# THE EFFECT OF SALT INTAKE ON THE SIZE AND FUNCTION OF THE SALT GLAND OF DUCKS

KNUT SCHMIDT-NIELSEN AND YOON T. KIM

THE salt gland or nasal gland of marine birds is capable of eliminating sodium chloride as a highly concentrated solution. This enables these birds to tolerate the ingestion of sea water or food with a high salt content. Terrestrial birds, which lack an extra-renal excretory mechanism have, in general, a low tolerance to salt because their kidneys cannot produce a urine with high salt content. Apparently all marine birds have utilized the extra-renal mechanism for salt elimination; an increased renal capacity for salt excretion does not seem to have been a feasible evolutionary approach to this problem. The few passerine birds that have a high salt tolerance, however, seem to represent an exception that may provide interesting material for the student of avian evolution.

The Australian Zebra Finch (*Taeniopygia castanotis*) and the Savannah Sparrow (*Passerculus sandwichensis beldingi*) can tolerate salt solutions more concentrated than sea water (Oksche *et al.*, 1963; Poulson and Bartholomew, 1962). While birds in general can concentrate the urine to about two times the plasma osmotic concentration the Savannah Sparrow can attain 4.5-fold concentration. It has generally been assumed that the bird kidney is incapable of producing such concentrated urine because extensive water reabsorption would cause precipitation of uric acid in the uriniferous tubules. This supposedly is the reason that marine birds, rather than using the kidney for eliminating salts, have developed extra-renal (nasal) salt excretion. The fact that the Savannah Sparrow has developed the kidney rather than extra-renal salt excretion weakens this line of reasoning. Is it possible that passerine birds in general are unable to develop a salt-secreting nasal gland and therefore are unable to evolve truly marine forms although some representatives are salt tolerant?

The difference in the size of the nasal glands between marine and terrestrial birds is striking (Technau, 1936). Seemingly without exception, marine birds have a large and well-developed gland. In all cases where the function of this gland has been tested, it has been found capable of secreting a fluid containing sodium chloride in concentrations equal to or higher than that of sea water (McFarland, 1959; Schmidt-Nielsen, 1960). Terrestrial birds, on the contrary, have small, undeveloped nasal glands which appear unable to produce any external secretion in measurable volume.

The present study attempts to contribute to the understanding of the functional development of the salt gland in the ontogeny of the individual bird. Heinroth and Heinroth (1926, vol. 3: 223) and Schildmacher (1932) reported that domestic ducks as well as eiders in captivity develop larger nasal glands when drinking salt water. However, since these investigators made no quantitative measurements of the increased size of the glands or their secretion we felt that further studies on ducks to establish the extent of the hypertrophy and the effects of the hypertrophy on salt excretion were needed. In particular, we wanted to know whether the larger glands from birds brought up on salt water produce greater volumes of fluid with higher salt concentrations.

## MATERIALS AND METHODS

The choice of experimental animals was influenced by the availability of young birds. A domestic form seemed preferable to wild birds which have a more limited reproductive season. Another consideration was that individuals of a species that has only a limited association with salt water in the wild might show greater responses than completely marine forms. It is known that in typically marine species the nasal glands remain relatively large even if the birds are brought up with fresh water (Schildmacher, 1932). Domestic ducks, on the other hand, have glands of intermediate size whose development depends on exposure to salt. That the gland in ducks is capable of secreting salt, although not to the same degree as in typically marine forms, had been shown by Scothorne (1959). We therefore decided to use domestic ducks as well as wild Mallards.

Most of our work was done with the white Peking duck, a highly domesticated variety of the Mallard (*Anas platyrhynchos*). For comparison we also used a number of wild Mallards, hatched from eggs collected in the marshes surrounding the Delta Waterfowl Research Station in Manitoba and transported by air to Durham, North Carolina.

The Mallard is a circumpolar species which in many areas lives at the coast, partially associated with salt water. It was therefore a surprise to us to find that the domestic variety was more tolerant to salt and also had a greater ability to develop the function of the salt gland than the wild form. In consequence, most of our work was done with domestic ducks rather than wild Mallards.

