PO_4, 6. The final osmolality of the saline perfusion solutions was adjusted by addition of NaCl (Table 1). The raffinose solution was prepared from a stock similar to that used for the saline solutions, except that $KHCO_3$ was substituted for $NaHCO_3$ and KCl was reduced from 34 to 9 mmol l^{-1} (Table 1). Amino acids (L-leucine, 4 mmol l^{-1}; L-lysine, 4 mmol l^{-1}) and glucose (5·5 mmol l^{-1}) were added to all saline perfusion solutions, as these compounds stimulate electrolyte absorption under some conditions (Lind, Munck, Olsen & Skadhauge, 1980; Skadhauge *et al.* 1984). [^{3}H]polyethylene glycol (PEG) was added to all solutions as a volume marker.

For each perfusion solution, the lower intestine was first flushed with a volume (approx. 20 ml) of body-temperature perfusion solution. Perfusion then commenced at a rate of 2 ml h^{-1}. Approximately 1–1·5 h was required for the collected fluid to reach equilibrium (stable values of electrolyte and PEG concentrations and osmolality). Therefore, each solution was perfused for at least 2 h, with collections each 0·5 h. The sequence of perfusion solutions was changed for each bird.

Blood samples (1·5 ml of plasma at the start and end of the experiments and 0·5 ml at the start of each new perfusion solution) were collected into heparinized syringes for determination of haematocrit, plasma electrolytes and osmolality (first and last sample only). The blood was transferred immediately to centrifuge tubes, and triplicate Strumia haematocrit tubes were filled. To separate the plasma, these blood samples were centrifuged at 15 000 rev. min^{-1} (15 600 ***g***) for 3 min in an Eppendorf model 3412 centrifuge. At the end of the experiments the gulls were killed by injection of saturated KCl, and the perfused segment was removed and its planar area measured.

Osmolality was measured by freezing point osmometry (Advanced Instruments model 31LAS). Chloride was measured by titration (Buchler Digital Chloridometer) and sodium and potassium by flame photometry (Instrumentation Laboratory Inc. model 143). PEG was assayed by liquid scintillation counting (Beckman model LS9000 scintillation counter). All samples were measured within 24 h of collection (osmolalities within 5 h) and most analyses were done in duplicate.

Calculations

The rate of volume absorption (J_v, $ml\,h^{-1}$) from each perfusion solution was calculated as the difference between perfusion rate and collection rate. Perfusion rate (J_i) was measured directly. Collection rate (J_o) was calculated from the change in concentration of the volume marker (Goldstein & Braun, 1986).

Solute absorption rates (J_x, $\mu equiv\,h^{-1}$) were calculated from the differences between the rates of perfusion of the electrolyte ($J_i\,[x_i]$) and the rates of collection of the electrolyte ($J_o\,[x_o]$), where x_i and x_o are the concentrations of solute x in the perfused and collected fluid, respectively. For sodium, we examined the absorption rate as a function of the mean luminal sodium concentration $[(Na_i + Na_o)/2]$.

The osmotic permeability of the intestinal epithelium was calculated from the rates of water reabsorption in the raffinose perfusion experiments (J_v/osmotic difference between plasma and intestinal lumen). We assumed that in the absence of any luminal sodium all water flux occurred in response to the transepithelial osmotic difference.

All transport rates have been converted to area-specific units (i.e. expressed per cm^2 of reabsorptive surface area).

The rates of solute-linked water reabsorption (μl water $\mu equiv^{-1}$ Na) were calculated from the isosmotic perfusion experiments (J_v/J_{Na}). This calculation assumes that, in the absence of any osmotic driving force, all water reabsorption was associated with reabsorption of sodium. Because these perfusions were actually slightly hyposmotic to plasma, we corrected our calculations for any osmotic water flow (assuming the same osmotic permeability coefficient as in the raffinose experiments). This correction was always a small proportion (approx. 5 %) of the total water flow from these isosmotic perfusions.

All results are reported as mean ± standard error. Group means were compared using *t*-tests. Sample size was six different birds, each perfused with four different perfusion solutions, for all groups except the FW raffinose perfusions, where $N = 4$.

