Nasal Salt Gland: Independence of Salt and Water Transport

Abstract. *The nasal salt-secreting gland of the domestic duck can produce a fluid with a sodium chloride concentration about three times that in blood plasma. To study the cellular mechanism responsible for the formation of the highly concentrated fluid, the gland was poisoned by retrograde injection of mercuric chloride into the lumen, decreasing the salt concentration to that in plasma while the volume of secretion was unchanged. Carbonic anhydrase inhibitor (acetazoleamide) caused a moderate decrease in salt concentrations, again with maintenance of volume of secretion. The results suggest that concentration and volume of the secreted fluid depend on two different cellular mechanisms.*

While a nasal gland is present in all birds it is particularly well developed in marine species. In these it secretes a highly concentrated solution of sodium chloride, and it seems that the exclusive function of the gland is that of osmoregulation (*1*). In the domestic duck the gland is of intermediate size, and both the size of the gland and its ability to secrete hypertonic salt solutions increases when the birds are regularly exposed to high salt intake (*2, 3*).

Because of the ease of obtaining and handling ducks we chose to use this species rather than wild marine birds which are more difficult to obtain and provide a less uniform material. White Peking ducklings (a highly domesticated variety of the wild mallard, *Anas platyrynchos*) were obtained commercially and fed on commercial bird feed. They were provided with a 3 percent solution of sodium chloride for drinking instead of fresh water, but they had the opportunity to drink fresh water for about ½ hour each day when the concrete floor of the pen was flushed with water for cleaning.

For the experiments the birds were anesthetized by intravenous injection of nembutal (about 40 mg/kg body weight). The ducts of both glands were exposed close to the gland and cannulated with thin polyethylene tubes (0.2 mm outside diameter). As the glands of anesthetized birds do not respond to osmotic loads (such as the injection of hypertonic sodium chloride solution) secretion was induced by the injection of methacholine chloride (Mecholyl, Merck) in amounts of 0.15-0.2 mg per kilogram of body weight (*4*).

Samples were collected from the gland on each side in 5-minute periods until the methacholine-stimulated secretion had subsided. One gland was then subjected to a retrograde injection of mercuric chloride or acetazoleamide (Diamox, Merck) while the other gland was subjected to a similar retrograde injection of the same volume of 1 percent sodium chloride to serve as a control. A second injection of methacholine was then used to induce renewed gland secretion and samples were again collected in 5-minute periods and analyzed for sodium, potassium, and chloride (*5*).

Figure 1 shows the effect of retrograde injection of mercuric chloride (0.08 ml of 0.05 percent solution) which was allowed to act upon the gland for 30 minutes before the second injection of methacholine. The volume of secretion was undiminished or perhaps slightly increased from the poisoned gland. The concentrations of sodium and chloride were decreased approaching the concentrations found in the blood serum.

Table 1 shows the effect of retrograde injection of carbonic anhydrase inhibitor (acetazoleamide) into the lumen of the gland. The flow rate was unaffected while sodium and chloride concentrations were somewhat decreased. Previous experiments have shown that although the intravenous injection of acetazoleamide stops secretion from an actively secreting salt gland, the secretory potential is maintained (*6*) and secretion is resumed if the gland is restimulated by methacholine injection (*4*). It was therefore suggested that the blocking effect of acetazoleamide is somewhere in the osmoregulatory reflex chain outside the salt gland itself (*1, 6*).

Table 1. Effect on secretion from salt gland after retrograde injection of carbonic anhydrase inhibitor (acetazoleamide). Secretion induced by injection of 0.15 mg methacholine per kilogram of body weight. Samples collected in 5-minute periods.