The birds were fed on commercial wild bird food and had available at all times fresh water or various salt solutions for drinking. All ducklings, in particular during cold weather, were adequately supplied with heat from brooders equipped with infrared heating lamps. Newly-hatched ducklings were quite intolerant to salt solutions and it was necessary to adapt them slowly to progressively increasing concentrations. This required a schedule of changes in the drinking solutions which varied from group to group, to be enumerated in detail in connection with the experiments reported below.

In the absence of acute osmotic stress the salt gland is at rest and produces no fluid. When we wanted to obtain fluid for measurements of the rate of flow or of concentrations, gland activity was induced by the intravenous injection in the leg of 10 per cent NaCl solution in an amount of 1 ml/100

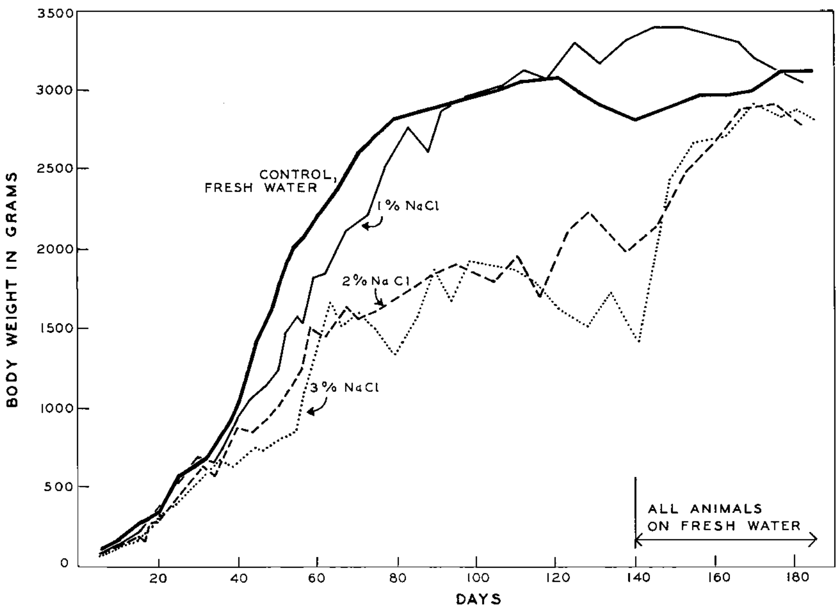


Figure 1. The growth of domestic Peking ducklings when provided various sodium chloride solutions for drinking. Since the adaptation to salt required some time, the details of this graph should be evaluated in conjunction with Table 1.

g body weight. Secretion from the gland usually began in about one to five minutes after such injection.

When the fluid was being collected, the ducks were immobilized by restraining their wings on a board with a cutout area for the body. This permitted them to remain in a nearly natural position with virtually no struggling or disturbance. Nasal fluid was collected in glass vials of known weight, and the amount of fluid was determined by weighing to the nearest mg. Concentrations of sodium were determined on a Baird flame photometer.

## RESULTS

### EFFECT OF SALT SOLUTIONS ON GROWTH

Four groups of Peking ducklings (five birds in each group) were brought up with various salt concentrations in the drinking water. We originally intended to use 1, 2, and 3 per cent NaCl, with the fourth group as control. However, these concentrations could not immediately be tolerated by the newly-hatched ducklings, and it was therefore necessary to adapt the birds slowly to increasing salt concentrations. Although previous investigators (Schildmacher and others) succeeded in supplying higher con-

TABLE 1

SCHEDULE OF CHANGES IN SALT SOLUTIONS PROVIDED TO PEKING DUCKLINGS DURING ADAPTATION TO HIGH SALT INTAKE*

| *1 per cent NaCl group* | | *2 per cent NaCl group* | | *3 per cent NaCl group* | |
|---|---|---|---|---|---|
| *Days* | *Concentration of NaCl (in per cent)* | *Days* | *Concentration of NaCl (in per cent)* | *Days* | *Concentration of NaCl (in per cent)* |
| 1 to 8 | fresh water | 1 to 8 | fresh water | 1 to 8 | fresh water |
| 9 to 14 | 0.5 | 9 to 14 | 0.5 | 9 to 16 | 0.5 |
| 15 to 55 | 1.0 | 15 to 40 | 1.0 | 17 to 22 | 1.0 |
| 56 to 59 | fresh water | 41 to 55 | 1.5 | 23 to 38 | 1.5 |
| 60 to 140 | 1.0 | 56 to 59 | fresh water | 39 to 59 | 2.0 |
| | | 60 to 66 | 1.5 | 60 to 63 | fresh water |
| | | 67 to 138 | 2.0 | 64 to 71 | 2.0 |
| | | | | 72 to 89 | 2.5 |
| | | | | 90 to 140 | 3.0 |

* The groups of five birds each are the same as those whose growth is represented in Figure 1.

centrations more rapidly, this was probably because they also gave fresh water to the birds for a short time each day. We decided not to follow this procedure, in spite of its success, because it would have been impractical or impossible to establish the proportion of salt and fresh water consumed.