Ureteral urine

Ureteral urine was collected by inserting closed-ended cannulae into the cloacas of gulls just removed from their cages. The closed end of the cannula prevented any contamination by cloacal fluid while a window in the side of the cannula was placed over the ureteral openings. Urine was centrifuged and the supernatant analysed for osmolality and electrolytes as above. Numbers of samples for ureteral urine were small (3 and 5 for FW and SW, respectively). Therefore, to avoid assumptions about

Table 2. *Composition of plasma and ureteral urine in FW- and SW-acclimated gulls*

	Osmolality (mosmol kg^{-1})	Na^+ (mequiv l^{-1})	K^+ (mequiv l^{-1})	Cl^- (mequiv l^{-1})	Haematocrit (%)
FW plasma ($N = 6$)	336·1 ± 2·6*	150·9 ± 1·1	3·3 ± 0·17	111·1 ± 1·8	43·7 ± 1·3
SW plasma ($N = 6$)	345·7 ± 2·8*	150·8 ± 2·1	3·1 ± 0·22	115·2 ± 1·5	49·1 ± 2·1
FW urine ($N = 3$)	501·0 ± 93·5	63·0 ± 5·1†	29·0 ± 6·7	20·8 ± 2·1	—
SW urine ($N = 5$)	548·0 ± 54·0	80·5 ± 5·1†	45·7 ± 13·1	41·3 ± 10·7	—

All values mean ± S.E. Values having the same symbol are significantly different from one another ($P < 0·05$).

sample distributions, we tested for differences between groups using the non-parametric Mann-Whitney U-test.

RESULTS

Body mass and plasma composition

The body masses of gulls acclimated to FW (796 ± 34 g) were not significantly different ($P > 0·05$) from those of gulls acclimated to SW (812 ± 26 g). Plasma osmolality was significantly increased in SW- *vs* FW-acclimated birds (Table 2). However, the plasma levels of Na^+, K^+ and Cl^- were not different in the two groups. Haematocrit was slightly higher ($0·05 < P < 0·1$) in SW- than in FW-acclimated gulls. Haematocrit and osmolality were only weakly correlated ($r = 0·41$, $P > 0·2$). Haematocrit, plasma [Na^+] and plasma [Cl^-] did not show any pattern of increase or decrease during the course of the experiments. However, plasma osmolality and [K^+] increased significantly ($P < 0·05$) over the length of an experimental day (by an average of 23 mosmol kg^{-1} and 0·8 mequiv l^{-1}, respectively). These increases were independent of the order in which the perfusion solutions were used.

Area of perfused segment

The area of the lower intestine was 4·41 ± 0·42 cm^2 in FW-acclimated gulls and 5·10 ± 0·39 cm^2 in SW-acclimated gulls. The difference was not significant ($P > 0·05$).

Electrolyte and water transport

Sodium was absorbed from all saline perfusion fluids. We are unable to define a Michaelis–Menten-type saturation curve for sodium transport over the range of sodium concentrations investigated (Fig. 1). In the sodium-free raffinose perfusion experiments, we could not detect any significant movement of sodium from plasma to lumen. The maximum sodium transport rates measured (from the hyperosmotic saline perfusion, mean luminal sodium concentration = 203 mequiv l^{-1}) were 37 ± 5·5 μequiv $cm^{-2} h^{-1}$. There were no significant differences between the sodium transport rates of gulls drinking FW and SW ($P > 0·15$ in all cases).

