WHAT MAKES PLUMAGE WATERPROOF?

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(This paper is a translation by the author of his original paper " Vad gör fåglarnas kroppsbeklädnad vattenavvisande " which appeared in Zoologisk Revy 18: 71-83. 1956).

WHEN a biological system is disturbed, this often gives a clue to the normal functioning of that system. This is the case with the ability of the plumage of birds to repel water. Under certain circumstances this vital ability is easily lost in birds kept in captivity. This is particularly true in the case of diving species, and the downy young are more sensitive in this respect than adult birds. Such disturbances, which make the downy plumage wet and lead to death with symptoms resembling pneumonia, cause severe losses in the rearing of poultry and waterfowl. In the Berlin Zoo Heinroth (1924) observed that such disturbances were rare in ducklings which had been hatched under their mother and were conducted by her, while they very commonly occurred in ducklings hatched in incubators or under hens. He assumed that the reason for this was that the ducklings hatched under their natural mother got preen gland secretion from contact with her feathers.

It has been a common belief that the plumage of birds is water-repellent because the feathers are anointed with the secretion from the oil gland. A comprehensive survey of the literature in this field has been given by Elder (1954). When I observed that some changes in the diet caused a loss of the waterproofing of the plumage of young Tufted Ducks, I supposed that these diet changes in some way interfered with the functioning of the oil gland (Fabricius 1945). The disturbances easily occurred when the ducklings were fed on fish, but disappeared if they were fed on insects. The oil gland, preen gland or uropygial gland is the only skin gland in the birds, and it is known that the skin glands of mammals are dependent for their proper functioning on some vitamins of the B-group.

Absolute or relative lack of some vitamins causes severe disturbances when the animals are given food containing the enzyme thiaminase, which is particularly abundant in raw fish (Suomalainen and Pihlgren 1955). One must therefore be very careful in using raw fish as food for furred animals, such as foxes and minks.

It would thus not be unimaginable that a diet consisting exclusively of raw fish would cause disturbances in the functioning of the oil gland. But if so, one wonders why several species of diving birds, such as the mergansers, are capable of living exclusively on fish, and why the young mergansers particularly easily lose the waterproofing of their plumage if they are fed on fish in captivity. The food of the ducklings of these species is, however, different from that of the adults, and one could imagine that the young birds would be more dependent on certain vitamins.

In the summers 1945 and 1946 I had an opportunity of making some observations and experiments on these problems in ducklings which were reared for behaviour studies. In all 66 Tufted Ducks (*Aythya fuligula*), 10 Eiders (*Somateria mollissima*) and 5 Shovelers (*Anas clypeata*) were reared for these purposes. The ducklings were hatched in an incubator, and the rearing technique has been described in a paper dealing with experiments on the following response and imprinting (Fabricius 1951).

The newly hatched ducklings were taken from the incubator and allowed to swim as soon as they looked dry, i.e. when their downy feathers had thrown off their horny sheaths. Their plumage was always waterproof at this first swimming test, and this overthrows the theory that the plumage of newly hatched ducklings is repellent to water because they get preen gland secretion from contact with the feathers of their mother.

In the beginning of my experiments I was mainly interested in the influence of the diet. To get an idea of the composition of the natural food of the ducklings in the archipelago off Hangö, where the studies were made, I had to shoot some ducklings of the Eider, the Velvet Scoter (*Melanitta fusca*), the Goosander (*Mergus merganser*) and the Tufted Duck, in all 15 specimens. It turned out that the young Goosanders had eaten mainly small crustaceans of the species *Neomysis vulgaris*, but also some adults of aquatic insects such as *Trichoptera*.

The young Goosanders thus showed a preference for free-swimming prey. The young Tufted Ducks and Scoters had, on the contrary, mainly been feeding on molluses of the genera *Theodoxus*, *Bythinia* and *Lymnea* which are abundant in the Fucus-vegetation of the shallow coastal waters in the Baltic Sea, and in addition they had consumed some adult midges of the genus *Chironomus*. The food of the young Tufted Ducks also contained much vegetable matter, mainly seeds of water plants of the genus *Potamogeton*. The young Eiders had eaten the aquatic snails mentioned above, but the bulk of their food consisted of three species of crustaceans which are abundant in the Fucus-vegetation, i.e. *Idotea baltica*, *viridis* and *granulosa*. The perference of the Eider for hard and comparatively large food objects thus appeared early. The food of the young Eiders had this composition up to an age of two weeks. In Eider ducklings three or four weeks old the bulk of the food consisted of mussels of the genus *Mytilus*.