The schedule for increasing the salt concentrations was adjusted to the general appearance and condition of the birds. In preliminary experiments we observed that newly-hatched ducklings were very intolerant of salt solutions, and only after the first week was NaCl supplied, first as a one-half per cent solution and then at gradually increased concentrations. If the condition of the bird indicated that the progress had been too fast, the concentration was lowered or the solution was, for a short time, replaced by fresh water. The schedule of increase in concentration for Peking ducklings is detailed in Table 1.

The growth of the four groups of ducklings is given in Figure 1. It is apparent that the birds which received 1 per cent NaCl grew as well as the fresh water controls. The birds receiving 2 or 3 per cent NaCl, on the other hand, grew conspicuously more slowly than the controls and the 1 per cent group. In fact, the weight curve for the groups receiving more than 1 per cent NaCl started deviating from that of the controls on the day when the concentration of salt was raised to 1.5 per cent (cf. Table 1). It thus seems that 1 per cent NaCl, which is slightly above the concentration in the blood but still within the capacity of the kidney to excrete, has no influence on the growth or body weight of the ducks. However, as low as 1.5 per cent retards the growth, and higher concentrations have a more pronounced effect. The 3 per cent group remained

TABLE 2

SCHEDULE OF CHANGES IN SALT SOLUTIONS GIVEN TO WILD MALLARD DUCKLINGS IN AN ATTEMPT TO ADAPT THEM TO HIGH SALT INTAKE

| *Group 1* | | *Group 2* | |
|---|---|---|---|
| *Days* | *Concentration of NaCl (in per cent)* | *Days* | *Concentration of NaCl (in per cent)* |
| 1 to 6 | fresh water | 1 to 6 | fresh water |
| 7 to 16 | 0.5 | 7 to 16 | 0.5 |
| 17 to 25 | 1.0 | 17 to 22 | 1.0 |
| 26 to 38 | 1.5 (some dead) | 23 to 38 | 1.5 (some dead) |
| 39 to 42 | fresh water | 39 to 42 | 2.0 (some dead) |
| 43 to 85 | 1.0 | 43 to 65 | 1.5 |
| | | 66 to 85 | 1.0 |

between 1,500 and 2,000 g, while the normal full-grown weight for the controls and the 1 per cent group was about 3,000 g.

After 140 days on the scheduled regime, all birds were transferred to fresh water. At this time the retarded birds increased in weight. It is noteworthy that the birds in the 3 per cent group now rapidly gained weight and approached 3,000 g, which had been reached by the control group two months earlier.

These observations are of interest in connection with findings on Glaucous-winged Gulls (*Larus glaucescens*) which also grow more slowly on salt solutions (Holmes *et al.*, 1961). Holmes *et al.* suggested that the slow growth of "salt-loaded" gulls was due to the increased size of the adrenal gland and an enhanced production of the glucocorticoid component of adreno-cortical secretion. We have no information about the adrenals of our experimental animals, but it is noteworthy that adrenalectomy in ducks abolishes the secretory function of the salt gland (Phillips *et al.*, 1961).

*Body weights of Mallards.*—The design of the experiment with wild Mallards was similar to that with the Peking duck, involving a slow increase of salts in the drinking water. The schedule of increase is given in Table 2. Very early in the experiment it became evident that the wild ducks were less tolerant to salt than the domestic variety, and as little as 1.5 per cent NaCl in the drinking water caused several deaths. As a result further experimentation was limited to birds that had been maintained on 1 per cent NaCl. However, not even these birds grew at the same rate as the controls. At the age of three months the control birds averaged 890 g, while the birds taking 1 per cent NaCl averaged only 650 g.

