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OBSERVATIONS ON THE INTAKE OF WATER AND ELECTROLYTES BY THE DUCK (*ANAS PLATYRHYNCHOS*) MAINTAINED ON FRESH WATER AND ON HYPERTONIC SALINE*

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INTRODUCTION

Transfer of the White Pekin duck from a diet including an *ad libitum* supply of fresh water to one containing hypertonic saline is accompanied by an increase in size of the nasal glands (Holmes, Phillips & Chester Jones, 1963). At the same time, the nasal glands show changes in their nucleic acid and protein composition and they develop an increased capacity to excrete sodium and potassium ions (Fletcher, Stainer & Holmes, 1967; Holmes & Stewart, 1968).

Studies on the renal function of these birds have shown that whereas the concentration of sodium in the urine was only one-seventh, the concentration of potassium in the urine was three times that found in the nasal gland fluid of the bird adapted to hypertonic saline (Holmes, Fletcher & Stewart, 1968). These studies therefore seemed to indicate that, under conditions where the birds were freely permitted to drink hypertonic saline containing sodium and chloride ions in concentrations equal to those found in 60 % standard sea water, the sodium chloride was primarily excreted via the nasal glands whilst the potassium chloride was excreted primarily via the kidneys.

The actual amounts of water and electrolytes that these birds consumed under laboratory conditions is not known. Furthermore, the relative distribution of the ingested water and electrolytes between the cloacal discharge and the nasal gland fluid is similarly obscure. The present study therefore attempted to elucidate these unknowns and relate them to the known functional capacities of the renal and extra-renal excretory pathways in these birds.

MATERIALS AND METHODS

Male Pekin ducks were obtained commercially and housed out of doors for at least 1 month before use. Prior to experimentation the birds were brought indoors and placed in individual cages maintained at 21° C. and 40–70 % relative humidity with a photoperiod of 12 hr. light and 12 hr. darkness.

In one group of birds the changes in plasma electrolyte concentrations were determined during the period of adaptation to hypertonic saline. At the beginning of the experiment a wing vein in each duck was cannulated and the bird was heparinized.

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At approximately 10 a.m. each day the drinking water was removed from the cage and the birds were given wet food (60 % water). At 1 p.m. the remaining food was removed and the drinking water was replaced. Blood samples were taken each day just before feeding and at 4 p.m. On the first day of adaptation an additional blood sample was taken at 10 p.m.

In the group of birds where the food and water intake was examined the birds were fed according to the following schedule. At 11 a.m. the drinking water was removed and each bird was given a ration of 308 g. commercial grower food (16 % protein) mixed with 460 ml. of tapwater. At 4 p.m. the remaining food was removed from the cage, weighed and the amount eaten was calculated. A bird 'water fountain' containing 2000 ml. of drinking water was then placed outside each cage and within reach of the bird via an access hole in the side of the cage. This procedure minimized the amount of water spilled and inhibited the use of water for preening. All birds were allowed to adapt to the experimental cages for 2 weeks prior to the commencement of the study. Daily measurements of food and water intake were then made for a period of 3–6 weeks. Following this the ducks were given hypertonic saline (284 mM/l. NaCl, 6·0 mM/l. KCl) and after 1 week of adaptation the daily measurements were resumed for a further period of 2–6 weeks. After 3 weeks the extra-renal excretory capacity of each bird was determined according to the method previously described (Fletcher *et al.* 1967).

Further experiments were conducted in which the concentration of the drinking water was varied after the birds had previously been adapted to a solution containing 284 mM/l. NaCl and 6 mM/l. KCl (see legends to tables and figures for precise protocol).

Water and cation content of cloacal outputs from fed birds was determined in freshwater-maintained ducks and in ducks which had been maintained on saline (284 mM/l. NaCl and 6·0 mM/l. KCl) for 1 month. At 11 a.m. each day the drinking water was removed and each animal was presented with a ration of commercial grower food (308 g. plus 460 ml. fresh water). At 12.30 p.m. the remaining food was removed and the drinking water was replaced. Each duck was trained on this feeding schedule for at least 2 weeks prior to experimentation. On the day of the experiment the birds were fed according to the above schedule and at 12.30 p.m. they were transferred to a room at 21–29° C. and 60–70 % R.H., placed on a board and cloacal outputs were collected for 24 hr. in a tared beaker immersed in ice. A few drops of chloroform were added to the excrement as the experiment progressed. At intervals during the course of the experiment the ducks were given water via a stomach tube. The total volume of water given to each bird was computed on the basis of the food intake of the individual. The volume of water was given in five equal loads at 4, 6·5, 8·5, 19·5 and 21·5 hr. after feeding.

The water contents of the food and excrement were determined by evaporating weighed samples to constant dryness at 50° C. Sodium, potassium, and calcium were determined by flame photometry (Eppendorf), chloride was estimated by amperometric titration against silver ions (Cotlove, 1963), inorganic phosphate was analysed by the method of Fiske & Subbarow (1925), and the total osmolality was measured by osmometry (Fiske, Model G-62).

