THE SECRETORY RATES AND THE CHEMICAL STIMULUS FOR SECRETION OF THE NASAL SALT GLANDS IN THE RALLIDAE

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Many birds possess functional nasal glands, or salt glands, which serve as auxiliary kidneys for the excretion of ingested salts at high concentrations. Functional salt glands are now known to exist in members of 11 avian orders, and have been thoroughly studied in several representatives of the marine orders, such as Charadriiformes (e.g., Fänge et al. 1958; Bonting et al. 1964) and Pelecaniformes (Schmidt-Nielsen et al. 1958), in which the glands are well developed. Except for detailed studies on domestic ducks (e.g., Scothorne 1959; Ellis et al. 1963; Lanthier and Sandor 1967), little is known about the function of the salt gland in most families of nonmarine birds.

The present study reports the rates and concentrations of the nasal secretion, and determines the chemical stimulus responsible for initiating salt gland secretion in the American Coot (*Fulica americana*) and the Guam Rail (*Rallus owstoni*). Both species are within the nonmarine family Rallidae, whose members typically occur in estuarine or marshy habitats. Water in many of these areas is sufficiently saline to present problems of ionic regulation to birds. The existence of functional salt glands in American Coots has been reported previously (Cooch 1964), but no detailed study has been made of the salt glands of any member of this large family.

MATERIALS AND METHODS

HABITATS, CAPTURE, AND MAINTENANCE OF EXPERIMENTAL BIRDS

Coots are ubiquitous inhabitants of lakes, sloughs, and lagoons in western North America. The 18 birds used in this study were captured in mist nets at San Elijo Lagoon, San Diego County, California, between November 1967 and March 1968. The western end of this lagoon joins a small inlet of the Pacific Ocean, and fresh water enters its eastern end from Escondido Creek and San Dieguito Reservoir. Water samples were collected at eight locations in the western half of the lagoon during the winter for analysis of chloride concentration.

The vegetation in these lagoons consists almost exclusively of pickleweed (*Salicornia* sp.), which grows in abundance on mud flats throughout San Elijo Lagoon. Field observations and stomach analyses indicated that this plant was the chief diet of coots. Samples of *Salicornia* collected in winter from six different locations in the western half of the lagoon were ground to a fine mash with a mortar and pestle, squeezed in cheesecloth, and the plant fluid collected and centrifuged. Samples of the supernatant were analyzed for chloride and sodium concentrations.

The captured birds were caged in groups in a shed that permitted exposure to natural photoperiods and ambient temperatures. Following an initial weight loss as they adjusted to captivity, the coots maintained weight at about 450 g on a diet of lettuce and chicken feed. They were given fresh water ad libitum, but were deprived of salt water. Experiments were begun within a few days of capture, while glands were of a normal size and function.

Guam Rails have greatly reduced wings and are capable of "flights" of only 3 m, which they accomplish chiefly by jumping with their powerful legs. These birds occur in all parts of Guam Island, and currently have a population of about 80,000 (Lint 1968). Alan M. Courtright, Wildlife Biologist for the Guam Department of Agriculture, has kindly forwarded to us his observations on the diet and habits of these rails. They are omnivorous and their diet includes snails, insects, carrion, slugs, fish, tomatoes, melon, and palm leaves. Rails are fond of fresh water, and large numbers of them bathe in puddles left by rains. There is apparently no evidence that they drink sea water or even brackish water.

We received four rails through the courtesy of the Department of Agriculture, Government of Guam, which we kept together in a large cage in a room with natural photoperiod and at temperatures that varied between 20 and 24°C. The birds weighed 170–189 g when they arrived, but their weights increased to 223–250 g on a diet of ground beef, chicken feed, and occasional pieces of lettuce. Both fresh water and sea water were available at all times during these experiments. Rails preferred to drink fresh water, but occasionally drank sea water as well. They bathed at least once each day, completely immersing themselves in the water.

CONCENTRATION AND RATE OF FLOW OF NASAL SECRETION

All birds were given solutions of 15 or 20 per cent NaCl by stomach tube in doses equal to 1 ml/100 g body wt to determine the concentration and rate of flow of the nasal secretion. All doses included fast green dye, which does not appear in the urine (Smyth and Bartholomew 1966) or in the nasal secretion. The dye was useful in distinguishing between any regurgitated solution and nasal secretion, and between the urinary and fecal portions of the cloacal discharge. Coots, which had a bulky and highly succulent diet, were deprived of food and water for 12 hr preceding

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TABLE 1. Measurements of salt excretion and weights of nasal salt glands in American Coots and Guam Rails.