The experimental birds were fed on fish (bleaks, herring), small crustaceans (*Neomysis*, *Praunus*) and grasshoppers (*Corthippus*, *Stauroderus*, *Mecostethus*) all in raw condition. In addition they were given dry oat flakes. At every feeding they were allowed to eat until they were quite satisfied, and it proved necessary to feed them at least 6 times daily, with intervals of 2-3 hours. To obtain the weight of the food consumed each bird was weighed immediately after every feed. Their daily consumption was considerable. It was 115% of their own body weight on a diet of crustaceans, 85% on fish, 38% on insects and 75% on oat flakes. The differences probably express mainly the differences in the specific weight of these substances, since the birds always fed until the crop was full, an almost constant volume. It should be noted that the birds always soaked the oat flakes in water before they swallowed them.

In addition to weighing at feeding, some observations were also made on the growth of the young. It turned out that the young Tufted Ducks, which newly hatched had a weight of about 38 grams, regularly lost weight during their first five days of life, and that the loss, about 5 grams, approximately equalled the weight of the internal yolk sack, about 5.4 grams, which remained in the body cavity at hatching. At an age of five or six days the yolk sack was completely absorbed, and it was not until then that the weight of the young began to increase. The weight increase was largest during sunny days, and during overcast and cold days it was small. At this early stage, before the insulating adult plumage is developed, the metabolic balance of the young seems to be very labile. In cold weather all the food seems to be needed for maintaining the body temperature, so that nothing is left for growth. It should be mentioned that no suitable artificial brooders were available for my birds.

The crustaceans of the genus *Neomysis* turned out to be the most favoured food. Young Eiders which for some days had been fed on these crustaceans became strongly conditioned to this kind of food. When they were offered a mixture of animals from the Fucus-fauna on a plate, they quickly selected and swallowed all the *Neomysis,* rejecting the crutaceans of the genus *Idotea* as well as the molluscs though these two groups of animals constitute the main food of Eider ducklings of this age in nature. The birds were fed on land. The fish was crushed, and the *Neomysis* were obtainable in such a quantity that they formed a ' porridge ' on the food plate.

At first the experiments confirmed my earlier observations. When the birds were fed on fish, the waterproofing of their plumage was very soon lost. But this also happened when they were fed on the *Neomysis,* and the young of the diving ducks turned out to be more sensitive in this respect that those of the dabbling ducks. As in my earlier experiments, the normal condition of the plumage could be restored if the birds were fed exclusively on insects, but this was also the case if they were put on a diet exclusively of dry oat flakes.

In addition, some new observations were made. For controlling the condition of the plumage, a number of swimming tests were made with the birds every day, and the degree of soaking was recorded. As mentioned in an earlier paper (Fabricius 1951, p.98), the birds after each swimming excursion came up on the shore and performed intense preening movements. This preening was continued until the plumage was completely dry, which could take more than an hour in the case of severe soaking.

The preening behaviour contains a number of fixed motor patterns which are repeated again and again. First the bird touches the nipple of the preen gland with the tip of its bill. Then the chin and the sides of the head are rubbed at the nipple, and after this the bird usually wipes the under side of the bill over the crop and the breast, by a pendulating movement from side to side. This is followed, in an irregular order, by a number of other movements. The sides of the head are rubbed over the back, the scapulars and the flanks. The neck and the under side of the head are scratched by the feet, and the bill is inserted into various parts of the plumage, and nibbling movements made. In this nibbling the bird, by cautious chewing movements, lets a small portion of the plumage glide through the bill. Then it performs swallowing movements and shakes the head to get rid of the water which has adhered to the bill, and finally it inserts the bill at a new place in the plumage and repeats the procedure. The largest portion of the time is spent in preening the plumage of the breast and belly in this nibbling manner.

The preening movements seem to be fixed motor patterns, but their orientation is apparently governed by local stimulation of the skin. This was shown by the fact that if the backs of the birds were experimentally soaked by water, the breast and belly being left dry, the birds spent most of their time preening the back in the nibbling manner. Now and then the preening was interspaced by shaking. The birds shook their body like wet dogs and fluttered their wings. This shaking is also performed immediately after the bird has emerged from the water, as an introduction to the preening behaviour.