RESULTS AND DISCUSSION

When the freshwater-maintained ducks were given hypertonic saline (284 ml. NaCl 6·0 ml. KCl) as their sole source of drinking water, a rapid increase in the total osmolality and in the plasma concentrations of sodium and chloride ions was apparent. This increase appeared to reach a maximum sometime between 6 and 10 hr. after first drinking the saline water. After 10 hr. of exposure to the saline drinking water both

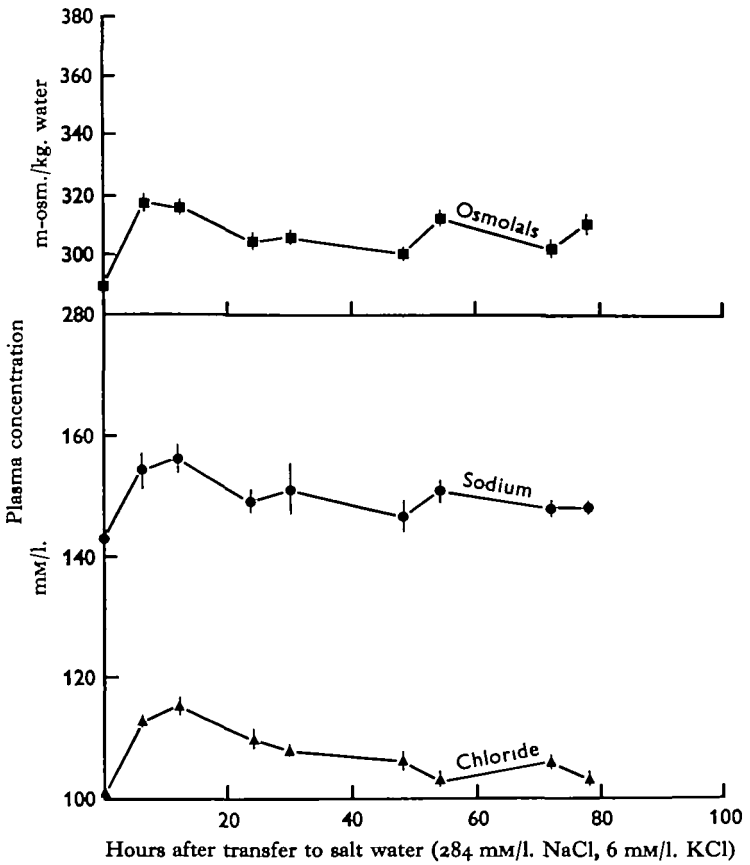

Fig. 1. Changes in plasma osmolality, and in concentrations of sodium and chloride when freshwater-maintained ducks were given hypertonic saline (284 mM/l. NaCl and 6·0 mM/l. KCl) as their sole source of drinking water. (Four ducks were used for this study. A wing vein was cannulated in each of the ducks on the day prior to the start of the experiment. The ducks were heparinized and blood samples were removed at the times indicated. Vertical lines represent the standard error of the mean for each point.)

plasma concentrations showed a steady decline, and by 50 hr. they were not significantly different from the levels observed before transfer to the saline water. The total osmolality also showed a slight decline after 10 hr. but it remained significantly higher than freshwater levels throughout the period of the experiment (Fig. 1). The plasma concentrations of potassium and calcium ions did not change significantly throughout the experimental period.

These observations suggested that the duck regulated its plasma electrolyte composition within a few hours after being transferred to the hypertonic saline water. Such an observation was not surprising in view of the fact that ducks have been maintained in this laboratory for many months under similar environmental conditions. These results, however, were in marked contrast to those obtained from ducks which had been transferred from fresh water to saline drinking water of a somewhat higher

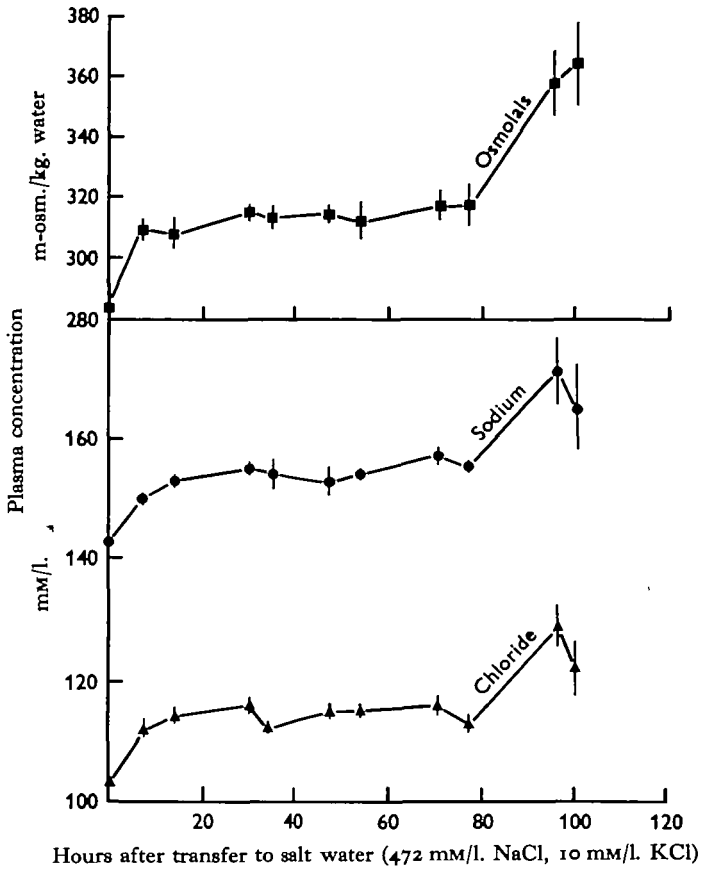

Fig. 2. Changes in plasma osmolality, and in concentrations of sodium and chloride when freshwater-maintained ducks were given hypertonic saline (472 mM/l. NaCl and 10·0 mM/l. KCl) as their sole source of drinking water. (Four ducks were used for this study. A wing vein was cannulated in each of the ducks on the day prior to the start of the experiment. The ducks were heparinized and blood samples were removed at the times indicated. Vertical lines represent the standard error of the mean for each point.)

concentration (470 mM/l. NaCl and 10·0 mM/l. KCl). In this case the plasma levels of total osmolals and of sodium and chloride ions again rose rapidly within the first few hours after exposure but the elevated concentrations did not decline during the experimental period (Fig. 2). Instead, they continued to increase for a period up to 14 days when the birds either died or were in a seriously deteriorated physiological state. Clearly, the ducks were unable to maintain homeostasis when exposed to this concentration of hypertonic saline drinking water.

