

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 nos-

trils. 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 chlo-

ride 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

uric acid. In fact, such an extrarenal mechanism may be a necessary prerequisite for these animals to take full advantage of the potentialities of uric acid excretion in water conservation. There is considerable evidence that water is reabsorbed in the cloaca of birds and reptiles (2). The urine produced in the kidney may have uric acid crystals suspended in it, but it must be relatively liquid in order to pass from the kidney through the thin ureters into the cloaca where water must be reabsorbed to produce the semisolid urine often observed in reptiles and birds. Experimental evidence, although not unequivocal, supports this concept. The removal of water from the cloacal contents could take place either through an active transport of water, or by the reabsorption of osmotically active substances with the water following passively through osmosis. If water were actively reabsorbed and cations such as sodium and potassium were to remain in the cloaca, the osmotic work involved would be very great (3) and would increase as the remaining fluid became more concentrated. If soluble cations were to remain in the cloaca they would finally form a highly concentrated solution, and it would be difficult to produce the almost dry urine pellets that are produced by reptiles and birds on a limited water intake.

The alternative hypothesis, that solutes are reabsorbed by active transport from the cloacal contents and that water follows passively is more plausible. The reptilian and bird urines produced by the kidney are always relatively dilute fluids. The reptilian kidney cannot produce urine more concentrated than the plasma, and the bird kidney in general can concentrate urine only to approximately twice the plasma concentration (the concentration limit for the mammalian kidney is approximately 17 times the plasma concentration). A simple improvement in the concentrating ability of the reptilian or bird kidney is probably not feasible because it would lead to the precipitation of so much uric acid in the kidney tubules that renal function would be impaired or blocked. The removal of a dilute or approximately isotonic fluid from the cloacal contents would be relatively inexpensive thermodynamically if the primary transport process were that of an active transport of cations with water following passively. If the same net result were achieved through an active transport of water, the expense would probably be several hundred times as

great. In fact, in no case has it been convincingly demonstrated that the primary mechanism in the transportation of fluid is an active transport of water.

Should the removal of water from the cloacal contents be achieved through the reabsorption of cations, such as sodium or potassium, this would necessitate another route for the final elimination of these cations from the body. The nasal salt secreting gland is precisely such a mechanism.

It is probable that both sodium and potassium are reabsorbed in the cloaca under circumstances which require the withdrawal of water from the urine. The relative abundance of these two ions in the food varies, potassium being high in plant food and sodium more abundant in food of animal origin. Thus, the relative amounts of sodium and potassium to be eliminated vary with the diet, and this would explain why more potassium than sodium was eliminated by a plant-eating reptile such as the iguana. It also explains why the major anion in the nasal secretion of this animal was bicarbonate; plant food yields an excess amount of cation because the anions in the food, mainly organic acids, are metabolized and not excreted.

If water reabsorption depends on sodium reabsorption in the cloaca in connection with extrarenal excretion of the salt, we also have an explanation for the observation that, when a heavy salt load is given to a gull, the sodium content of cloacal urine often falls to very low values (1). This can better be understood if the response of the avian organism to an osmotic load is to achieve water conservation through an increased cloacal sodium reabsorption.

It has previously been suggested that the cloaca serves the function of sodium reabsorption (4). Evidence in favor of this opinion includes experiments in which the ureters of chickens were connected directly to the exterior so that the cloaca was bypassed. Such birds underwent excessive sodium loss but could be kept alive if sodium was added to the drinking water.

It is interesting to note that water conservation in the mammalian kidney is likewise achieved through an active transport of sodium from the urinary fluid to the blood, a transport which through the counter-current multiplier system permits an efficient withdrawal of water in the collecting ducts and thus the achievement of a high urine concentration (5). It now appears that the withdrawal of water from the urine

of birds and reptiles may also be achieved through an active transport of sodium or potassium from the urinary fluid to the blood with water following passively. An extrarenal excretory mechanism is a necessity for the function of such a mechanism; it is possible that extrarenal excretion is a prerequisite for the evolution of birds and reptiles adapted to highly terrestrial habitats and that it is a prerequisite for these animals to utilize fully the advantage offered by the excretion of uric acid as the final metabolic end product of protein metabolism.

Obviously, water conservation is not always needed in a reptile or bird; at times they produce copious volumes of urine, and in this event there would be no need for the mechanism just presented (6).

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Synthesis of α -Linolenic Acid by *Leishmania enriettii*

Abstract. *The zooflagellate Leishmania enriettii synthesizes α -linolenic acid as determined by experiments with stearic acid uniformly labeled with C^{14} . This is the first demonstration of the synthesis of α -linolenic acid by a non-photosynthetic organism.*

One of the few generalizations possible concerning the phylogenetic distribution of fatty acids is that higher plants synthesize α -linolenic acid (*cis*, *cis*, *cis*-9,12,15-octadecatrienoic acid) while higher animals do not (1). A further refinement of this statement resulted from the study by Erwin and Bloch (2) of the fatty acids of certain phytoflagellates. When grown in the light, *Euglena gracilis* contained α -