In most cases the preening movements considerably improved the ability of the plumage to repel water. Even on a diet of raw crushed fish it was possible to make the plumage of the ducklings almost waterproof by repeatedly allowing them to preen, swim, preen again, and so on, without feeding them between these performances. It is apparent that the secretion of the oil gland is distributed over the plumage by the preening behaviour, particularly by the rubbing and wiping movements of the head and bill. When the feathers were dyed in Sudan III, the droplets of the oil gland secretion could be distinctly seen on microscopic examination, even on feathers from those ducklings which had lost the waterproofing of their plumage. The oil gland is a tubular gland, and each of the numerous tubules consists of an epthelium built up by several layers of cells surrounding a central lumen. In microscopic preparations dyed in Sudan III considerably amounts of secretion could be seen as dark masses in the lumen of the tubules irrespective of whether the plumage of the bird from which the gland had been taken had been waterproof or not.

My observations here differ from those of Madsen (1941, 1943) and Veselovsky (1951), who claim that the oil gland is not functional in newly hatched diving ducks, which swim and dive without wetting their plumage. Madsen was not able to squeeze secretion out of the oil glands of Eider ducklings by manual manipulation, and he could not detect any secretion droplets on feathers of waterbirds by microscopic examination. In my ducklings one could not press out secretion of the gland either, as long as they were living, but immediately after death it was quite easy to squeeze out considerable amounts of the secretion by gentle manual maniplulation. Apparently the powerful sphincter musculature around the external openings of the ducts of the gland makes it impossible to squeeze secretion out of the gland of a living bird, unless one uses such force that the bird is damaged.

As mentioned already the secretion was distinctly visible on microscopic preparations of feathers from ducklings of the species used in my experiments, and one could also watch how it was spread over the plumage by the preening movements. But when feathers from adult ducks were examined, it was found that the secretion was present in such small quantities that it could be seen only with great difficulty. This probably explains the difference between Madsen's and my own observations, since Madsen made his Sudan III tests on feathers from specimens of Black-headed Gulls and Goosanders which were probably adult. Elder (1954) has also confirmed that the oil gland is functional in newly hatched ducklings.

Irrespective of weather the plumage of the ducklings was wettable or water-repellent, their oil glands were thus functioning and the secretion was present in their feathers. This undoubtedly speaks against the theory that changes in the condition of the plumage obtained by altering the experimental diet was due to changes in the functioning of the oil gland. Several authors, for example Paris (1913), have denied that the oil gland has anything to do with the water-repellent quality of the feathers, because this quality has not always been lost when the oil gland has been removed. In such removal experiments, which have also been made by Kossmann (1871), Hou (1928) and Madsen (1941, 1943) adult birds have generally been used. Thus, one cannot exclude the possibility that secretion from the oil gland might have been present on the feathers at the time of operation, and might have remained there for a considerable period, affecting the condition of the plumage*. Madsen and Elder have, however, found that after completion of the moult the water-repellent quality of the plumage was restored in glandless birds. To be absolutely sure that the ability of the plumage to repel water is not primarily dependent on the secretion of the oil gland, one would have to remove the gland from birds which definitely have no oil gland secretion on their feathers. In newly hatched ducklings the downy feathers are enclosed in totally isolating horny sheaths. Not until about six hours after hatching are these sheaths thrown off and the downy feathers unfolded, making the duckling look dry.

In 14 young Tufted Ducks I removed the oil gland immediately after hatching, the downy feathers still being enclosed in their horny sheaths. The operation was made under ether anaesthetic. The skin was opened by a T-shaped incision and the gland and its nipple was carefully excised. Treatment by alum solution made the loss of blood very small, and the wound was closed by adhesive plaster. In all cases the wound healed quickly, and the operated birds behaved quite normally. It was observed that they performed all the normal preening movements, including touching the bill to the area where the nipple of the oil gland had been situated, and all the rubbing and wiping movements of the head over different parts of the body.

In order to avoid all possibilities of contact with oil gland secretion, the glandless birds were kept isolated in a separate cage, while a control group of unoperated young Tufted Ducks of the same age was kept in another cage. All the birds were allowed to swim as soon as they had thrown off the horny sheaths of their feathers. It turned out that the plumage of the glandless birds was just as waterproof as that of the unoperated ones. All the ducklings swam and dived without wetting their plumage, which indicates that the water-repellent quality of the plumage is not primarily dependent on the oil gland secretion. One could, of course, object that the horny sheaths of the feathers in the newly hatched ducklings might perhaps contain some substance similar to the oil gland secretion, but no droplets of secretion were found on the feathers of the glandless birds on careful microscopic examination.