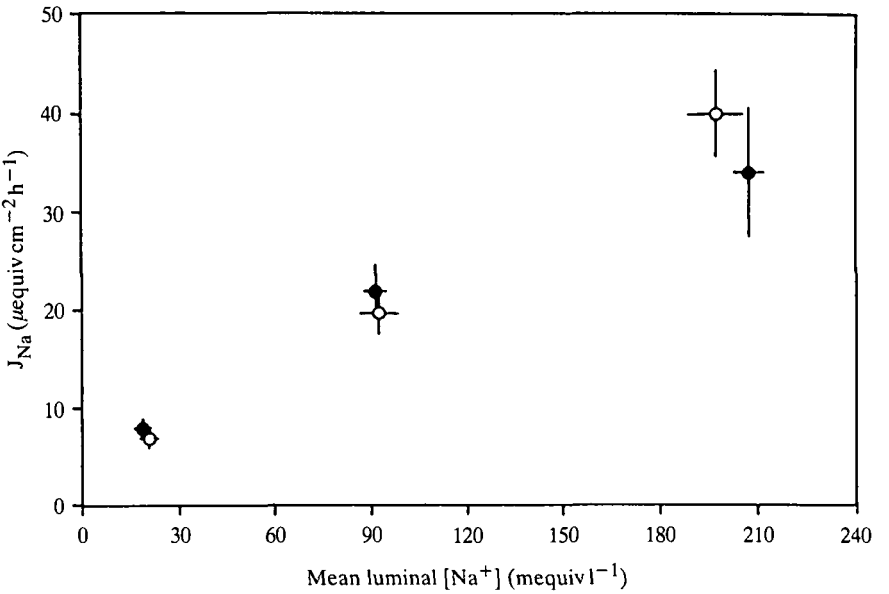

Fig. 1. Sodium reabsorption rate as a function of mean luminal sodium concentration. Error bars encompass one standard error. $N = 6$ for each group. ○, freshwater-acclimated gulls; ●, seawater-acclimated gulls.

Potassium was almost always secreted from plasma to intestinal lumen in FW isosmotic perfusions (five out of six cases), FW hyperosmotic perfusions (five out of six cases) and SW hyperosmotic perfusions (all six experiments). Potassium was reabsorbed from FW hyposmotic perfusions (four out of six), SW hyposmotic perfusions (six out of six) and all raffinose perfusions. Potassium was secreted in three and reabsorbed in three of the SW isosmotic perfusions. There were no significant differences ($P > 0{\cdot}15$ for all cases) between FW- and SW-acclimated gulls for any perfusion solution. Potassium transport rates were not related to plasma potassium concentrations ($r = 0{\cdot}17$, $P > 0{\cdot}25$). There was a weak negative correlation between potassium transport rates and sodium reabsorption rates in the saline perfusion experiments (Fig. 2).

Chloride was reabsorbed from all perfusion solutions (Table 3). The rate of chloride reabsorption was significantly correlated with the rate of sodium reabsorption (Fig. 3). From the isosmotic saline perfusion, the difference in rates of chloride reabsorption between gulls drinking SW and those drinking FW approached significance ($0{\cdot}05 < P < 0{\cdot}1$); there were no significant differences for the other three perfusion solutions ($P > 0{\cdot}4$ in all cases).

The intestinal epithelium of the gull had a significant solute-linked water flow. In FW-acclimated gulls this value was $3{\cdot}5 \pm 0{\cdot}4$ μl μequiv^{-1} Na^+, and it was $3{\cdot}4 \pm 0{\cdot}5$ μl μequiv^{-1} Na^+ in SW-acclimated gulls ($P > 0{\cdot}4$). The effective Na^+ concentration of the reabsorbed fluid was 285 mequiv l^{-1}. The net volume flow of water from the hyperosmotic saline perfusion (average $130 \pm 5{\cdot}8$ mosmol kg^{-1} hyperosmotic to plasma) was near 0 ($0{\cdot}032 \pm 0{\cdot}071$ ml h^{-1} in FW gulls, $0{\cdot}005 \pm 0{\cdot}11$ ml h^{-1} in SW gulls). This suggests that the solute-linked water reabsorption was able

to balance osmotic water loss into the intestinal lumen up to an osmotic difference of approximately 130 mosmol kg^{-1}.

The serosal-to-mucosal osmotic permeability coefficient for the lower intestine of *L. glaucescens* was $0{\cdot}206 \pm 0{\cdot}043$ $\mu l\,cm^{-2}\,h^{-1}$ (mosmol $kg^{-1})^{-1}$ for FW gulls and $0{\cdot}172 \pm 0{\cdot}044$ $\mu l\,cm^{-2}\,h^{-1}$ (mosmol $kg^{-1})^{-1}$ for SW gulls ($P > 0{\cdot}6$).

