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THE FUNCTION OF THE SALT GLAND IN THE BROWN PELICAN

BY KNUT SCHMIDT-NIELSEN AND RAGNAR FANGE

It has long been a matter of speculation how oceanic birds cover their needs for water. Some marine birds remain at sea for weeks or months, hundreds of miles from land and any possible sources of fresh water. Sea water is known to be toxic to man and most other mammals, the reason being its high salt content. Some authors have stated that marine birds do drink sea water (Murphy, 1936: 337), while others have maintained that they can subsist wholly on water obtained from the food (Smith, 1953: 163).

In order to profit from the ingestion of sea water it is necessary for an animal to excrete salts in a concentration at least as high as that in the water ingested. The elimination of the salt would otherwise require an additional amount of water which would be taken from the body tissues. Therefore, if the organism cannot excrete a highly concentrated salt solution, the drinking of sea water only will lead to a progressive dehydration or a harmful accumulation of salt.

The bird kidney is able to excrete salts in a concentration only about one-half of that found in sea water. Hence, if the bird kidney should excrete the salts from a given amount of sea water, it would be necessary to produce twice as much urine as the amount of water ingested. Thus, the kidney is not able to keep a marine bird in a favorable water balance if it drinks sea water.

However, it was recently discovered that in marine birds a major part of the ingested salt is excreted extrarenally. The nasal glands, or salt glands, are able to produce a highly concentrated salt solution, making it possible to tolerate drinking of sea water (Schmidt-Nielsen *et al.*, 1957, 1958). Cormorants as well as a number of other marine birds have been found to secrete salt in high concentrations from the salt gland, and there is little doubt that this is the general avenue for salt excretion in all marine birds. This function is well correlated with the size of the salt gland, which is large in marine birds, as contrasted with terrestrial birds, which have a very small nasal gland. Our findings on the function of the salt gland in the Brown Pelican are here reported.

Materials and Methods

The experimental animals were common Brown Pelicans (*Pelecanus occidentalis carolinensis*). They were caught on the Gulf Coast of Florida immediately before being brought to the laboratory for the physiological studies. Altogether eight birds were used, four with

mature plumage (average weight 3.36 kg.), and four with juvenal plumage (average weight 2.59 kg.). Most of the birds were unwilling to eat in captivity, and force feeding resulted in vomiting. The experimental work was therefore done on fasting animals.

The purpose of the investigation was to establish whether the salt gland plays the same role in salt excretion in the pelican as it does in other marine birds. Stimulation of the gland was accomplished in two different ways, either by imposing a heavy salt load by infusion of hypertonic sodium chloride solution, or by injection of a solution of mecholyl, a synthetic drug with an effect similar to that of parasympathetic nerve stimulation. Although these stimuli do not correspond precisely to the normal situation the bird meets in nature, the salt load is an exaggerated representation of the physiological effects of ingestion of sea water, and the mecholyl injection simulates the action of the secretory nerves that normally control the gland.

All injections were made intravenously in the foot of unanesthetized birds. We have found in other species of marine birds that anesthesia blocks the normal response of the gland to a salt load. Samples of the secretion from the salt gland were collected by means of thin polyethylene tubings introduced one or two mm into the narrow external nares. Occasional samples were taken of urine and of lacrymal fluid for comparative purposes.

The sodium and potassium content of the samples was determined by means of a flame photometer, and chloride by a modification of the Volhard titration method (Rehberg, 1926).

RESPONSE TO A SALT LOAD

A salt load was imposed by injection of various amounts of a 10% sodium chloride solution in four pelicans (2 adult and 2 juveniles). Within 1 to 5 minutes after the injection, drops of a clear, water-like liquid appeared at the external nares. The liquid ran down along the grooves on the upper side of the beak until it reached the tip of the beak, where it dripped off. The head shaking which was characteristic in the behavior of cormorants during secretion from the salt gland (Schmidt-Nielsen, *et al.*, 1958) was not observed in pelicans. The secretion continued for some one to two hours.