Because of the lack of success in adapting the wild Mallards to salt

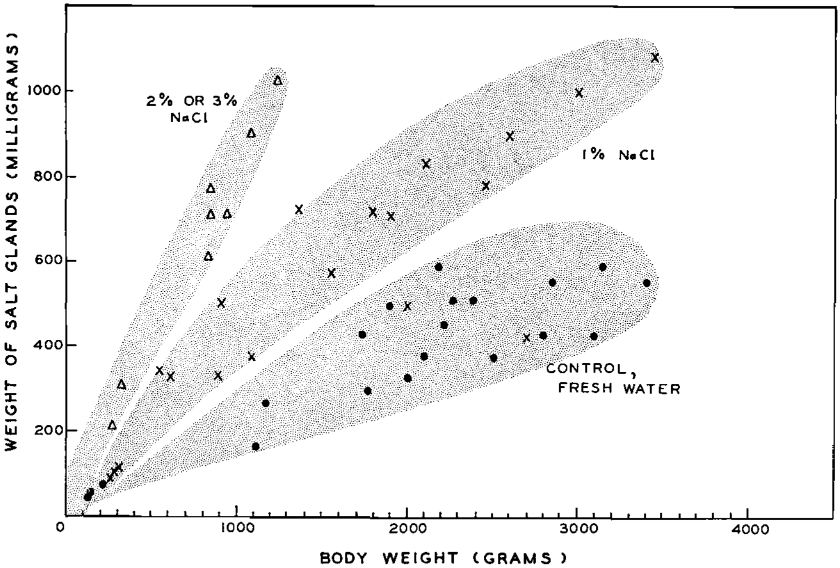


Figure 2. The size of the salt glands in ducks given various salt solutions for drinking. The figures indicate the combined weight of the right and left gland from each individual.

solutions, further work was concentrated on the domestic duck, and only a small number of Mallards was subjected to detailed studies.

### Size and Weight of the Salt Gland

The size of the salt glands was determined in 47 Peking ducks that had been brought up on various solutions. The results are plotted in Figure 2, which shows the difference in the size of the glands between ducks brought up on fresh water, on 1 per cent NaCl, and on higher concentrations of NaCl. The relatively small number of individuals studied does not permit any conclusion as to possible differences between the ducks on 2 and 3 per cent NaCl; but both these groups have significantly larger salt glands than the other groups.

(In evaluating these data it should be remembered that the ducks drinking 2 and 3 per cent salt solutions had a smaller body size than the control birds of the same age. Since none of the birds brought up on solutions of these two concentrations reached a body weight as large as the controls, it is an open question whether the size of the gland can best be related to body weight, as done here, or should be related to some other parameter, as, for example, the age of the individual.)

There was also a difference in appearance of the glands. Those of the fresh water control group were more grayish than those of the salt water

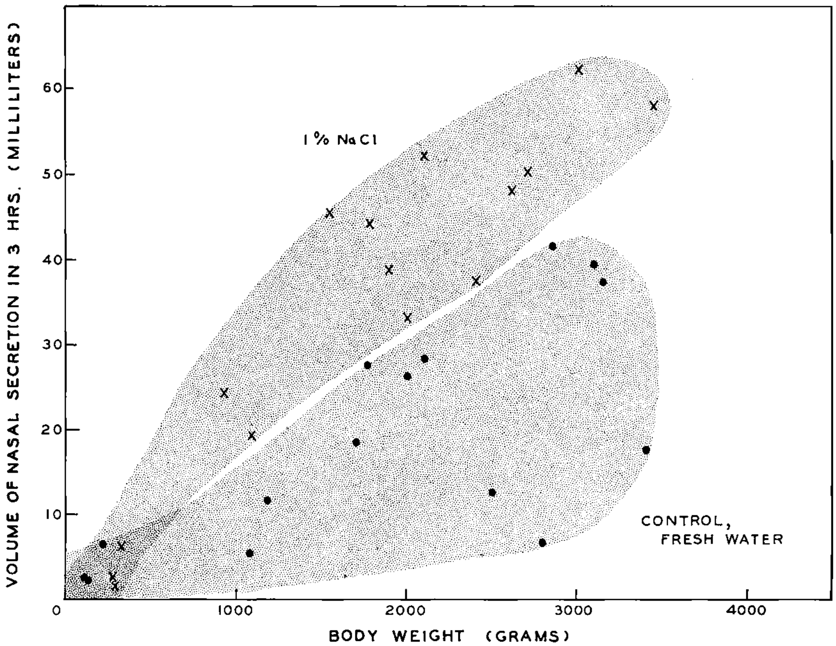


Figure 3. The volume of nasal secretion in response to a salt load in ducks drinking 1 per cent NaCl and in controls drinking fresh water.

groups, which had a fresh reddish-pink color and appeared to be much more heavily vascularized.