Time (min)	Flow rate (mg/g of gland per min)	Na (meq/liter)	Cl (meq/liter)
	Experimental side		
0– 5	46.2	370.5	350
5–10	26.9	367.0	352
Injection of 30 mg acetazoleamide in 0.15 ml of 1% NaCl			
70–75	47.4	239.0	222
75–80	29.5	237.5	220
	Control side		
0– 5	56.8	344.5	320
5–10	35.8	351.0	328
Injection of 0.15 ml of 1% NaCl			
70–75	64.2	369.0	356
75–80	37.0	344.5	337
	Blood serum		
		158.5	125.5

Since acetazoleamide influences sodium and chloride concentrations without affecting flow rate from the gland, these experiments, as well as the mercuric chloride effect, suggest an independence of the volume of fluid produced and the ionic transport mechanism. If this is the case it is easier to understand that, in the nor-

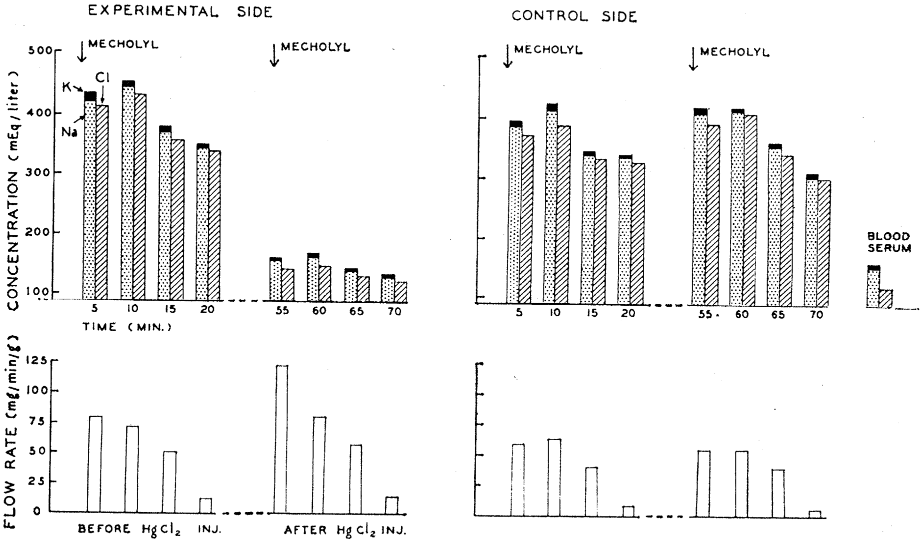

Fig. 1. Effect on secretion from salt gland of retrograde injection of mercuric chloride. Secretion induced by injecton of 0.13 mg methacholine per kilogram of body weight. Samples collected in 5-minute periods.

mally secreting gland, the ionic concentrations are extremely uniform and independent of wide variations in flow rate (*1*; *7*).

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Nasal Salt Excretion and the Possible Function of the Cloaca in Water Conservation

Abstract. *Secretion of concentrated salt solutions from the nasal region was observed in several terrestrial birds and reptiles. In the secreted fluid potassium usually exceeded sodium concentrations, with chloride and bicarbonate as the major anions. It is suggested that the extrarenal excretion of salts is related to the reabsorption of water in the cloaca, that it is necessary for the production of urine with a particularly low water content, and perhaps was prerequisite for the evolution of efficient cloacal water conservation.*

Marine birds and reptiles tolerate a high salt intake because they possess nasal glands that secrete a fluid with high concentrations of salt, mainly sodium chloride (*1*). Similar secretion of large volumes of highly concentrated salt solutions has not been reported for terrestrial birds and reptiles, and since these forms normally are not exposed to a high salt intake, such a mechanism appears to be less essential to them.

However, we have recently found that several terrestrial reptiles and birds do secrete significant quantities of salt from the nasal region, although not in the conspicuously large amounts found in their marine relatives.