Species	$\bar{x}$ wt. nasal gland		$\bar{x}$ concn. nasal secretion		$\bar{x}$ max. rate Cl^- excretion	$\bar{x}$ max. urine concn.
	mg	mg/kg	Cl^- (mEq/l)	Na^+ (mEq/l)	(mg/min)	(mEq/l)
American Coot	293.3 (10, 79–497)[a]	587 (10, 190–868)	542 (128, 412–680)	530 (54, 410–680)	1.06 (7, 0.65–1.37)	178 (8, 110–220)
Guam Rail	19.5 (4, 16.2–23.0)	82 (4, 68–103)	785 (28, 667–900)	Not measured	0.33 (3, 0.24–0.49)	222 (3, 219–229)

[a] Sample size and range.

a dose, but this was generally not done with the rails. Birds were always allowed at least three days on their normal laboratory diet before being used in a subsequent experiment.

Several techniques were used for collection of nasal secretion. Samples were initially gathered as drops fell or were shaken from the beak onto a sheet of waxed paper beneath a caged bird. These drops were immediately drawn up by pipette and frozen in sealed vials for later analysis of sodium and chloride concentrations. All cloacal samples produced during this time were also collected immediately off the waxed paper and saved for chloride analysis. This method was used for determining concentrations only, but was unsatisfactory for measuring the rates of flow because some of the secretion adhered to the wires of the cage.

Rates of secretion from the rails were extremely small, and measurement of salt concentration was determined most accurately by periodically collecting a drop of secretion from the nares with a micropipette, then immediately measuring its chloride concentration.

Rates of salt secretion by both species were measured by taping a 3-dr plastic vial over a bird's beak. The vial was half filled with cotton to absorb the secretion. During the several hours following a salt load, vials were replaced with clean ones at half-hour intervals. The total amount of chloride in each vial was determined by first drying the vial and cotton, then adding 5 ml of distilled water and measuring the chloride concentration.

Both the rate of flow and the concentration of the secretions from coots were measured simultaneously when birds were placed in a wooden restrainer that was cut away at the rear to allow excreta to fall into a glass dish (Stafford 1969). The bird's head was held stationary between two boards, so that drops of secretion could not be shaken off the beak. The secretion then dripped from the beak and fell into a large funnel to which a small vial was attached by a piece of rubber tubing. The funnel was filled with mineral oil which prevented any evaporation from the secretion before it was collected. The secretion was withdrawn at half-hour intervals with a hypodermic needle inserted through the rubber tube, and the volume was recorded. All samples were frozen in sealed vials and later analyzed for sodium and chloride concentrations. Rates of secretion from rails were too small to permit accurate determinations of volumes by this method.

STIMULUS RESPONSIBLE FOR NASAL GLAND SECRETION

A series of experiments was undertaken to determine what changes in constitution of the blood stimulate the function of the salt glands in these birds. At least six coots were given each of the following solutions by stomach tube in doses equal to 1 ml/100 g body wt: 15 or 20 per cent NaCl, 20 per cent $MgCl_2 \cdot 6H_2O$, saturated $NaHCO_3$ (approximately 11 per cent), and 50 per cent urea. Two rails died during various stages of this study, but the same solutions were given to at least three of these birds. Four coots were also given an equal dose of 20 per cent KCl.

Between 0.5 and 1.0 ml of blood was withdrawn from a wing vein into a heparinized syringe within 5 min after the first drop of secretion appeared on the beak of a salt-loaded bird. If no secretion appeared, a blood sample was taken 1–3 hr (usually at 2 hr) after the solution was given to the bird. Blood samples were also collected from four coots within 2 hr of their capture, and from three coots that were shot in the field. Normal blood samples were taken from the four rails in the absence of any salt load. All blood samples were centrifuged and the plasma was sealed in 2-ml vials for later analysis.

All chloride determinations in this study were made on an automatic chloride titrator (American Inst. Co.), and sodium concentrations were measured with a flame photometer (Beckman Inst. Co., model DU). A vapor pressure osmometer (Hewlett-Packard Co.) measured total osmotic concentrations.

The salt glands from five coots killed in the field and from two rails that had continuous access to sea water were removed and weighed for comparative purposes.