### THE FUNCTION OF THE SALT GLAND

Secretion from the salt glands was induced in ducks of both the fresh water and salt water groups by the intravenous injection of a salt load. In response to this injection, secretion from the salt gland usually appeared within a few minutes, and for three hours all of the fluid was collected continuously, but measured also for each interval of 15 or 20 minutes. The rate of secretion was in general much higher in the ducks reared on salt water, but in individual birds (whether control or salt water) it varied a great deal, even during a single experiment. The concentration of sodium in the secretion, however, remained very constant during each experiment, in spite of the variations in volume of the fluid produced. Therefore, the details of the 15 to 20 minute collection periods are of peripheral interest, and only mean concentrations over the three hour period are reported here.

*Volume of fluid secreted.*—The greater size of the glands in ducks brought up with salt water was reflected in their ability to secrete fluid at a higher rate than could the ducks reared on fresh water. The difference in two groups of 15 ducks each is illustrated in Figure 3. Except for the very youngest birds, which had not yet developed any appreciable secretory ability, the ducks reared on salt water had a considerably higher secretory rate than the controls. However, there was considerable variation within each group, in particular within the fresh water group. (It should be remembered that each bird could be used for an acute salt load experiment only once because the salt injection employed to induce secretion would cause further hypertrophy of the gland and invalidate later observations.)

The average rate of secretion, when related to body size, gave a mean value for ducks reared on fresh water of 0.064 ml/kg body weight/minute, and the corresponding figure for ducks reared on salt water was 0.113 ml/kg body weight/minute. In other words, in response to an injected salt load, ducks brought up with salt solutions on the average produced almost twice as much secretion as ducks brought up on fresh water.

*Sodium concentration in the fluid.*—In ducks reared on fresh water the fluid produced in response to an injected salt load ranged in concentration from 270 to 523 mEq Na/liter with a mean of 435 ± 14(S.E.) mEq/liter. In the 29 ducks which had been brought up on various concentrations of salt water, the concentration of the fluid varied from 372 to 599 mEq Na/liter with a mean concentration of 525 ± 10(S.E.) mEq/liter. Of the 29 ducks reared on salt water, 22 individuals had concentrations above 500 mEq/liter while of the 22 ducks reared on fresh water only 3 exceeded 500 mEq/liter.

Determinations of concentrations in the secreted fluid were carried out on a few Mallards. Three individuals brought up on fresh water had an average concentration of 546 mEq Na/liter (range, 518 to 561); five individuals drinking salt solutions averaged 583 mEq Na/liter (range, 471 to 661). It is noteworthy that, in spite of the higher concentrations attained in the nasal secretion of the Mallards, these birds were considerably less tolerant than the domestic ducks to salt in the drinking water.

*Amount of sodium excreted.*—The difference in the capacity for excretion of the salt gland in ducks on fresh water and those on salt water was particularly clear during the initial stages of a salt load. When the amounts of sodium eliminated during the first hour were compared, it appeared that the latter might eliminate up to five times as much sodium as the ducks of the same size brought up on fresh water (Figure 4). Furthermore, the ducks reared on fresh water showed no increased ability for secretion (as related to body weight) with increasing age. The "salt water" ducks, on the other hand, secreted increasing amounts of salt (per unit body weight) with increasing age, so that the difference between the two groups became more pronounced with time.