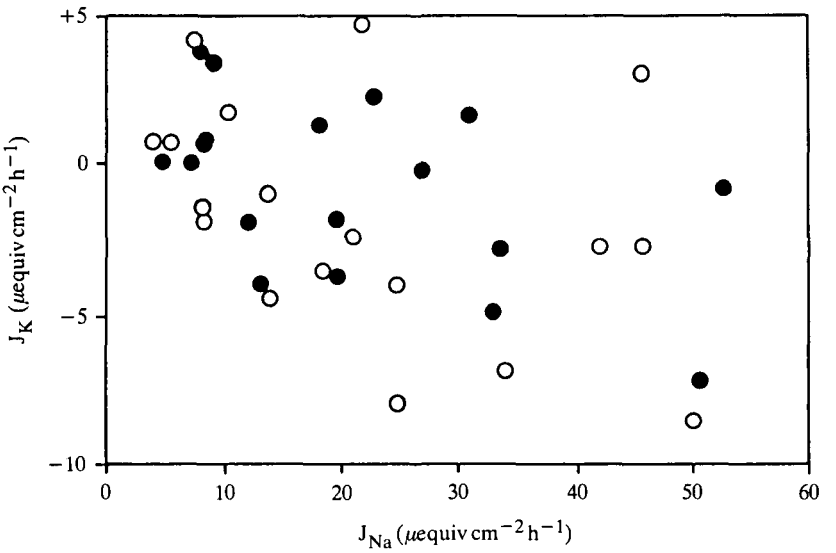

Fig. 2. Potassium transport rates related to rates of sodium reabsorption ($N = 36$, $r = -0{\cdot}39$, $P > 0{\cdot}1$). Transport rates greater than 0 indicate net reabsorption, less than 0 indicate net secretion. ○, freshwater-acclimated gulls; ●, seawater-acclimated gulls.

Table 3. *Transport rates of water (J_v), sodium (J_{Na}), potassium (J_K) and chloride (J_{Cl}) in lower intestine of FW- and SW-adapted gulls*

Perfusion solution	J_v ($\mu l\,cm^{-2}\,h^{-1}$)	J_{Na} (μequiv $cm^{-2}\,h^{-1}$)	J_K (μequiv $cm^{-2}\,h^{-1}$)	J_{Cl} (μequiv $cm^{-2}\,h^{-1}$)
		FW-adapted gulls		
Hyposmotic	121·3 ± 13·9	6·98 ± 0·75	0·56 ± 0·88	3·90 ± 0·93
Isosmotic	76·0 ± 8·9	19·62 ± 2·10	−2·63 ± 1·76	10·58 ± 1·63
Hyperosmotic	1·7 ± 10·9	39·83 ± 4·40	−3·33 ± 1·67	24·75 ± 3·56
Raffinose	−46·5 ± 10·9	−0·92 ± 0·80	3·86 ± 0·36	1·80 ± 0·23
		SW-adapted gulls		
Hyposmotic	131·2 ± 22·1	7·95 ± 0·77	1·64 ± 0·67	4·59 ± 0·88
Isosmotic	87·5 ± 18·1	21·80 ± 2·70	0·25 ± 0·74	16·42 ± 2·47
Hyperosmotic	3·8 ± 19·3	33·80 ± 6·50	−3·89 ± 0·87	23·25 ± 5·89
Raffinose	−40·8 ± 11·1	−0·028 ± 0·30	3·52 ± 0·94	1·37 ± 0·44

$N = 6$ for all groups except FW raffinose, where $N = 4$.
All data presented as mean ± S.E.
Negative transport rates indicate net secretory flux (from plasma to lumen).