It was apparent from the above observations that the ducks living on saline water

containing 284 mM/l. NaCl and 6·0 mM/l. KCl were maintaining a steady state in respect of the intake and the excretion of water and electrolytes. Just what the intake of these birds was, and how it could be related to their ability to excrete water and electrolytes via the renal and extrarenal excretory pathways was unknown. During the ensuing months experiments were therefore carried out to determine the food, water, and electrolyte intake of birds maintained on the freshwater and hypertonic

Table 1. *The changes in body weights and the daily intakes of drinking water and wet food by ducks when transferred from fresh drinking water to hypertonic saline drinking water*

(Daily food and water intakes were measured when ducks were maintained on fresh drinking water for 3–6 weeks. Following this, the birds were given saline drinking water (284 mM/l. NaCl and 6·0 mM/l. KCl) and, after 1 week of adaptation, the daily food and water intakes were again measured for at least 2 weeks. The differences in food and water intake were obtained by subtracting the mean intake for each bird when drinking saline, from the corresponding value for that individual when drinking fresh water. The differences in body weights were obtained by subtracting the body weight of each duck after 3 weeks of drinking hypertonic saline from its initial body weight before transfer to saline. Single tailed 't' tests were performed on the differences obtained. All values are expressed as means ± S.E.)

	No. of birds	Freshwater-maintained	Saline-maintained	Difference
Body weight (g.)	6	2706 ± 58·4	2542 ± 58·4	168*** ± 41·2
Drinking water intake (ml./kg. body wt./day)	6	117 ± 10·7	89·1 ± 10·1	27·5*** ± 5·06
Wet food intake (g./kg. body wt./day)	6	174 ± 2·74	151 ± 5·96	22·5* ± *8·29

Significance level of decline: * $P < 0.025$, ** $P < 0.01$, *** $P < 0.005$.

saline regimens. While the ducks were being maintained on fresh drinking water their body weights and food and water intakes remained fairly constant throughout the 3- to 6-week period of observation. Upon transfer to saline drinking water (284 mM/l. NaCl and 6·0 mM/l. KCl), however, each duck began to lose weight, and after 3 weeks the body weight of each individual was significantly lower than it was before transfer to the saline regimen (Table 1). In the ducks which were observed for longer periods of time the body weight tended to stabilize after the first 3 weeks but some birds did continue to lose weight while others eventually regained what they had lost. The drop in body weight upon transfer to saline was accompanied by a simultaneous reduction in the food and water intake (Table 1). When maintained on fresh water the ducks drank 0·67 ml. of water per gram of wet food eaten and the corresponding value for the saline-maintained birds was 0·59 ml. per gram of wet food. It is evident that, regardless of whether the ducks were maintained on fresh water or on hypertonic saline, they obtained 50% of their total daily water intake from the ingested food (cf. Tables 2–4). The water consumption of the duck appeared to be similar to that of the laying chicken observed by Medway & Kare (1959), but it was considerably higher than other values reported for the chicken (Korr, 1939; Hart & Essex, 1942; Dicker & Haslam, 1966). Since these latter values were obtained from chickens consuming dry food, it may be that the high volume of total water consumption observed for the ducks in the present study was in some way related to the wet food they received. Preliminary observations on the water consumption of a duck transferred from wet to dry food, however, seems to preclude this conjecture. During a 3-week period the

Table 2. *The amounts of water and electrolytes contained in the food ingested by ducks which were first maintained on fresh drinking water and subsequently transferred to hypertonic saline water*

(Daily food and water intakes were measured for ducks maintained on fresh drinking water for 3–6 weeks. Following this the ducks were given hypertonic saline (284 mM/l. NaCl and 6·0 mM/l. KCl), and after 1 week of adaptation, the daily food and water intakes were again measured for at least 2 weeks. All values are expressed as means ± S.E.)

	No. of birds	Food intake (ml. or mM/kg. body wt./day)					
		H_2O	Na^+	K^+	Ca^{2+}	Cl^-	PO_4^{3-}
Freshwater-maintained	6	104 ± 2·65	3·05 ± 0·0706	11·9 ± 0·365	2·85 ± 0·116	3 85 ± 0·071	6·28 ± 0·248
Saline-maintained	6	90·5** ± 3·00	2·65** ± 0·0914	10·4* ± 0·408	2·48* ± 0·108	3·35** ± 0 116	5·48* ± 0·183

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, with respect to corresponding value for the freshwater-maintained birds.

Table 3. *The amounts of water and electrolytes contained in the drinking water consumed by ducks which were first maintained on fresh drinking water and subsequently transferred to hypertonic saline drinking water*

(Daily food and water intakes were measured for ducks maintained on fresh drinking water for 3–6 weeks. Following this, the ducks were given hypertonic saline (284 mM/l. NaCl and 6·0 mM/l. KCl), and after 1 week of adaptation, the daily food and water intakes were again measured for at least two weeks. All values are expressed as means ± S.E.)

	No. of birds	Fluid intake (ml. or mM/kg. body wt./day)					
		H_2O	Na^+	K^+	Ca^{2+}	Cl^-	PO_4^{3-}
Freshwater-maintained	6	117 ± 10·7	0·233 ± 0·0529	0·008 ± 0·00097	0·173 ± 0 0168	0·101 ± 0·009	< 0·001
Saline-maintained	6	89·1 ± 10·1	25·3*** ± 2·92	0·535*** ± 0·0604	0·133 ± 0 0147	25·8*** ± 2·86	< 0 001

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, with respect to corresponding value for the freshwater-maintained birds.