Finally, it was of interest to examine the ability of the ducks to eliminate a given salt load. All birds under observation were given an injection of

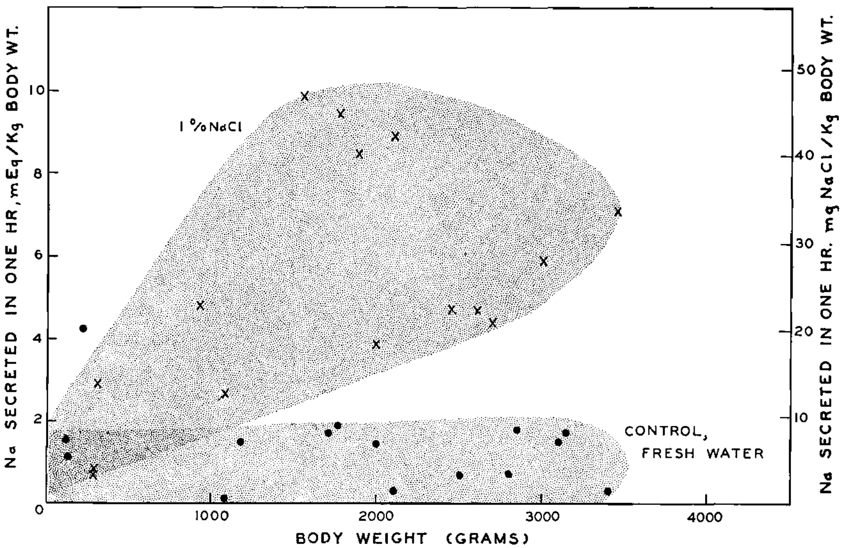


Figure 4. Amount of sodium excreted during the first hour of a salt load experiment.

10 per cent NaCl solution in the amount of 1 ml/100 g body weight. The illustration in Figure 5 shows the fraction of the injected load which was excreted by the nasal gland in the first hour. The elimination by ducks reared on fresh water ranged up to slightly above 20 per cent, while the ducks reared on salt water were able to eliminate up to 80 per cent of the load during the time. This shows the conspicuous improvement in the ability to eliminate excess salt loads in birds habituated to intake of salt water.

## DISCUSSION

The findings reported in this paper show that when ducks are brought up with salt solutions for drinking they develop larger salt-secreting (nasal) glands than control animals brought up with fresh water only. In addition to the increased size of the gland, its capacity to secrete is greatly increased, in particular with respect to the volume of fluid that can be produced. The concentration of sodium in the fluid is also increased, but the difference is not as great as it is in respect to the size of the gland and the volume of fluid produced.

These findings are of interest in connection with several previous observations on various birds associated with salt and fresh water.

The difference in the size of the nasal gland between marine birds on the one hand and terrestrial and fresh water birds on the other was clearly

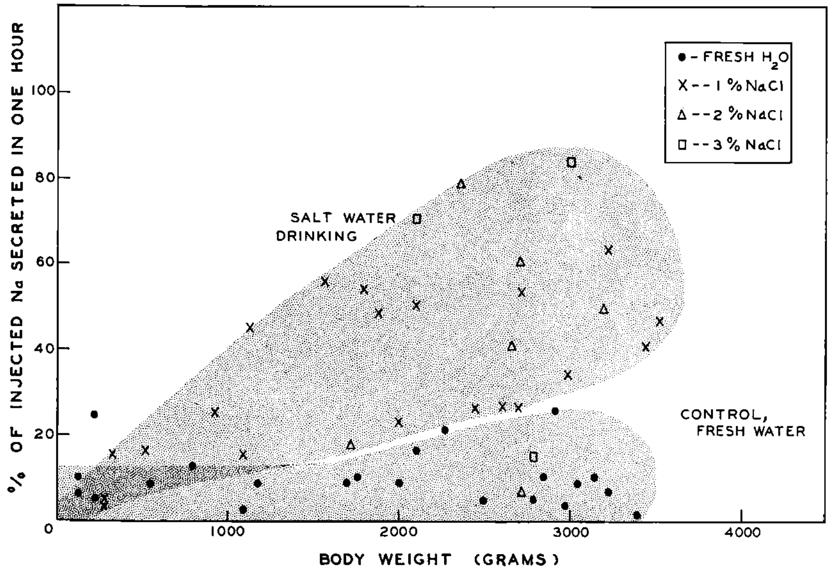


Figure 5. Fraction of an injected salt load which was excreted in one hour by ducks reared on salt water and on fresh water, respectively.

pointed out by Technau, who examined anatomical material from a large number of birds (1936). Technau also carefully reviewed the existing literature in the field. He pointed out that not only do marine birds have large nasal glands, but the size of the gland is different in different subspecies or races of one species and again is related to the degree of association with sea water.