In a typical salt load experiment with a pelican (2.54 kg. body weight) 28 ml of a 10% NaCl solution were injected intravenously. Within one minute of the beginning of injection the nasal secretion had started. During an initial period of 7 minutes the rate of secretion increased rapidly. When it had reached a high level it continued at a rather constant rate for 110 minutes and then declined abruptly and

ceased altogether during the next 15 minutes. Except for the terminal observation period the flow remained between 0.26 and 0.31 ml/minute (see table 1).

TABLE 1

VOLUME AND COMPOSITION OF NASAL SECRETION IN A PELICAN SUBJECTED TO SALT LOAD

Time, min.	*Min.*	*Vol. of secr. ml.*	*ml per min.*	*Conc. mEq/liter*		
				Na	*Cl*	*K*
0–7	7	—	—	650	—	11
7–17	10	2.885	0.29	637	656	10
17–27	10	2.686	0.27	700	695	12
27–37	10	2.997	0.30	764	850	15
37–57	20	6.155	0.31	736	740	16
57–77	20	5.879	0.29	721	730	14
77–97	20	5.209	0.26	704	708	14
97–117	20	5.119	0.26	696	704	13
117–132	15	2.815	0.19	676	694	14
	Total:	33.745	Aver.: 0.27	698	722	13

The total amount of liquid secreted from the salt gland in this experiment was 33.75 ml. In the same period four samples with a total volume of about 22 ml of cloacal contents were passed (most of this was only slightly contaminated with fecal material). The amount of liquid produced by the salt gland therefore exceeded the amount produced by the kidney. However, the important difference in the roles of these two organs appears when the salt concentrations are compared.

While the average salt concentration in the nasal secretion was over 700 mEq/liter (ab. 4 g NaCl per 100 ml), the average urine concentrations were about 250 mEq/liter (ab. 1.5 g NaCl per 100 ml) (see table 2). With the smaller volume of urine and its much lower salt concen-

TABLE 2

VOLUME AND COMPOSITION OF URINE SAMPLES DISCHARGED DURING THE EXPERIMENT DESCRIBED IN TABLE 1

Urine vol.	*Conc. mEq/l*		
ml	*Na*	*Cl*	*K*
6.7	222	251	18
7.1	207	205	7
5.9	261	316	38
1.9	156	269	52
21.6	212	260	29

trations, it appears that the amount of salt eliminated by the kidney is about one fifth of the total, while about four-fifths of the salt was excreted from the salt gland in the observation period of slightly more than two hours (see table 3).

In this connection it is desirable to emphasize that the salt load imposed in this experiment was in the form of a salt solution about three times as concentrated as sea water. Such loads would not occur in nature. The total volume of nasal secretion (33.75 ml) exceeded the injected volume of salt solution (28 ml). Its concentration of salt (ab. 700 mN), although not as high as in the injected solution (1710 mN) was well above that of sea water (ab. 550 mN). In other words, the salt gland has the capacity to excrete the salts contained in ingested sea water.

TABLE 3

THE AMOUNTS OF SALT EXCRETED IN A PELICAN DURING TWO HOURS AFTER THE INJECTION OF A SALT LOAD OF 28 ML OF 10% NaCl SOLUTION

	NaCl injected	*Nasal excretion*	*Renal excretion*	*Total excretion*
Volume, ml	28	34	22	56
Total NaCl, mEq	47.9	23.9	5.3	29.2
Total NaCl, gram	2.8	1.4	0.3	1.7

RESPONSE TO OTHER STIMULATION

Previous work on cormorants has shown that the secretion from the salt gland is stimulated not only by a load with sodium chloride, but also by a general osmotic load in the absence of increased salt concentrations (Schmidt-Nielsen *et al.*, 1958). This was shown by the injection of hypertonic solutions of sucrose, which stimulated a secretion similar to that observed after a salt load.