Table 4. *The total dry food, water and electrolytes consumed by ducks which were first maintained on fresh water and then transferred to hypertonic saline drinking water*

(Daily food and water intakes were measured for ducks maintained on fresh drinking water for 3–6 weeks. Following this, the ducks were given hypertonic saline (284 mM/l. NaCl and 6·0 mM/l. KCl), and after 1 week of adaptation, the daily food and water intakes were again measured for at least 2 weeks. All values are expressed as means ± S.E.)

	No. of birds	Total intake (g., ml. or mM/kg. body wt./day)						
		Dry food	H_2O	Na^+	K^+	Ca^{2+}	Cl^-	PO_4^{3-}
Freshwater-maintained	6	69·7 ± 2·24	221 ± 8·04	3·27 ± 0·116	11·9 ± 0·365	3·03 ± 0·0817	3·95 ± 0·531	6·28 ± 0·268
Saline-maintained	6	60 7* ± 2·20	180* ± 10 9	28·0*** ± 2·86	10·9* ± 0 183	2·62** ± 0 0816	29·2*** ± 2·74	5·48* ± 0·168

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, with respect to the corresponding value for freshwater-maintained birds.

ducks consumed an average of 181 ± 5·76 ml. of water per kg/body weight/day when given wet food but when given dry food for an additional 4 weeks the water intake did not change significantly (169 ± 5·29 ml. water/kg body weight/day).

Since the drinking water contributed only 4·9 % of the potassium ion ingested by the ducks maintained on saline it was evident that the food contributed the major portion of the potassium ion intake. The sodium ion content of the food, on the other hand, was quite low and comprised only 9·5 % of the total sodium ion ingested by the saline-maintained birds.

Table 5. *The concentrations of electrolytes in nasal gland fluid and maximum extra-renal excretory rates of ducks maintained on hypertonic saline for* 3 *weeks*

(Daily food and water intakes were measured for ducks maintained on fresh drinking water for 3–6 weeks. Following this, the ducks were given hypertonic saline (284 mM/l. NaCl and 6·0 mM/l. KCl), and after 1 week of adaptation, the daily food and water intakes were again measured for at least 2 weeks. After 3 weeks of maintenance on hypertonic saline the maximum extra-renal excretory rates were determined by the intravenous infusion of 10% NaCl. All values expressed as means ± S.E.)

	Concentration of nasal fluid (mM/l.)			Maximum extra-renal excretion (ml. or mM/kg. body wt./day)			
No. of birds	Na^+	K^+	Cl^-	H_2O	Na^+	K^+	Cl^-
6	613 ± 8·28	15·9 ± 0·577	610 ± 12·5	286 ± 23·2	175 ± 15·5	4·58 ± 0·555	174 ± 15·5

After at least 3 weeks of observation the maximum extra-renal excretory rates of the saline-maintained ducks were determined (Table 5). Upon comparing the electrolyte intake and the extra-renal excretory capacity of each individual it was apparent that the total intake of sodium and chloride ions were only 16·0 ± 1·08 % and 16·8 ± 1·08 % respectively of the maximum extra-renal excretory capacity. The total intake of potassium ion, however, was more than twice (251 ± 22·1 %) the capacity of the nasal glands to excrete this ion. The sodium:potassium ratio of the nasal gland fluid from these ducks has always been observed to be constant. Assuming, therefore, that all of the ingested sodium and potassium ions were absorbed by the intestine and that all of this sodium ion was excreted extra-renally, then only about 6·7 % of the total potassium ion intake could be simultaneously excreted by the nasal glands; the remaining 93 % must have been excreted renally. It is of interest to note that a precisely similar relationship between the ingested sodium and potassium ions and the inability of the extra-renal pathway to excrete the potassium ion from a potassium ion-rich diet has been described for the salt gland of the green turtle *Chelonia mydas mydas* (Holmes & McBean, 1964).

It is apparent that the duck cannot survive an abrupt transfer from a freshwater diet to a diet composed of drinking water containing 472 mM/l. NaCl and 10·0 mM/l. KCl. Previously, we have established that the ability of the duck to excrete sodium chloride extra-renally increased seven- to eight-fold during the first 2 weeks of exposure to saline containing 284 mM/l. NaCl and 6·0 mM/l. KCl (Fletcher *et al.* 1967). In view of this observation a group of birds were first allowed to develop their extra-renal capacity on the lower concentration of saline before being exposed to drinking water containing 472 mM/l. NaCl and 10·0 mM/l. KCl. The daily food and water intake of a group of four ducks given saline containing 284 mM/l. NaCl and 6·0 mM/l. KCl, was followed

for a 3-week period. These birds were then transferred to drinking water containing 472 mM/l. NaCl and 10·0 mM/l. KCl and their daily food and water intakes were again measured. This study indicated that the prior adaption of the birds to dilute saline did not increase their survival upon transfer to the more concentrated saline drinking water. Since all of the ducks died within 7–14 days, only the data for the first week is presented (Table 6). Each bird lost considerable weight during the first week of exposure to the high concentration of saline, and this was accompanied by a reduction of water intake to a value which was one-half of that consumed when the birds were maintained on the

Table 6. *Changes in body weight, drinking water and wet food intake of ducks when transferred from saline equivalent to* 60 % *standard sea water to saline equivalent to* 100 % *standard sea water*

(Daily food and water intakes were measured for ducks maintained on saline equivalent to 60 % standard sea water (284 mM/l. NaCl and 6·0 mM/l. KCl) for a period of 3 weeks. Following this the ducks were given saline equivalent to 100 % standard sea water (472 mM/l. NaCl and 10·0 mM/l. KCl) and daily food and water intakes were again measured for 1 week. Differences in food and water intakes were obtained by subtracting the mean intake for each duck while drinking 100 % standard sea water from its mean intake when drinking 60 % standard sea water. The differences in body weights were obtained by subtracting the body weight of each duck after 1 week of drinking 100 % standard sea water from its body weight just before transfer to this concentration. Single tailed '*t*' tests were performed on the differences. All values expressed as means ± S.E.)