A specimen of the tropical lizard *Iguana iguana* which was kept in the laboratory was occasionally found with white incrustations around the nostrils. The material was water soluble, and preliminary analysis showed large amounts of potassium as well as sodium. Closer observation of the lizard while kept in a glass-walled terrarium revealed that the animal had the habit of pushing its nose against the wall, thereby leaving a salty deposit on the glass. A total of 160 mg of this deposit was collected and analyzed; it consisted of sodium and potassium chlorides and bicarbonates. Potassium was present in an amount three times as high as the sodium; the corresponding anions were in the proportion of two parts of bicarbonate to three parts of chloride. These four ions accounted for 83 percent of the total weight of the deposit.

A large iguana (1.9 kg) was then subjected to a heavy salt load by intraperitoneal injection of 29 ml of 10 percent sodium chloride solution, a procedure similar to that used in marine birds to stimulate secretion from nasal salt glands. After 2 hours, droplets of fluid appeared at the nostrils of the iguana and on the walls of the container, and samples were collected and analyzed. Over a period of 4 hours the sodium concentration in the samples varied from 340 to 894 meq/liter with a mean of 507 meq/liter while the potassium concentrations varied from 316 to 862 meq/liter with a mean of 497 meq/liter. The samples were obtained as soon as possible after the fluid appeared at the nostril, but there was no way of preventing evaporation nor of evaluating to what extent evaporation had taken place in the nasal passages.

The total volume of the secretion was difficult to estimate because of the irregular occurrence of the droplets, but it appeared to be in the order of 0.5 ml per hour, which is about 1/50 of the rate of secretion commonly observed in the herring gull. Two days later the iguana was still secreting fluid from the nose at a moderate rate. A sample contained 728 meq/liter sodium and 290 meq/liter of potassium, that is, the proportion of sodium relative to potassium had increased, presumably as a response to the heavy sodium load used to stimulate secretion.

Analogous experiments carried out with the American desert lizard, *Dipsosaurus dorsalis* gave similar results. Secretion was stimulated with a salt load, and the concentration of the fluid over a 2-hour period averaged 494 meq/liter sodium and 1387 meq/liter potassium. Two days after the sodium chloride load, the concentrations had changed to 1032 meq/liter sodium and 640 meq/liter potassium.

The Old World desert lizard *Uromastyx aegyptius* showed a response to salt load similar to that observed in *Dipsosaurus*, with sodium concentrations (mean = 639 meq/l) less than one-half of the potassium concentration (mean = 1398 meq/l) during the first 3 hours.

Among desert birds we have observed nasal secretion of fluids with high concentrations of salts in the desert partridge, *Ammoperdix heyi* and in the ostrich, *Struthio camelus*. In these birds secretion from the nasal region occurred without osmotic stimulation (injection of salt) when the birds were exposed to high temperature. In the desert partridge small amounts of nasal secretion were also produced in response to salt loads; in this case the fluid had a high sodium concentration and only a moderate or low potassium concentration, similar to the composition usually observed in marine birds. We have experimented with only one ostrich which, because of its value, has not yet been subjected to salt loads. When the bird is exposed to high temperatures and simultaneously deprived of drinking water it secretes fluid which contains high concentrations of potassium, sodium, calcium, and chloride. Considerable variations were found in the composition of nasal secretion of the ostrich; in some samples sodium and potassium concentrations were similar, in others potassium was five to ten times as high as sodium.

Thus, the nasal secretion of various salts has been observed in a number of terrestrial reptiles and birds. Most of the observed species are from arid or desert habitats and therefore are adapted to an extreme degree of terrestrialism. However, the iguana is a typical humid-tropical form, and nasal secretion is therefore not restricted to arid-adapted forms.

Since it now seems that nasal secretion of salts occurs widely in birds and reptiles, the copious nasal secretion in marine forms can perhaps be regarded as a highly developed specialization of a general extrarenal excretory mechanism.

We should like to suggest that the extrarenal excretion of salt may be related to the capacity of birds and reptiles to withdraw water from the urine in the cloaca and that it is an integral part of their capacity to produce a semisolid urine consisting mostly of