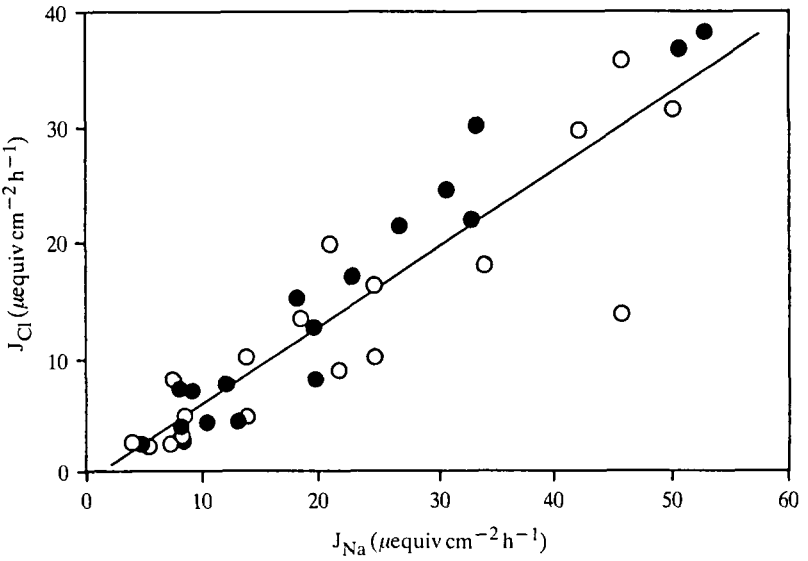

Fig. 3. Rates of chloride reabsorption related to rates of sodium reabsorption. Solid line is linear regression of all data points ($y = 0{\cdot}60x - 0{\cdot}12$; $N = 36$, $r = 0{\cdot}88$, $P \ll 0{\cdot}01$). ○, freshwater-acclimated gulls; ●, seawater-acclimated gulls.

Composition of ureteral urine

The osmolality of ureteral urine from three FW-acclimated gulls averaged 501 mosmol kg^{-1} (Table 2). The urines of two of the three birds were strongly hyperosmotic to plasma (591 and 598 mosmol kg^{-1}), and the urine of the third bird was slightly hyposmotic (314 mosmol kg^{-1}). In all cases sodium, potassium and chloride concentrations were low, together accounting for less than 25 % of total osmolytes.

Ureteral urine from SW-acclimated gulls was similar in osmolality to that of gulls acclimated to FW, but sodium, potassium and chloride concentrations were all slightly elevated (only sodium significantly, Table 2).

DISCUSSION

The most striking feature of our results is the absence of any differences in rates of movement of water and electrolytes across the lower intestines of FW- *vs* SW-acclimated gulls. This contrasts with the situation in both the terrestrial, granivorous chicken *Gallus domesticus* (Bindslev & Skadhauge, 1971) and the aquatic, herbivorous duck (Skadhauge *et al.* 1984). Following acclimation to a high-salt diet, rates of electrolyte transport in the lower intestine were reduced in both of these species. In addition to this difference in the effect of salt acclimation, examination of the rates of water and electrolyte transport in the gull lower intestine also reveals some interesting comparisons with other species. We will first examine these comparisons, and then return to the role of the lower intestine in acclimation of the gull to salt-water drinking.

Acclimation of gulls to sea-water drinking

The osmoregulatory response to drinking sea water was quite evident in this study, as the plasma osmolality of gulls drinking SW was significantly increased over that of gulls drinking FW (Table 1). As in previous studies with this species (Roberts & Hughes, 1984*b*), this increase in plasma osmolality was not accompanied by an increase in plasma sodium or chloride.

Resorptive surface area

The lower intestine of glaucous-winged gulls is small (4·75 cm^2, or 0·59 cm^2 100 g^{-1} body mass). This mass-specific area is only 20–50 % as large as the area of lower intestine in those terrestrial birds which have been examined (Goldstein & Braun, 1986) and is just half as large as the mass-specific area of the lower intestine of the domestic duck (Skadhauge *et al.* 1984). *Post-mortem* examination of the gulls (after the perfusion experiments) did not reveal uric acid in the small intestine cephalad to the caeca. The area of epithelium available for post-renal modification of the urine is thus probably no greater than the small segment of lower intestine.