	No. of birds	Sea water equivalent		Difference
		60 %	100 %	
Body weight (g.)	4	2540 ± 92·0	2218 ± 130	323*** ± 54
Drinking water intake (ml./kg. body wt./day)	4	86·2 ± 8·25	45·0 ± 4·19	41·3*** ± 7·0
Wet food intake (g./kg. body wt./day)	4	153 ± 4·25	124 ± 17·1	28·3 ± 13·8

Significance level of decline: * $P < 0.025$, ** $P < 0.01$, *** $P < 0.005$.

lower saline concentration. Since no significant drop in food intake occurred during this period, it must be concluded that the body-weight loss during the first week was primarily due to dehydration. Birds which survived the first week reduced their water intake to less than 20 ml./kg. body weight/day and the food consumption dropped to less than 10 % of the normal intake. To test whether a shortage of water or the high concentration saline was responsible for the physiological deterioration of the birds, a group of four ducks were given wet food but no drinking water. In contrast to the saline-maintained ducks above, these birds reduced their food intake to less than 20 % of normal during the first 48 hr. and during the first week their body weights had fallen by 639 ± 83 g. All of the birds died within 8–14 days. Thus it would appear that the water in the food was not sufficient to sustain these birds.

The sodium chloride intake of the ducks maintained on 284 mM/l. NaCl and 6·0 mM/l. KCl (24·5 ± 2·4 mM/kg. body weight/day) and on 472 mM/l. NaCl and 10·0 mM/l. KCl (21·2 ± 2·0 mM/kg. body weight/day) did not differ significantly. Again, this amount of sodium chloride was well below the maximum extra-renal excretory capacity of the nasal gland and it would appear that, even up to the point of death these ducks did not, or could not, utilize the full excretory capacity of their extra-renal pathway.

From these investigations it would appear that the Pekin duck would be unable to survive on a diet containing 100 % sea water. It is interesting to note in this regard that the herring gull (*Larus argentatus smithsonianus*) also appears to have a low ability to survive on sea water (Harriman & Kare, 1966). Harriman (1967) indicated that whereas the herring gull had a low survival rate when maintained on sodium chloride solutions equivalent to 50 % standard sea water, the more pelagic adult laughing gull (*Larus atricilla*) was able to live and maintain its body weight on 100 % sea water throughout the 10-day period of observation.

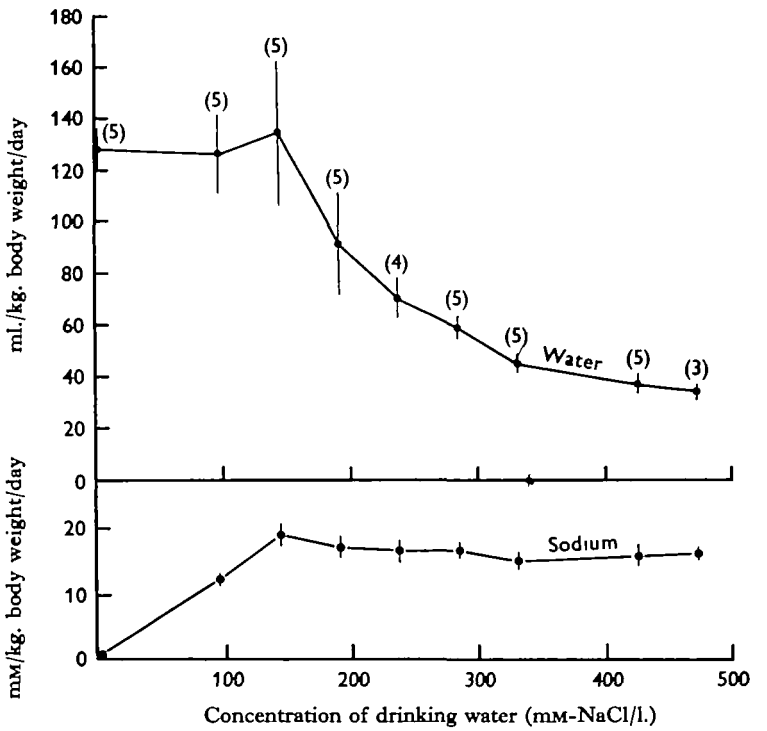

Fig. 3. Volume of water and amount of sodium ingested in the drinking water by ducks given various concentrations of sodium chloride as their sole source of drinking water. (Daily food and water intakes were measured for ducks maintained on fresh water for a period of 2–3 weeks. The ducks were then given hypertonic saline (284 mM/l. NaCl) as their sole source of drinking water, and daily food and water intakes were again observed for an additional 3-week period. Following this the ducks were given various concentrations of sodium chloride to drink, and the daily food and water intakes were measured for periods of 5–10 days. Vertical lines represent the standard error for each point. Numerals in parentheses represent the number of ducks used for the determination.)