Studies on gulls, which will be described in another publication, have shown that the innervation of the salt gland is of parasympathetic nature, and that secretion from the gland can be stimulated by mecholyl (methacholine chloride), a drug that mimics parasympathetic stimulation and causes secretion from a number of glands. It was therefore of interest to compare the stimulation by mecholyl in the pelican with its effect on gulls. Mecholyl was injected intravenously in amounts of from 0.1 mg to 0.17 mg per kg body weight. Secretion from the salt glands as well as secretion of tear fluid started immediately and continued for periods up to ten minutes. The rate of secretion from the salt glands was rather low, the highest rate observed under mecholyl

stimulation was 0.17 ml/minute for a five minute period. Hence, some samples obtained were too small for complete analysis, but sodium determinations could be made on five samples. These ranged from 590 to 750 mEq Na/liter (aver. 652 mEq/1). In other words, the concentration was similar to that obtained by a salt load (see table 1). Potassium was from 10–18 mEq/1, and chloride from 632 to 708 mEq/1.

The mecholyl stimulation also provided an opportunity to obtain samples of lacrymal fluid. In the three samples obtained the sodium concentrations were 52, 83 and 93 mEq/liter, respectively. This is lower than the sodium concentration of the plasma, which is about 150 to 160 mEq/liter, and it clearly shows that the glands that produce the lacrymal fluid have no role similar to that of the salt gland in the excretion of salt.

THE MAJOR GLANDS IN THE ORBITAL REGION

In the Brown Pelican the salt gland, or nasal gland, is located in the upper anterior portion of the orbital cavity of the skull close to the interorbital septum (see figure 1). A shallow depression in the underside of the bony roof of the orbit (praefrontale) marks the place of the gland. The position of the gland is the same as reported by Technau (1936, p. 560) in *Pelecanus onocrotalus*. The gland has an oblongate pear-shaped form with a length of 2.6–3 cm and a width of 0.6–0.8 cm. The surface of the gland is slightly lobulated. The attenuating anterior end continues forward horizontally as a duct that is about 1 cm long

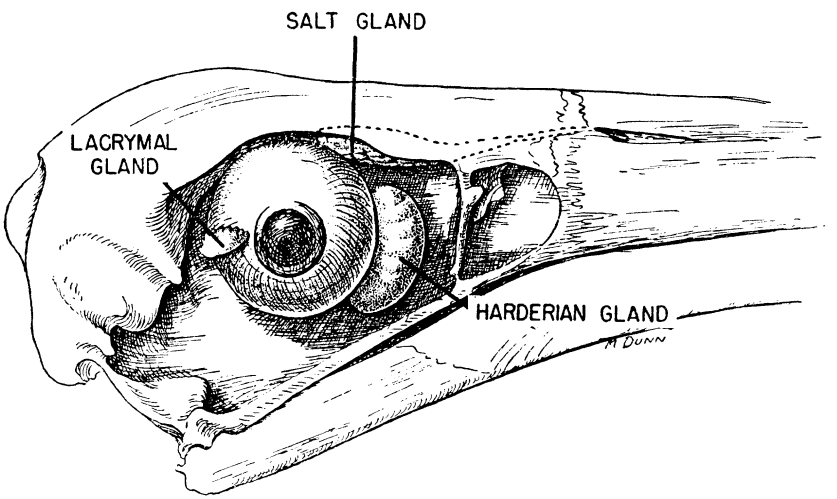

FIGURE 1. Orbital region of Brown Pelican, showing location of major glands.

and opens into a narrow cavity a few mm behind the external nares. A gland taken from a bird which has just been secreting has a reddish color, probably due to the rich blood supply. According to one single observation a non-secreting gland is paler and of a somewhat smaller size than a secreting gland. The microscopical structure is very similar to that of the salt gland of gulls (manuscript in preparation). The secretory elements consist of parallel closely packed glandular tubules radiating from central ducts. The gland tissue is surrounded by a thin connective tissue membrane. Several blood vessels and thin nerves pass into the gland but the anatomy of these was not studied.

The weights of the major glands of the orbit were determined in six pelicans. The results of these weighings are tabulated in table 4.