RESULTS

FIELD MEASUREMENTS

The chloride concentration in water samples from San Elijo Lagoon ranged from 40.0 to

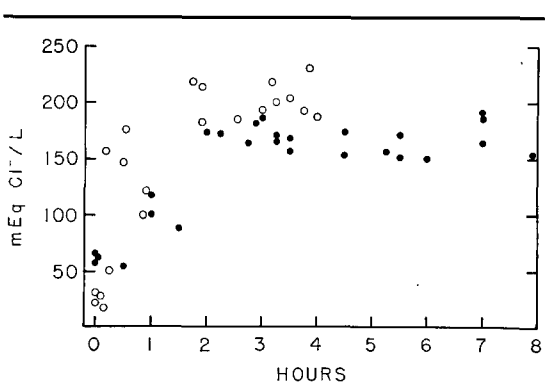

FIGURE 1. Urinary chloride concentrations produced by coots (shaded circles) and rails (unshaded circles) at the indicated times following 1 ml/100 g body wt. of 15 per cent or 20 per cent NaCl solution.

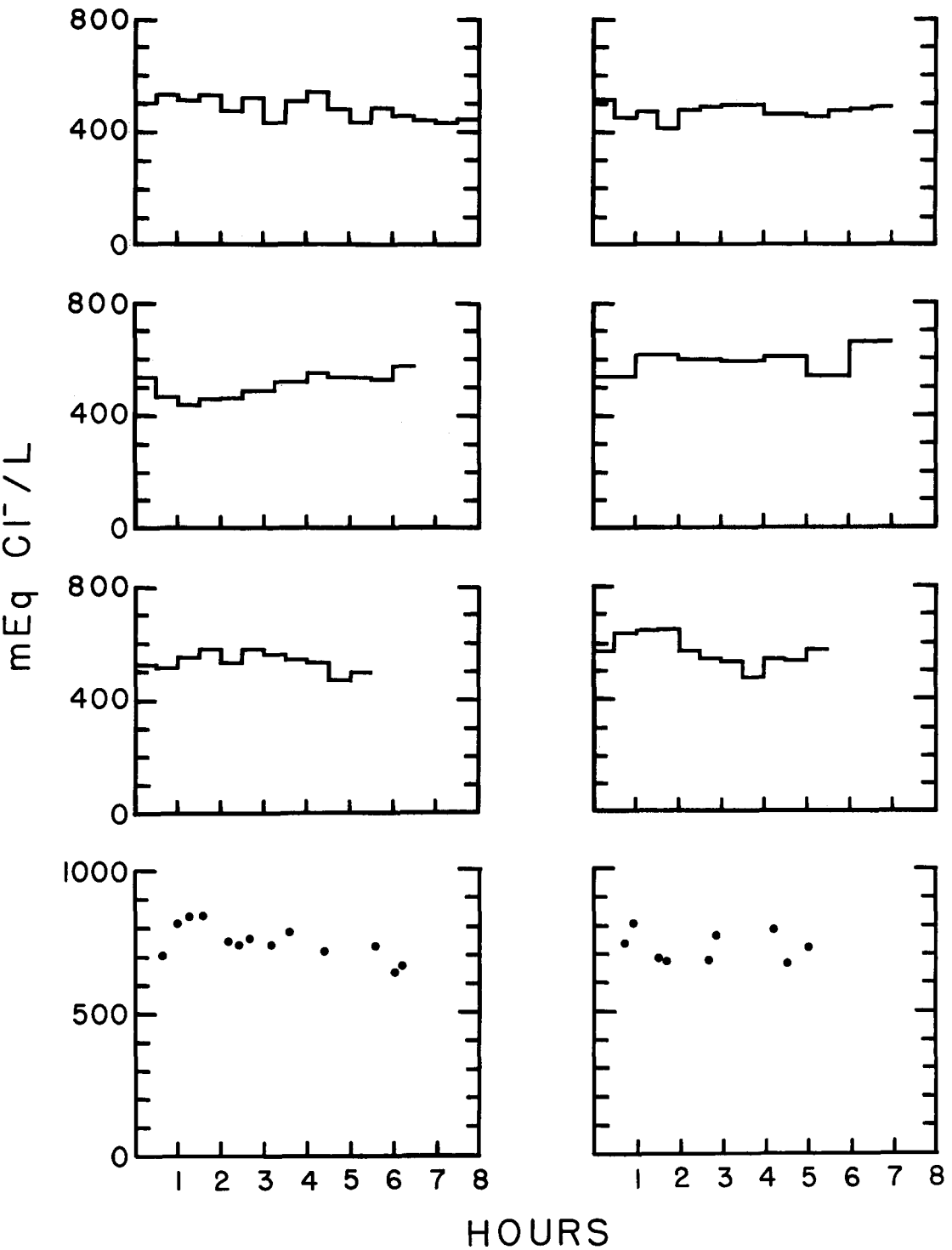

FIGURE 2. Chloride concentrations of the nasal secretions from six coots (top six graphs) and two rails (bottom graphs) given 1 ml/100 g body wt. of 15 per cent or 20 per cent NaCl solution. Samples from coots were obtained at 30-min intervals from oil-filled funnels. Secretions from rails were taken directly from the external nares with micropipettes. Data are plotted from time of first secretion.