The constancy of the sodium ions intake by birds maintained on saline solutions equivalent to 60 and 100 % standard sea water suggested the possibility that these birds may be able to regulate the amount of sodium ion consumed in their drinking water. To investigate this possibility a group of ducks were first adapted to saline equivalent to 60 % standard sea water. These birds were then randomly exposed for periods from 5–10 days to equivalent concentrations of sodium chloride varying from 20 to 100 % standard sea water. Although the volume of water consumed progressively declined when solutions of sodium chloride equivalent to 30 % standard sea water and above

were presented, the intake of sodium chloride remained essentially constant (Fig. 3). The variation between individuals in the volumes of water consumed were considerable and therefore the detailed patterns of consumption were masked when the mean data was considered. For example, most of the ducks studied showed a consistantly higher

Table 7. *A comparison of the concentrations and amounts of dry food, water, and electrolytes ingested by fresh water and hypertonic saline-maintained ducks*

(The saline-maintained ducks were maintained on hypertonic saline (284 mM/l. NaCl and 6·0 mM/l. KCl) for at least 1 month prior to the experiment. At 11 a.m. each day the drinking water was removed and each duck was offered 308 g. of dry feed mixed with 460 ml. tap water. At 12.30 p.m. the food was removed and the drinking water was replaced. Each duckwas trained on this feeding schedule for at least 2 weeks prior to the experiment. On the day of the experiment the birds were fed as above, but at 12.30 p.m. they were removed from their cages and placed on a board where the total cloacal discharge was determined over a 24 hr. period. Each duck was given, by stomach tube, a volume of water calculated on the basis of the amount of food eaten on the day of the experiment. Freshwater ducks were given 0 67 ml. of tap-water/g. wet food eaten and the saline-maintained ducks were given 0·59 ml. of saline (284 mM/l. NaCl and 6·0 mM/l. KCl) per g. wet food eaten. The total volume of water was given to the ducks in five equal loads at 4, 6·5, 8·5, 19 5 and 21·5 hr. after feeding. The concentrations of sodium and potassium in the intake were computed on the basis of the total water taken in by the birds during the 24 hr. of observation. All values are expressed as means ± S.E.)

		Concentration of intake (mM/kg. water)		Amount of intake (g./kg. body wt./day)		(mM/kg. body wt./day)	
	No. of birds	Na^+	K^+	Dry matter	H_2O	Na^+	K^+
Freshwater-maintained	4	10·8 ± 0·500	42 5 ± 2·50	44·5 ± 1·12	141 ± 2·70	1·53 ± 0·055	6·00 ± 0·25
Saline-maintained	4	147*** ± 0·354	42·8 ± 1·12	53·8 ± 3·97	180* ± 15·0	26·5*** ± 2 06	7·73* ± 0·61

* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$, with respect to the corresponding value for freshwater-maintained birds.

intake of water when drinking sodium chloride solutions equivalent to 30 % standard sea water. Also it should be noted that at higher concentrations of saline (sodium chloride solutions equivalent to 60–100 % standard sea water) the birds' ability to survive indefinitely was not studied. It would appear from the data, however, that the ducks possessed the ability to regulate the amounts of sodium chloride consumed in their drinking water, at least during the short time they were observed. Quantitatively similar observations within the range of 0·1–2·0 M-NaCl have been observed for the laughing gull (Harriman, 1967). This author defined the reduction in water intake as 'rejection or aversion' but we believe that 'regulation' may be a more apt physiological description of the phenomenon.

The observed ability to regulate the sodium chloride intake must be added to the already well-known renal and extra-renal excretory pathways as being an important factor contributing to the birds, ability to survive in environments in which hypertonic saline solutions are the only available drinking water. Also important in this regard is the apparent ability of the birds to select drinking water which is most suited to their survival. Studies on the herring gull and laughing gull have indicated that when these birds are simultaneously presented with distilled water and hypertonic saline they drink more of the former (Harriman & Kare, 1966; Harriman, 1967).

To obtain an estimate of the combined role of the renal and intestinal excretory

pathways in the total water and electrolyte excretion, freshwater-maintained and saline-maintained (284 mM/l. NaCl, 6 mM/l. KCl) birds were allowed to feed *ad libitum* before the total cloacal discharge was measured over a period of 24 hr. During the 24 hr. period each duck received five equal loads of water administered by stomach

Table 8. *A comparison of the concentration and amounts of cloacal excretion by freshwater-maintained and saline-maintained ducks*

(The saline-maintained ducks were maintained on hypertonic saline (284 mM/l. NaCl and 6·0 mM/l. KCl) for at least 1 month prior to the experiment. At 11 a.m. each day the drinking water was removed and each duck was offered 308 g. of dry feed mixed with 460 ml. tap water. At 12.30 p.m. the food was removed and the drinking water was replaced. Each duck was trained on this feeding schedule for at least 2 weeks prior to the experiment. On the day of the experiment the birds were fed as above, but at 12.30 p.m. they were removed from their cages and placed on a board where the total cloacal discharge was determined over a 24 hr. period. Each duck was given, by stomach tube, a volume of water calculated on the basis of the amount of food eaten on the day of the experiment. Freshwater ducks were given 0·67 ml. of tap-water/g. wet food eaten and the saline-maintained ducks were given 0·59 ml. of saline (284 mM/l. NaCl and 6·0 mM/l. KCl) per g. wet food eaten. The total volume of water was given to the ducks in five equal loads at 4, 6·5, 8·5, 19·5 and 21·5 hr. after feeding. The concentrations of sodium, potassium, and ammonium in the cloacal discharge were computed on the basis of the cloacal excretion of water by the birds during the 24 hr. observation. All values were expressed as means ±S.E.)