In a series of experiments no differences between the glandless birds and those of the unoperated group could be found in the following respects:

1. When the birds were fed on raw crushed fish or raw *Neomysis* the water-repellent quality of their plumage was lost if the food was offered on a plate on land.

2. The water-repellent quality could be restored by a change to a diet of insects or dry oat flakes.

3. Even when the birds were fed on raw crushed fish, the water-repellent quality of their plumage persisted if they were never fed on land, but only when swimming in clean water. The pieces of fish had to be thrown in the water one by one allowing the birds to dive for them.

*Elder (op. cit.) removed the oil gland from young Redheads, but he did not test the water-repellent quality of their plumage while they were still in the downy stage.

4. The ability of the plumage to repel water was improved by the preening movements, in spite of the fact that in the glandless birds no secretion could be applied to the feathers by such movements.

5. The ability of the plumage to repel water was always poorest in the morning, at the first swimming test which was made immediately after the birds had been released from the narrow brooder where they had been crowded during the night. It was, however, much improved during the course of the day if they were allowed to preen repeatedly outdoors.

6. When the birds were offered dry oat flakes, they repeatedly took some flakes in the bill and ran to the water, where they soaked them before they were swallowed, returning then to the plate for more flakes. When this occurred on a rock at the edge of the water, a wet track was formed between the water and the food plate. The bellies of the running birds touched the wet rock, and if a swimming test was made immediately after this, it was observed that the birds became wet on the under side.

7. If a bird was rubbed during handling, this could destroy the water-repellent quality of its plumage, so that it became wet to the skin if placed in the water immediately afterwards.

8. The ability of the plumage to repel water was gradually lost if a bird was prevented from preening. This could be done either by force or by leaving the bird alone in a cage. The birds were imprinted to their keeper, and if left alone they continuously searched for him and for their group companions, and this apparently blocked their preening behaviour.

In connection with these experiments, a careful microscopic examination was made of feathers of ducklings in which the plumage was perfectly waterproof, as well as of feathers of ducklings which had lost the water-repellent quality of their plumage. A feather consists of a quill from which the barbs branch out. At the portion closest to the quill, each barb carries numerous fine barbules. These are lacking in the terminal portion of the quills, the barbules are equipped with rows of small hooks which keep the vane together and maintain the barbules at a constant and very small distance from each other. In feathers of downy ducklings these hooks are poorly developed, but the barbules bear small protrusions of an irregular shape, which probably have a similar function.

It was observed that the barbules were disarranged in feathers of ducklings which had lost the water-repellent quality of their plumage. Several barbules would stick together in groups, or cross each other, so that broad gaps formed between them. On the other hand, the barbules were in perfect order and at an even distance from each other in feathers from ducklings in which the plumage was repellent to water. When a duckling in this normal condition emerges from diving, one can only see some narrow wet stripes at the surface of the plumage, formed by the naked bristle-like terminal parts of the quills, but the deeper layers of the plumage, where the barbules occur, are perfectly dry.

According to the previously mentioned papers by Madsen, which were not available to me in Finland during the war, the water-repellent quality of the plumage of birds is due to the presence of air among the finest ramifications of the feathers. The barbules are maintained at constant distances from each other, and the spaces between them, as well as between the individual feathers, are so narrow that water with a normal surface tension is not able to penetrate them. But as soon as gaps are formed, water penetrates into the feathers, replacing the air and wetting the plumage. Contact with fluids, such as oils, which have a smaller surface tension than water, has the same disastrous consequences. The feathers of water birds are, in contrast to those of most passerine birds, densely and evenly distributed over the skin, and special muscles maintain them tightly together. When these muscles cease to function in a dead bird, gaps are formed between the feathers and water can penetrate the plumage. This explains the experience of duck shooters, that dead ducks soon become wet to the skin if they fall into water. Madsen also assumed that the barbules were maintained in their correct order by the preening movements.

My experiments seem to confirm the results of Madsen. The water-repellent quality of the plumage is lost if the fine barbules of the feathers become disarranged by contact with smearing substances, or by mechanical action. The first condition arises, for instance, when the birds lie in a plate of crushed fish or wet crustaceans when feeding, or when they become smeared by faeces while enclosed in a narrow brooder during the night. Probably a mechanical action is also concerned in these cases, but particularly must this be so when the water-repellent quality of the plumage is lost after manual manipulation, or after the bird has rubbed its under side to a wet rock when running to and fro between the water and the food plate to soak oat flakes. A case described by Elder (1954), where Redhead ducklings became wet when jumping at the edges of a wash tub, might be explained in a similar way.