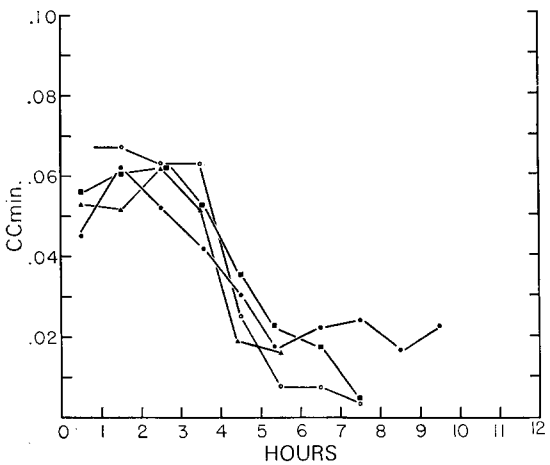

FIGURE 3. Rates of flow of nasal secretion from four coots given NaCl. Data are plotted from time of first secretion.

298 mEq/l, depending upon their proximity to sources of fresh or sea water. The mean concentration was 116 mEq/l.

Chloride concentrations in the fluid from *Salicornia* ranged from 510 to 1051 mEq/l, with a mean of 687 mEq/l. Sodium concentrations were between 580 and 1040 mEq/l, with a mean value of 680 mEq/l.

When the four rails were given only sea water to drink with a diet of chopped meat and some lettuce, between 9.0 and 12.1 per cent of body weight was lost in two days. Normal weights were regained in four days when we again provided fresh water ad libitum. Weight maintenance on various diets and salt solutions was not measured for coots.

CLOACAL ELIMINATION OF SALTS

It was assumed that the cloacal excreta was urine if it was free of fast green dye or obvious fecal material. Volumes of urine of 0.5–2 ml were usually voided by both species throughout the period of nasal secretion, generally at intervals exceeding 1 hr.

Following a dose of NaCl, maximum urine concentrations (table 1) were reached within about 2 hr by both species, and maintained at these levels throughout the period of secretion (fig. 1).

CONCENTRATION OF NASAL SECRETION

Secretion began in all birds 15–45 min after administration of a dose of NaCl. Maximum or near maximum concentrations of nasal secretion were usually reached during the first 30 min of secretion, and concentrations were maintained at approximately the same level (fig. 2, table 1).

RATE OF FLOW OF NASAL SECRETION

Secretion began at a maximum or near maximum rate of flow, and was maintained at this level for as long as 3 hr, after which it gradually declined until secretion ceased (fig. 3). The maximum rate of flow averaged 0.064 ml/min in four coots given NaCl. The maximum flow rates from four rails were between 0.015 and 0.0066 ml/min, and these rates declined with time in a pattern similar to that of coots.

The rates of chloride excretion through the salt glands of both species were measured directly by absorption of the secretion in cotton, or, for some coots, were calculated from data on volumes and concentrations (fig. 4, table 1).

Several coots given NaCl ceased secretion approximately 2 hr after they began, and shortly thereafter suffered convulsions and died. Blood samples taken from these birds immediately after death were viscous and the chloride and total osmotic concentrations of the plasma were as high as 163 mEq/l and 470 mOsmol/l. Secretion also ceased if coots were handled, but it resumed once the birds were left undisturbed for a while.

Initial doses of 50 per cent urea were regurgitated by two rails, and a second dose was then given to each one. After 2–3 hr these birds showed poor coordination and loss of equilibrium. Fluid was withdrawn from their crops and fresh water was added in an effort to revive them, but both birds died. Their blood was extremely viscous, and the total osmotic concentrations were 614 and 645 mOsmol/l. Two other rails showed normal coordination and survived plasma osmotic concentrations of 428 and 500 mOsmol/l.

STIMULUS RESPONSIBLE FOR SALT GLAND SECRETION

Nasal secretion occurred in all coots and rails given doses of NaCl and $NaHCO_3$. No secretion occurred in birds given $MgCl_2$ or urea. Coots that were given KCl did not secrete and died within one hour after this dose was given.