TABLE 4

WEIGHTS IN MG OF THE MAJOR GLANDS IN THE ORBITAL REGION OF THE BROWN PELICAN

		Salt gland				*Harderian gland*			
Animal No.	*Body wt. kg*	*L*	*R*	*Total*	*mg/kg BW*	*L*	*R*	*Total*	*mg/kg BW*
A (ad.)	3.74	520	474	994	266	1776	1805	3581	958
C (ad.)	3.17	483	480	963	304	2065	2053	4118	1290
D (ad.)	3.41	—	536	— est.	314	2491	2487	4978	1462
E (juv.)	2.86	382	384	766	268	1894	1935	3829	1339
F (juv.)	2.36	370	353	723	306	2082	2052	4134	1753
G (juv.)	2.54	540	530	1070	421	2194	2126	4310	1697

The most striking finding is that although the salt gland (nasal gland) is quite large, the Harderian gland is some four to five times as large again. This gland forms a white or yellowish rounded mass in front of the eye bulb. Its histological structure is vesicular and different from the salt gland. The lacrymal gland is situated behind the eye. It is a small gland which in three cases weighed from 8 to 12 mg.

The normal function of the large Harderian gland is not known with certainty. However, it is likely that the "tears" that appeared under mecholyl stimulation (see above) came from the Harderian gland. The amount of "lacrymal" fluid that was obtained in about a minute ran as high as 342 mg, and it is unthinkable that this amount of fluid was secreted by the lacrymal gland which weighs only some 10 mg. These "tears" could, on the other hand, easily be produced by a gland as large as the Harderian gland. As described earlier, the fluid is hypotonic, and it is viscious and slow flowing. It could well serve for protection of the eye of a diving bird, where the high viscosity would be a help in keeping it from being washed away.

In contrast, the secretion from the salt (nasal) gland is always high in salt concentration and water-like in consistency. With the rates of secretion observed, which ranged up to 0.38 ml/minute (Pelican C) it can be estimated that the salt glands can secrete a volume of liquid about four tenths of their weight per minute. This is indeed a very high rate of secretion, particularly in view of the considerable osmotic work involved in the secretion.

DISCUSSION

While sea water is known to be toxic to most mammals and terrestrial birds, it has been debated whether marine birds drink sea water. For an animal to tolerate drinking of sea water it is necessary to excrete the salts in a concentration at least as high as in the water taken in. While the bird kidney cannot produce a urine as concentrated as sea water, the excretory function of the salt gland (nasal gland) is very efficient, producing a fluid with salt concentrations higher than that in ingested sea water, thereby leaving a net gain of water.

It is well known that the nasal gland is particularly well-developed in marine birds. The significance of this has been discussed, and the commonly accepted conclusion has been that the large nasal gland produces a secretion which will rinse away the harmful or irritating effect of sea water that penetrates into the nasal cavity (Marples, 1932). Of 83 species of birds examined by Technau (1936) the 24 species that had particularly large glands were all marine. It is interesting to note that Technau's careful investigations also revealed a correlation with the habitat of the bird within a single genus. For example, among gulls the size of the gland increases as we move from the European Black-headed Gull (*Larus ridibundus*), through the Mew Gull (*Larus canus*) and the Herring Gull (*Larus argentatus*) to the Great Black-backed Gull (*Larus marinus*). In Europe the Black-headed Gull is mostly a fresh water species; it breeds at fresh water and spends much of the year on the big European rivers. The Great Black-backed Gull, on the other hand, has the most pronounced marine habitat of all the species mentioned. The same trend to a correlation with the extremeness of the marine habitat is evident in other birds listed in Technau's well compiled tables.

It has, furthermore, been shown that the size of the salt gland to some extent depends on the adaptation of the bird to its habitat. For example, Schildmacher (1932), working in the Berlin Zoo, found that when ducks of the same species were brought up in salt water and in fresh water, those brought up in salt water had considerably larger nasal glands.

While these correlations between the size of the salt gland and the marine environment are well established, it is necessary to modify the interpretation that the function of the gland is to protect the nasal membranes against sea water. Instead, it is evident that the gland has the unique role of being the main organ for excretion of salt in marine birds.

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SUMMARY

The salt gland (nasal gland) of the Brown Pelican can excrete a highly concentrated solution of sodium chloride. The excretory capacity of the salt gland permits the bird to tolerate ingestion of sea water, and to profit from it because the salt is excreted in a concentration higher than in sea water. Quantitatively, the role of the salt gland in the elimination of sodium chloride is greater than that of the kidney.

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