Electrolyte transport by the lower intestine

Previous studies in several species of birds have shown that the lower intestinal epithelium generates a lumen-negative electrical potential difference (average approximately 40 mV, see Skadhauge, 1981, p. 109, for summary), indicating active sodium reabsorption. We were unable to demonstrate saturation of the sodium transport system in our experiments; therefore the maximum sodium transport rates that we measured may or may not represent the maximum of which the tissue is capable. Nevertheless, the maximum J_{Na} values that we measured (approx. 37 μequiv cm^{-2} h^{-1}) are substantially higher than the J_{max} measured for sodium in the lower intestine of terrestrial birds (approx. 21 μequiv cm^{-2} h^{-1} in three species; Goldstein & Braun, 1986). From a luminal concentration of 100–150 mequiv l^{-1}, the sodium transport rate of a unit area of gull lower intestine also significantly exceeds that of the domestic duck. The latter species transports sodium at a rate of up to 16·6 μequiv cm^{-2} h^{-1} from a perfusion fluid containing sodium at 138 mequiv l^{-1} (Skadhauge *et al.* 1984). J_{Na} for the gull was 20·7 μequiv cm^{-2} h^{-1} from a perfusion fluid containing 110 mequiv l^{-1} sodium. However, because of its substantially larger surface area, the lower intestine of the duck has a greater total sodium transport capacity.

The potassium concentration was the same in all saline perfusion solutions. However, the pattern of potassium flux was different for the three different solutions. In the low-sodium (hyposmotic) perfusion, potassium was usually reabsorbed, whereas potassium was secreted into the high-sodium (hyperosmotic) solution. The situation was intermediate for the isosmotic solutions. These results suggest some form of linkage between sodium and potassium transport (Na/K exchange), as seen in the domestic fowl (Bindslev & Skadhauge, 1971) but not in the galah *Cacatua roseicapilla* (Skadhauge, 1974).

The fluxes of chloride followed the same pattern as in other birds: chloride was always reabsorbed, and higher intraluminal concentrations resulted in higher absorption rates. We found no evidence for saturation of chloride transport in these experiments.

Movement of water across the lower intestinal epithelium

The rate of solute-linked water absorption (3·4 μl μequiv^{-1} Na^+) in *L. glaucescens* is intermediate among the values found for terrestrial birds (1·1–5 μl μequiv^{-1} Na^+; Bindslev & Skadhauge, 1971; Skadhauge, 1974; Goldstein & Braun, 1986) and is also intermediate between the values determined for FW-acclimated (2·5 μl μequiv^{-1} Na^+) and SW-acclimated (5·7 μl μequiv^{-1} Na^+) ducks (Skadhauge *et al.* 1984). This solute-linked reabsorption enables the gull to reabsorb water against an osmotic difference of up to 130 mosmol kg^{-1}, a capacity similar to that of the dehydrated chicken (Bindslev & Skadhauge, 1971) but greater than that of either the hydrated chicken (Bindslev & Skadhauge, 1971) or the house sparrow (Goldstein & Braun, 1986).

The osmotic permeability of the lower intestine of the gull (0·19 μl cm^{-2} h^{-1} (mosmol kg^{-1})$^{-1}$) is at the lower end of the values measured in birds (Goldstein & Braun, 1986).

Adaptation versus *acclimation of gulls to drinking sea water*

The results of our experiments may be viewed from two perspectives. First, we can think of the gull as a bird adapted to salt water, and we can compare the physiological capacities of this species with terrestrial or freshwater birds. This is a valid comparison in the case of our experimental animals, because they were raised in captivity with access only to fresh water. From this perspective, we see that the transport capacities of the lower intestines of gulls drinking FW were higher than have been measured in other species. The glaucous-winged gull, a coastal marine resident, is not likely to be often in a situation where it has an inadequate salt intake. The high reabsorptive capacity of the gull lower intestine, present even in birds raised on fresh water, probably does not serve to conserve salt. Rather, this capacity relates to the likelihood of a high salt intake, and the consequent need to reabsorb water and to recycle salt to the salt glands.