A one-factor analysis of variance revealed differences among the mean concentrations of sodium in the plasma of each species given the various salt solutions ($P < 0.01$). This procedure also demonstrated differences among the mean plasma chloride concentrations and among plasma osmotic concentrations of each species on the same series of salt loads. Plasma concentrations on each salt load were further compared with Tukey's w-procedure (Steel and Torrie 1960), and are summarized in tables 2 and 3.

Although the patterns of increase in sodium,

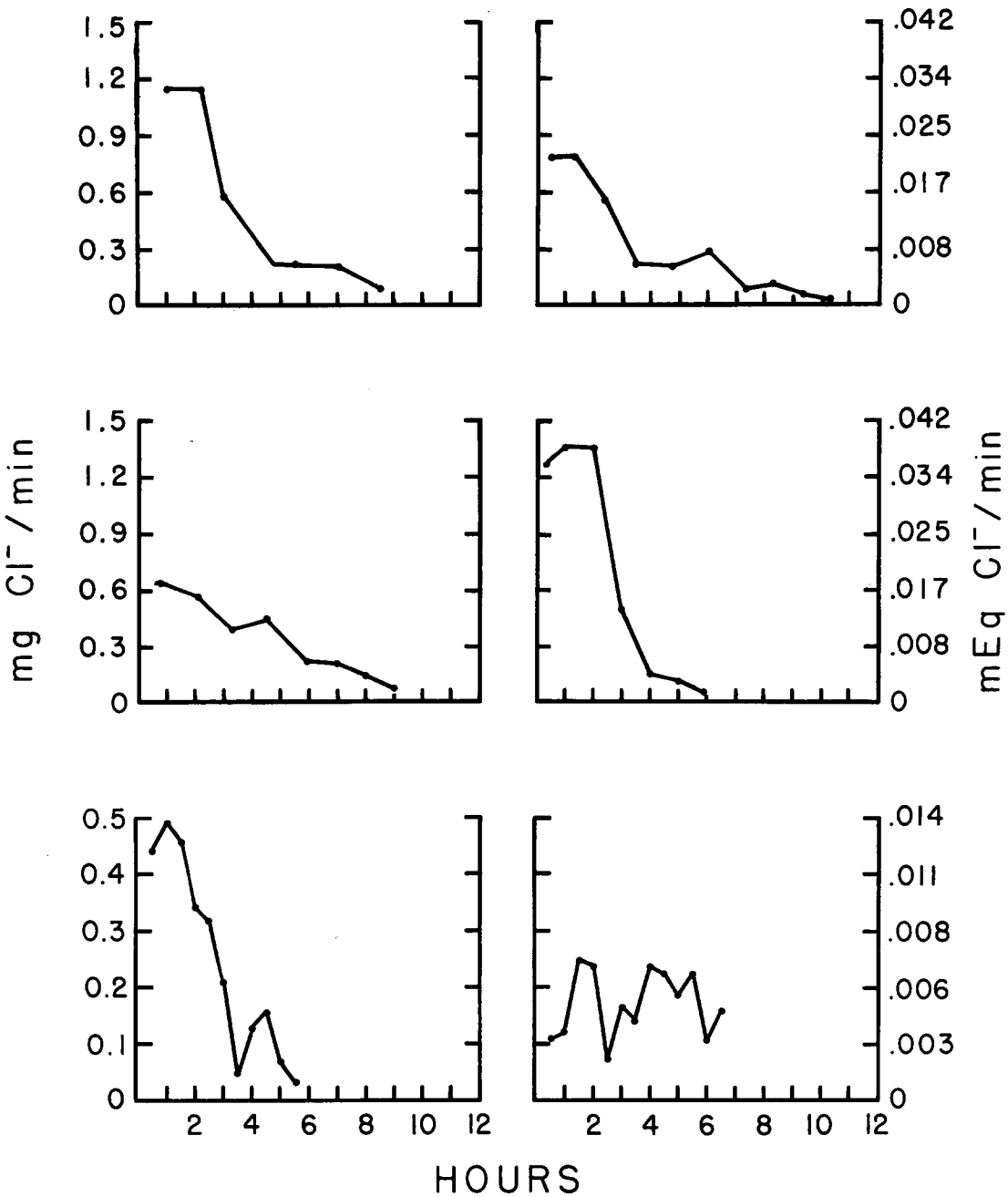

FIGURE 4. Rates of nasal chloride secretion from four coots (top four graphs) and two rails (bottom graphs) given NaCl. Samples for coots were obtained from oil-filled funnels and vials filled with cotton. Secretions from rails were gathered with cotton-filled vials. Data are plotted from time of first secretion.

chloride, and osmotic concentrations of the plasma were similar in the two species, the plasma concentrations of the rails under all conditions were generally higher than the corresponding values for coots.