An excellent illustration showing the different size of the gland in subspecies of Mallards was given by Stresemann (1934: 52). The drawings show the relatively small nasal (supraorbital) glands of the central European race *Anas p. platyrhynchos* compared with the Greenland race *A. p. conboschas.* The latter, which has tremendously well-developed nasal glands, lives along the coast of Greenland in close association with salt water.

Bock (1958) in his monograph of the plovers (Charadriinae) carefully reviewed the size of the nasal gland and its influence on the ossification of the supraorbital rims in a large number of species and subspecies of plovers. The interest in this subject stems from the possibility of using the characteristic impression of the nasal gland on the cranial bones as a taxonomic character. Bock concluded that this skull character was invalid because it was modified by the size of the nasal gland, which again was determined by environmental factors (the salinity of the habitat). Although the actual function of the nasal gland was unknown when Bock's monograph was prepared, the later understanding of the excretory function of the gland lends further support to the conclusions that Bock reached on zoogeographical evidence.

The effect of salt on the morphological development of the nasal gland was demonstrated experimentally by Schildmacher (1932), who in the Berlin Zoo brought up ducks with and without salt water to drink. The birds that had salt water (but also had daily access to fresh water) developed conspicuously larger nasal glands. Unfortunately, Schildmacher did not carry his experiments beyond the qualitative observation that the glands were larger and more highly vascularized in the birds reared on salt water. His observations are, of course, not invalidated by the fact that he worked under the contemporary misconception that the function of the nasal gland in marine birds is to rinse away salt water that may penetrate to the sensitive nasal membranes.

The conclusion to be drawn from the experimental work described in this paper and from the reports discussed above is that the development of the size of the salt-secreting (nasal) gland in birds depends on two factors, one primary genetic factor and a secondary phenotypic effect of salt stress. The genetic factor is evident in terrestrial birds, which always have a very small gland which is unable to excrete salt. For example, Scothorne (1959) exposed pigeons to salt loads but was unable to obtain any secretion from the nasal gland. The same situation prevails in the domestic chicken. These birds, then, do not have the ability to develop a functional salt-secreting gland from the rudimentary anatomical material present. On the other hand, marine birds without exception have a large nasal gland. Even if they are brought up on fresh water, the nasal gland develops to an appreciable size, as observed by Heinroth on eiders in the Berlin Zoo (Schildmacher, 1932). Genetically, marine birds, therefore, possess large nasal glands, irrespective of the presence or absence of salt stress.

The other factor in the development of the nasal gland is that, if the gland is anatomically present and capable of developing as a salt-excreting organ, its size and capacity for excretion are directly influenced by the amount of salt taken in by the individual. This has been demonstrated in the present paper on the domestic duck, and by Holmes *et al.* (1961) on the Glaucous-winged Gull.

The fact that the size of the nasal gland is phenotypically modified by salt intake makes it difficult to evaluate information such as the difference in gland size between the European and Greenland races of the Mallard (see above). Is the Greenland race provided with a large gland which makes it better suited to the coastal life, or is the different size of the gland in this race a result of its living in and being exposed to a saline environment? This question can, at the present time, only be answered by obtaining breeding stock of the various races or subspecies involved and rearing these individuals under various well-defined conditions of salt load. This should clarify the extent to which differences are genetically or phenotypically determined.

### ACKNOWLEDGMENTS

This work was supported by National Institutes of Health Grant number H-2228, and by NIH Research Career Award 1-K6-GM-21, 522-01 from the National Institute of General Medical Sciences. We wish to express our gratitude to Dr. Peter Klopfer who generously provided us with newly-hatched wild Mallard ducklings.

### SUMMARY

Domestic ducks of the white Peking variety were raised with various concentrations of sodium chloride (NaCl) added to their drinking water. One per cent NaCl was well tolerated but 2 and 3 per cent NaCl retarded the growth of the birds.

All ducks drinking salt solutions developed larger salt-secreting glands (nasal glands) than fresh water controls. The hypertrophied glands were able to secrete fluid at a much higher rate than the glands from fresh water controls. However, the salt concentrations in the secreted fluid were only slightly higher in the salt-adapted birds. Thus the increase in extra-renal, salt-excreting capacity which occurs in response to salt intake results primarily from increases in the size of the salt glands and in the volume of secreted fluid.

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*Department of Zoology, Duke University, Durham, North Carolina.*