Secondly, we can think of the gull as a bird which is able to acclimate to drinking salt water, and we can compare the physiological responses of the lower intestine of the gull with the responses in other birds. From this perspective, we can see that, unlike the chicken (Bindslev & Skadhauge, 1971) or the domestic duck (Skadhauge *et al.* 1984), the lower intestine of the gull does not respond to salt-water drinking by a reduction in transport capacity. (Conversely, the FW-acclimated gull does not respond by increasing transport capacity.) Once again, the lower intestine of the SW-acclimated gull is able to reabsorb salt and water, and the salt can be recycled for excretion to the salt gland.

Together, these two views suggest that the physiology of the lower intestine of the glaucous-winged gull is indeed adapted to a marine environment: FW-acclimated

gulls have high transport capacities, and these capacities do not respond to SW acclimation in a manner similar to those of terrestrial or freshwater-adapted birds.

Is the lower intestine important in recycling urinary salt and water?

Schmidt-Nielsen *et al.* (1963) predicted that the lower intestine of marine birds should maintain, or even enhance, its capacity to reabsorb NaCl when the birds are on a high-salt diet. The lower intestine could then reabsorb a portion of the NaCl and water present in ureteral urine, and this salt could be recycled to the supra-orbital salt glands for excretion with minimal loss of water. As predicted, the lower intestinal epithelium of the glaucous-winged gull does have a relatively high capacity (on an area-specific basis) for reabsorption of NaCl, and this capacity remains undiminished in birds with a high salt intake. However, the role of the lower intestine in recycling ureterally excreted electrolytes and water remains in question for several reasons.

First, the planar area of the lower intestine is very small in *L. glaucescens*. This in itself is suggestive of a reduced significance of this organ in conservation of water and electrolytes.

Second, the composition of ureteral urine does not favour reabsorption of sodium and water after passage into the lower intestine. In both FW- and SW-acclimated glaucous-winged gulls, the ureteral urine is generally strongly hyperosmotic to plasma and, as in herring gulls (Douglas, 1966), low in sodium. Osmotic dilution of this urine in the lower intestine would further reduce the already low sodium concentration, as might mixing with fluids coming from the small intestine. It is possible that other constituents of the urine, such as phosphate or ammonia, could be reabsorbed (Skadhauge & Thomas, 1979). However, sodium reabsorption appears to be the primary determinant of solute-linked water reabsorption (Skadhauge & Thomas, 1979) and is also most significant with respect to recycling to the salt glands of ions lost in the urine. We have not explored the possibility that a significant quantity of sodium might be trapped in the urates of the ureteral urine.

The composition of excreted cloacal fluids also suggests that refluxing of ureteral urine may be of minor importance in *L. glaucescens*. Conscious caged gulls fed herring and maintained on increasingly more concentrated sea water excreted cloacal fluid which ranged between 464 (FW) and 643 (90% SW) mosmol kg^{-1} (Hughes, 1977). These high osmolalities, particularly those in the highest salt group, could not be maintained in the lower intestine, which could maintain an osmotic difference only up to approx. 130 mosmol kg^{-1} hyperosmotic to plasma in our *in vivo* perfusion experiments.

Together, these lines of evidence suggest that the lower intestine may be of minor significance in modifying ureteral urine in *L. glaucescens*. We suggest (as did Douglas, 1970) that the majority of the sodium ingested in food and drinking water is absorbed during the initial passage through the gastrointestinal tract. The small intestine may be particularly important in this regard, as segments of this organ do increase their transport capacities in response to salt acclimation (Roberts & Hughes, 1984*b*). The relatively high sodium transport rates in the lower intestine could reclaim a further portion of the ingested salt. The kidneys also do an effective job of

reclaiming sodium and chloride. Thus, most of the sodium chloride is excreted by the nasal salt glands; the salts remaining in the urine would appear to be most effectively excreted without first passing across the epithelium of the lower intestine.

Thus, the hypothesis of Schmidt-Nielsen *et al.* (1963), that the cloaca of marine birds possesses a strong capacity for reabsorbing urinary water and electrolytes under conditions of high salt intake, is substantiated only in part by our studies. The epithelium of the lower intestine does have relatively high transport capacities, and these capacities are maintained under conditions of high salt intake. However, the reabsorptive area of the lower intestine is small, and probably does not serve as a significant site of post-renal reabsorption of urinary water and sodium.

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