DISCUSSION

RATES OF SALT EXCRETION

The amount of salt lost in the nasal secretion of various marine birds is 1–10 times the amount lost in the urine (Schmidt-Nielsen et al. 1958; Schmidt-Nielsen 1960). Four coots had a higher ratio (26) for the amount of chloride lost by these two routes than reported for any other bird. This suggests that when coots are deprived of sufficient water, the nasal glands become more important for them, relative to the kidneys, than for other birds.

The ratio of nasal to cloacal chloride excretion by rails was quite variable; it ranged

TABLE 2. Mean values for sodium, chloride, and osmotic concentrations of the plasma of American Coots given various solutions.

Treatment[a]	Sodium concn. (mEq/l)	Chloride concn. (mEq/l)	Osmotic concn. (mOsmol/l)
Normal (field)	135.0 (7, 15.9)[b]	96.6 (8, 4.5)	258.8 (4, 11.8)
NaCl	189.4 (9, 6.4)	133.0 (9, 8.2)	347.8 (9, 17.7)
$NaHCO_3$	189.3 (8, 5.5)	91.8 (8, 7.3)	336.2 (8, 10.9)
$MgCl_2$	167.1 (6, 10.5)	128.0 (7, 15.4)	352.1 (7, 16.8)
Urea	170.5 (5, 4.2)	107.2 (6, 9.1)	422.5 (6, 5.2)
Significant differences in plasma concentrations with indicated solutions	NaCl, $NaHCO_3$ > $MgCl_2$, urea, and normal ($P < 0.05$) NaCl, $NaHCO_3$, $MgCl_2$, and urea > normal ($P < 0.01$)	NaCl and $MgCl_2$ > urea, normal and $NaHCO_3$ ($P < 0.01$) Urea > $NaHCO_3$ ($P < 0.05$)	Urea > $MgCl_2$, NaCl, $NaHCO_3$ and normal ($P < 0.01$) Urea, $MgCl_2$, NaCl, and $NaHCO_3$ > normal ($P < 0.01$)

[a] Solutions which stimulated secretions are underlined.
[b] Sample size and SD.

from a value of one to as high as 71 in one bird that produced a negligible amount of cloacal excreta during the 4 hr following a salt load. The mean ratio of nasal to urinary chloride loss in rails (2.5) was similar to the moderate values of ducks (Scothorne 1959). The great difference between coots and rails in their nasal : cloacal ratios is largely the result of rails having both higher urine chloride concentrations, and a lower rate of nasal chloride excretion (only one-third that of the coots).

The rates of chloride secretion from the glands of coots and rails are far below the rates of excretion from the large glands of some marine birds, such as members of the family Laridae (Schmidt-Nielsen 1960). Perhaps the closest ecological equivalents to coots found locally are some of the Anseriformes. Several species of ducks, including Mallards (*Anas platyrhynchos*) and Pintails (*Anas acuta*), inhabit these coastal lagoons and presumably are faced with similar osmotic stresses. It is not surprising, therefore, that the concentra-

TABLE 3. Mean values for sodium, chloride, and osmotic concentrations of the plasma of Guam Rails given various solutions.

Treatment[a]	Sodium concn. (mEq/l)	Chloride concn. (mEq/l)	Osmotic concn. (mOsmol/l)
Normal	178.0 (4, 172.0–185.0)[b]	117.6 (4, 115.4–119.3)	335.2 (4, 320–342)
NaCl	215.9 (4, 205.0–225.0)	145.7 (4, 141.0–149.0)	383.5 (4, 368–400)
$NaHCO_3$	225.0 (3, 218.7–231.2)	117.2 (3, 110.9–123.2)	361.3 (3, 321–401)
$MgCl_2$	189.6 (3, 187.5–193.8)	136.0 (3, 124.0–144.1)	372.7 (3, 350–393)
Urea	186.2 (4, 175.0–200.0)	124.2 (4, 111.0–141.3)	546.8 (4, 428–645)
Significant differences in plasma concentrations with indicated solutions	$NaHCO_3$ and NaCl > $MgCl_2$, urea, and normal ($P < 0.01$)	NaCl and $MgCl_2$ > $NaHCO_3$ ($P < 0.05$)	Urea > NaCl, $MgCl_2$, $NaHCO_3$, and normal ($P < 0.01$)

[a] Solutions which stimulated secretions are underlined.
[b] Sample size and range.

tions and total rates of secretion of chloride from ducks (Scothorne 1959) are similar to the values obtained for coots.