	No. of birds	Concentration of cloacal output (mM/kg. water)			Amount of cloacal output (g./kg. body wt./day)		(mM/kg. body wt./day)		
		Na^+	K^+	NH_4^+	Dry matter	H_2O	Na^+	K^+	NH_4^+
Freshwater-maintained	4	10 2 ±1·12	50·8 ±3·57	111 ±2·29	11·9 ±0·707	85·3 ±9·75	0·913 ±0·18	4·23 ±0·374	9·38 ±1·00
Saline-maintained	4	40 5** ±5·1	71·3* ±4·72	134* ±6 90	17·8*** ±0·50	64·0 ±3·12	2·60** ±0·36	5·38 ±0·158	8·53 ±0 133

* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$, with respect to the corresponding value for freshwater-maintained birds.

tube, the total amount of water administered having been determined from food consumption of the individuals on the day of the experiment (0·67 ml. water per g. wet food for the freshwater-maintained ducks and 0·59 ml. of water per g. wet food for the salt water-maintained ducks). On the day of the experiment the saline-maintained ducks ate more food than the freshwater-maintained ducks. Thus, the volume of water given to saline-maintained birds was higher than that given to the freshwater-maintained birds. The concentrations of sodium and potassium in the intake were computed on the basis of the total daily water intake (Table 7). In the freshwater-maintained ducks the concentrations of sodium and potassium ions in the intake (Table 7) were within the ranges of those previously observed in the urine of starved ducks (Holmes *et al.* 1967). When the concentrations of sodium and potassium ions in the intake (Table 7) were compared to the concentrations of these ions in the cloacal discharge (Table 8) no significant difference was observed for the freshwater-maintained birds. A similar comparison for the saline-maintained birds, however, showed that although the potassium ion concentrations were of the same order of magnitude the concentration of sodium ion in the cloacal discharge was significantly lower than that of the ingested material (cf. Tables 7 and 8). It is clear then that all the ingested electrolytes could be

excreted by the freshwater-maintained birds without the involvement of the nasal glands. On the other hand, since the sodium ion concentration of the ingested material was more than three times that of the cloacal discharge from the saline-maintained birds, the excretion of sodium ions via the nasal gland appeared necessary for the maintenance of homeostasis.

Although the output of dry matter was significantly higher in the saline-maintained birds, the cloacal output of water did not differ in the two groups of birds (Table 8). Further, it is of interest to note that the rates of cloacal water excretion in both groups

Table 9. *Percentage of intake recovered in the cloacal output of freshwater-maintained and saline-maintained ducks*

(Percentages calculated from data included in Tables 7 and 8.)

	No. of birds	Percentage of intake recovered in cloacal output			
		Dry matter	H_2O	Na^+	K^+
Freshwater-maintained	4	27·0 ± 1·00	60·3 ± 6·35	59·5 ± 11·4	71·3 ± 7·50
Saline-maintained	4	33·8** ± 1·12	36·5* ± 3·04	10·0** ± 1·58	71·3 ± 4·72

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, with respect to the corresponding value for freshwater-maintained birds.

did not differ significantly from the rates of urine flow previously reported for the starved duck (Holmes *et al.* 1968). In contrast, the cloacal excretory rates of sodium ions were only approximately half the previously reported urine excretory rates of this ion by starved birds (Holmes *et al.* 1968). This decrease probably reflected a reduced osmotic space in the urine of fed birds compared to that of the starved birds. The ammonium output in the urine of the fed birds was, however, similar to that of starved birds (Holmes *et al.* 1968).

By expressing the cloacal discharge of each component as a percentage of the total intake of that component, an estimate of the percentage recovery of the intake was made. From these estimates it was immediately apparent that although the recovery of potassium ions from the freshwater-maintained and saline-maintained birds was the same, the recoveries of water and sodium ions from the saline-maintained birds were only one-half and one-sixth respectively of the corresponding recoveries from the freshwater birds (Table 9). Since only 10 % of the ingested sodium ion was recovered in the cloacal discharge from the saline-maintained birds it appeared that approximately 90 % of this ion was excreted extra-renally. The recovery of water from the freshwater-maintained birds represented only 60 % of the intake, suggesting that a loss equivalent to approximately 56 ml./kg. body weight/day occurred via pathways other than the excretory pathways. An evaporative water loss of 16·8 ml./kg. body weight/day has been reported for chickens of similar weight maintained between 60 and 75° F. (Barott & Pringle, 1941). These authors indicated, however, that the rate of respiratory water loss increased several fold when the environmental temperature rises from 75 to 85° F., a temperature to which the ducks were exposed for at least part of the day when the cloacal discharge was collected. Furthermore, the wings of the birds used in the present experiment were taped to the side of the body and thereby the rate of

heat loss by radiation was probably restricted. Considering these experimental variables, it may be that a rate of evaporative water loss from the respiratory surfaces equivalent to 5·6 % of the body weight per day is not too much in excess of the actual value.

The actual amounts of sodium and potassium ions which were not recovered from the freshwater birds were quite small and were equal to approximately 0·62 mM and 1·8 mM/kg. body weight/day respectively. Since the birds were somewhat restrained during the collection period the possibility existed that some change in the distribution of these ions between the intracellular and extracellular spaces occurred. Assuming that the unrecovered quantities of sodium and potassium ions from the saline-maintained birds were of the same order as those described above, then the amount of sodium ion excreted via the nasal glands of these birds was approximately 23·3 mM/kg. body weight/day at a sodium concentration of 613 mM/l. in the nasal gland fluid (Table 5), this represented 38 ml. of nasal gland fluid/kg. body weight/day. Since the potassium ion concentration of the nasal gland fluid was 15·9 mM/l., the amount of potassium ion excreted in 38 ml. of nasal gland fluid would equal 0·6 mM/kg. body weight/day. The difference between the intake and the cloacal output of potassium ion was 2·38 mM/kg. body weight/day (Tables 7 and 8). If we assume, therefore, that the unrecovered amount of potassium ion from the saline-maintained birds was 1·8 mM/kg. body weight/day then the remaining 0·55 mM k^+/kg. body weight/day was probably excreted extra-renally. This value compared well with estimated values of 0·6 mM/kg. body weight/day. This rate of extra-renal potassium ion excretion does not differ significantly from the earlier estimation (6·7 %) made on the basis of the data contained in Tables 4 and 5.