A comparison of the estimated dietary salt intake of coots with their rates of nasal salt secretion indicates that their nasal glands serve strictly as an auxiliary to the kidneys. In the laboratory each bird ate approximately 250 g of lettuce per day, suggesting that they normally consume a similar quantity of *Salicornia.* The salt content of the least concentrated *Salicornia* (510 mEq/l) is low enough that birds could excrete this salt with a net gain of free water. Their rate of nasal salt excretion, however, is so low (630 mEq Cl^-/hr) that in 24 hr a coot could eliminate the salt from only 57.5 g of *Salicornia.* This amount is so far below the probable daily food consumption that it is likely that coots rely on drinking water to remove, via the kidneys, most of the salt ingested with a greater consumption of this plant.

The problem of salt excretion would be greatly increased if coots ate plants without regard to salt content, thus consuming juice with a mean chloride concentration of 687.4 mEq/l. Drinking fresh or mildly brackish water would be necessary for survival on this diet.

Water of the maximum salinity measured in San Elijo Lagoon is well above the maximum urine concentrating capacity of their kidneys, and would impose an additional salt load on coots that already were secreting the salt in their food at maximum rates. However, water of average or minimal salinity in this location (116 mEq Cl^-/l) is below the concentrating ability of their kidneys, and could conveniently be consumed for renal removal of salts.

Salt glands are probably of little importance to Guam Rails. They apparently have high water requirements as indicated by their fondness for water and their inability to maintain weight on a succulent diet when deprived of water. A high water requirement, however, would not appear to be a problem, since any need for water in addition to that in their food could easily be provided by rainfall. Average precipitation in Guam during the driest month (March) is 44 mm, and the lowest rainfall recorded for any month during a 10-year period was 15 mm (U.S. Department of Commerce 1968). Rainfall exceeds 62 mm during all other months, and from August through October, average precipitation is over 310 mm per month.

STIMULUS FOR NASAL SECRETION

The initial paper on salt gland function reported that intravenous infusion of sucrose stimulated a cormorant to produce a nasal gland secretion of a concentration similar to that induced by infusion of NaCl solution (Schmidt-Nielsen et al. 1958). These workers concluded that any elevation of osmotic concentration of the blood will stimulate secretion, and subsequent workers have accepted this conclusion in studies with all other birds possessing salt glands.

The results of the present study demonstrate conclusively that the salt glands of two members of the Rallidae do not secrete in response to a simple increase in the osmotic concentration of the plasma. These birds did not secrete when given doses of $MgCl_2$ or urea, but osmotic concentrations of their plasma were equal to, or greater than, the threshold plasma concentrations of birds given NaCl or $NaHCO_3$ (tables 2 and 3). Examination of chloride concentrations in the plasma (tables 2 and 3) indicates that elevations of plasma chloride are also not the stimulus for secretion.

Secretion occurred only when the concentrations of sodium in the blood were significantly above those of non-secreting birds. Sodium concentrations also increased in the plasma of birds given $MgCl_2$ and urea, but these levels did not reach the threshold levels of secreting birds. Thus, the salt glands of both species appear to respond specifically to an increase in plasma sodium.

The site at which an elevation in plasma sodium has an effect is uncertain. McFarland (1964:1203) attributed secretion in gulls to stimulation of the osmoreceptors of the central nervous system that regulate the secretion of the salt glands, and suggested that this is "probably brought about by the cellular shrinkage caused by the increased osmolarity associated with elevated intravascular NaCl concentration. . . ." In coots loaded with $MgCl_2$ or urea, the osmotic concentration of the plasma was as high as in birds loaded with NaCl, and any cellular shrinkage was presumably as great.

Lanthier and Sandor (1967) infused various solutions into the wing veins of Peking Ducks. These compounds could be divided into two groups, based on the secretory responses of the salt glands. Both the concentrations and rates of secretion were similar in birds given NaCl, $NaHCO_3$, mannitol, and sucrose. Ducks given solutions of NH_4Cl, urea, and dextran produced secretions that were only one-half the concentration, and at approximately one-

eighth the flow rates, of those from birds given the first group of compounds. The rate, but not the concentration, of nasal secretion was also below normal when sucrose was infused into a cormorant (Schmidt-Nielsen et al. 1958).

Lanthier and Sandor (1967) concluded that compounds in the first group did not pass freely across the membranes of the osmoreceptors. Presumably, when these compounds were added to the blood, the osmoreceptors shrank and stimulated secretion according to the sequence outlined by Fänge et al. (1958) and McFarland (1964). Lanthier and Sandor suggest that the osmoreceptors are more freely permeable to the second group of compounds, and quickly reached osmotic equilibrium with the surrounding fluids. As a result, the slight shrinkage of the receptors stimulated only slight secretion, in spite of the increase in plasma concentrations. Their conclusion, therefore, is in agreement with the original one that an increase in osmotic concentration of the blood will stimulate secretion, but with the qualification that the substance added must not pass freely through the membrane of the receptor cells.

Lanthier and Sandor also report the plasma sodium concentrations for their ducks both before infusion of a solution and during secretion, and these data appear to offer an alternative conclusion that is consistent with that of our study. The maximum elevation in concentration of plasma sodium was only 12.5 mEq/l, and was measured in those ducks given NaCl. This elevation was approached by the increases in concentrations of plasma sodium that followed the infusion of all other solutions, although the increases were generally smaller with compounds that stimulated only slight secretion. This fact suggests to us that an increase in plasma sodium is an equally likely explanation for secretion in these ducks, but that the threshold level for secretion is quite low compared to the average increases required for secretion in coots (54 mEq/l) and rails (38 mEq/l). Elevations in the concentration of plasma sodium also occurred with all solutions given to coots and rails, but these concentrations never reached the higher threshold levels necessary for secretion by these birds.

It now appears that the "osmoreceptors" of coots and rails are, in fact, sodium receptors. The similarity in responses of these two species suggests that sodium receptors are present throughout the members of the Rallidae.

There remains the question of whether other birds possessing salt glands have receptors that are sodium specific. Most research on the function of avian salt glands has involved the administration of NaCl solutions, and increases in concentration of plasma sodium have frequently been measured as indices of increases in osmotic concentrations. The concentrations of sodium in the plasma of coots and rails at initial secretion (190 and 216 mEq/l, respectively) are higher than values reported during secretion in ducks (160 mEq/l, Phillips et al. 1961; 163 mEq/l, Lanthier and Sandor 1967), albatrosses (164 mEq/l, Frings et al. 1958), and most Falconiformes (160–190 mEq/l, Cade and Greenwald 1966). Plasma sodium concentrations of secreting sea gulls (190 mEq/l, McFarland 1964) are similar to the values for coots. The differences between normal and secreting sodium concentrations are also greater in coots and rails than in these other species. Because blood samples from these other birds were taken at various times following the start of nasal secretion, the significance of the sodium concentrations in various species is unclear.

These increases in plasma sodium levels in all secreting birds could, however, lend support to either the original idea that receptors respond to any increase in osmotic concentration of the plasma or to our conclusion that the receptors are sodium specific. If the salt glands of all birds are homologous, then it seems likely that systematic investigation with a variety of compounds and with careful attention to plasma concentrations, would show sodium receptors, rather than osmoreceptors, to be the rule. A receptor sensitive to sodium would seem fully as advantageous as one sensitive to a general osmotic increase. Most of the avian groups possessing salt glands inhabit marine or brackish waters, and the primary source of an increase in osmotic concentration of the plasma would be the sodium chloride ingested in food or with drinking water. A sodium receptor, furthermore, would be most sensitive to the substance secreted by the gland that it regulates.

SUMMARY

The performance of nasal salt glands was studied in American Coots and Guam Rails of the family Rallidae. Mean maximum concentrations of the nasal secretion from coots and rails were 542 and 785 mEq/l, respectively. The salt glands of coots produced chloride at a maximum rate of 1.06 mg/min, and rails

secreted 0.33 mgCl^-/min. These rates of salt excretion appear to be insufficient to allow either species to meet all of its normal water needs by consumption of sea water, and these birds probably rely on fresh or mildly brackish water, which is abundant in their habitats.

Various compounds were given to these birds through a stomach tube in quantities sufficient to elevate the concentrations in their plasma. Nasal secretion occurred only when sodium concentrations in the blood reached levels significantly above the sodium levels in non-secreting birds. Elevations of plasma chloride concentration or plasma osmotic concentrations in the absence of significantly high sodium levels did not stimulate secretion. This pattern conflicts with previous explanations that nasal secretion will be stimulated by an increase of plasma osmotic pressure caused by the addition of any substance to the blood. We conclude that the "osmoreceptors" that initiate secretion in members of the Rallidae are actually sodium receptors. Detailed study of salt glands in other birds may show that sodium receptors are widespread among the class Aves.

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