Under the conditions maintained during measurements of food and water intake, if we consider that the saline-maintained ducks were in an isorrhoeic state, (Wolf, 1950) then the following relationship should have existed between the intake and excretion of water or of any other constituent of the urine and nasal gland fluid:

intake (Z) = respiratory loss (W) + cloacal excretion (X) + extra-renal excretion (Y).

If the concentration of sodium ion in the cloacal discharge observed over the 24 hr. collection period (Table 8) may be considered to be representative of that normally found in ducks adapted to saline drinking water, an estimation of the distribution of ingested water and electrolytes between the cloacal discharge and nasal gland fluid can be made. Assuming the rate of respiratory water loss at 60–75° F. to be 16·8 ml./kg. body weight/day (Barott & Pringle, 1941) and using the rates of intake of water and sodium and the concentration of sodium ion in the nasal gland fluid, derived from ducks maintained on saline for a prolonged period of time (Tables 4, 5), then the extra-renal and cloacal excretory rates may be estimated for these fed birds by solving the following pair of simultaneous equations:

$$(Z) = (W)+(X)+(Y), \tag{1}$$

$$(Z).(Z_{Na}) = (W).(W_{Na})+(X).(X_{Na})+(Y).(Y_{Na}), \tag{2}$$

where W, X, Y, and Z are respiratory water loss, rate of cloacal discharge of water, rate of nasal gland secretion, and rate of water intake, respectively, in ml./kg. body weight/day, and W_{Na}, X_{Na}, Y_{Na} and Z_{Na} are the concentrations of sodium ions in respiratory water, cloacal discharge, nasal gland fluid and ingested material, respectively, in mM/ml.

Substituting the experimental values in (1) and (2)

$$180 = 16{\cdot}8 + X + Y, \tag{3}$$

$$28 = 0 + 0{\cdot}0405X + 0{\cdot}613Y. \tag{4}$$

Solving for Y:

$$7{\cdot}29 = 0{\cdot}068 + 0{\cdot}0405X + 0{\cdot}0405Y, \tag{5}$$

$$28{\cdot}0 = 0 + 0{\cdot}0405X + 0{\cdot}0613Y. \tag{6}$$

Subtracting (5) from (6)

$$20{\cdot}7 = 0{\cdot}068 + 0{\cdot}573Y,$$

$$Y = 36{\cdot}3 \text{ ml./kg. body weight/day.}$$

Substituting 36·3 for Y in equation (3)

$$X = 127 \text{ ml./kg. body weight/day.}$$

Therefore, under the conditions prevailing during the observations of food and water intake, the nasal glands would have excreted 36·3 ml./kg. body weight/day while the cloacal discharge would have been 127 ml./kg. body weight/day. It is quite apparent that this estimation for the cloacal excretory rate of water is considerably higher than that found during the 24 hr. observation period (Table 8). This difference may have been due to a high rate of evaporative water loss produced by the experimental conditions of the observation period. It should be noted, however, that the discrepancy between the estimated and observed cloacal excretory rates of water have virtually no effect on the amounts of sodium ion excreted via renal and extra-renal excretory pathways.

The actual amount of evaporative water loss by the duck may play a critical role in determining the ability of this animal to live on saline. Since the duck appears to have a maximum sodium ion intake, any increase in evaporative water loss could not be compensated for by drinking. Thus a decrease in urine flow would occur. Since the kidneys are responsible for the excretion of nitrogenous waste products and apparently for all ingested electrolytes except sodium chloride, then the urine flow could only be reduced to a minimal level, below which the bird would be unable to sustain itself.

From the present studies on water and electrolyte intake and cloacal excretion in fed ducks, and from the previous studies on renal excretion in starved ducks (Holmes *et al.* 1968), it is evident that the nasal glands of the duck constitute the major pathway for the excretion of sodium and chloride ions, while the kidneys are responsible for the excretion of potassium. Although estimates can be made as to how the ingested water and electrolytes distribute themselves between the cloacal and extra-renal excretory pathways, by use of simultaneous equations, the actual details of their distribution can only be revealed by studying intake and excretion simultaneously under controlled conditions of temperature and humidity, over extended periods of time utilizing free-living birds.

SUMMARY

1. Intake of food, water and electrolyte by ducks maintained on fresh water and on hypertonic saline were measured over periods up to several months.

2. Transfer to saline approximately equivalent to 60% sea water was followed during the first 24 hr. by a sharp rise and fall in the plasma concentrations of sodium and chloride, which thereafter remained similar to the concentrations found in the freshwater-maintained birds.

3. Transfer to saline equivalent to 100% sea water resulted in a rise in these concentrations during the first 10 hr., which continued for a period up to 14 days, after which the birds either died or became unhealthy.

4. Upon transfer to saline drinking water (284 mM/l. Na^+, 6·0 mM/l. K^+) there was a gradual loss of body weight accompanied by a reduction in the food and water intake. Body weights tended to become stable after about 3 weeks, but some individuals continued to lose weight while others regained what they had lost.

5. When the concentration of sodium chloride in the drinking water exceeded 143 mM/l. the amount of sodium chloride ingested remained constant. Thus there was progressive decline in the volume of water drunk as the concentration increased. It would appear therefore that the saline-adapted duck possessed some mechanism whereby the daily intake of sodium chloride was regulated.

6. The cloacal output from saline-adapted ducks over a 24 hr. period showed that only 10% of the ingested sodium was excreted via this pathway as compared with over 70% of the ingested potassium. Most of the sodium appeared to be excreted via the nasal glands.

7. The possible interactions between the renal and extra-renal excretory pathways in the maintenance of homeostasis during adaptation to diets including hypertonic saline or seawater are discussed.

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