The waterproof condition of the plumage can be restored by the preening behaviour, and probably the nibbling movements of the bill in particular are effective in bringing the barbules back into their normal positions. It has been assumed by several authors, among others Sick (1937) and Madsen (1941), that electricity produced in the plumage by friction caused by the preening movements may contribute to the maintenance of the correct distances between the barbules.

The reason why the water-repellent quality of the plumage could be restored and maintained by feeding on insects and oat flakes was simply that this kind of food was dry and did not smear the feathers. Even when the birds were fed exclusively on crushed fish, the ability of their plumage to repel water could be maintained, provided that the food was given in such a way that it never got in contact with the feathers, i.e. if they were allowed to dive for the food in clean water. The water-repellent quality is more easily lost in downy young than in adult birds apparently because the feathers of the young in the downy stage are not so stiff and capable of resisting mechanical action as those of older birds, and in addition the hooks are poorly developed in the downy feathers. The consequence of wetting are also most severe at the downy stage, and particularly during the first week of life it very easily causes death, probably because of the labile condition of the metabolic balance at this early age. Downy young at this stage have a very great need for warmth, and apparently they are not capable of maintaining their body temperature for any length of time, for they can only be kept alive if allowed to rest under their mother or in an artificial brooder several times a day.

It is not difficult to understand why diving ducks in captivity lose the water-repellent quality of their plumage more easily than dabbling ducks. The tarsi of diving ducks are shorter than those of dabbling ducks, and the position and posture of the legs is such that, when moving on land, the diving ducks much more easily touch the ground with the under side of their body. This easily causes disarrangement of the plumage or smearing, particularly at feeding or when the birds are kept under crowded conditions. All these circumstances show that in rearing waterfowl of diving species one should avoid all conditions which could cause smearing of the plumage. Food of a smeary nature should not be given, the birds should only be fed when swimming in clean water, not when moving on land, and crowding in too narrow enclosures or brooders should be avoided. Finally, such birds should not be handled, and particularly not when they are wet, or by wet hands.

Thus, the ability of the plumage of birds to repel water is apparently not primarily dependent on the secretion of the oil gland, but on the delicate structure of the feathers, which is maintained by the preening behaviour. It is evident, however, that the preening behaviour also includes movements which apparently serve to distribute the oil gland secretion over the plumage, and one wonders what the function of this secretion might be. It has been shown by the Chinese physiologist Hou (1928) that the secretion of the oil gland contains ergosterol which changes into vitamin D when subjected to sunlight on the feathers, and that birds obtain this vitamin by the swallowing movements they perform during the nibbling type of preening. Hou also found that birds developed rickets when kept in darkness on a diet free of vitamin D, and that this could be cured by ultraviolet light in normal birds, but not in specimens from which the oil gland had been removed. Because of the thick, insulating plumage, vitamin D cannot be produced in the skin of birds by sun radiation as in many other animals, and therefore nature has apparently relied on the indirect method of letting the provitamin be irradiated at the surface of the plumage and then subsequently be swallowed.

In domestic ducks from which the oil gland had been removed Hou also observed that all droplets of secretion had disappeared from the feathers about one month after the operation. At this time the birds began biting their plumage so frantically that the barbs and barbules were broken and disarranged, which caused a deterioration of the water-repellent quality of the plumage. A similar degeneration of the plumage in birds from which the oil gland had been removed has been observed by Madsen (1941, 1943) and Elder (op. cit.) . I could not keep my operated Tufted ducklings alive long enough to study this phenomenon. All, as well as those of the control group, died when about a week old, after having become wet to the skin during a torrent of rain.

Even if the secretion of the oil gland is not primarily necessary for the plumage to repel water, it apparently indirectly affects this ability in the course of time, by maintaining the feather structure and preventing degenerative changes of the plumage. It seems also possible that the secretion could affect the conditions of surface tension at the areas where the feathers are in contact with the water, in a way which would reinforce the effect of the delicate structure of the feathers. To solve these problems team work would be necessary, involving at least a physiologist, a biochemist specialising in methods of analysing microscopic quantities of organic substances and a physicist specializing in problems of surface tension and capillary action. In addition, a thorough study would be needed of the very complicated structure of the feathers, including careful measurements of the distances between the different structures under various conditions.

Summary

Ducklings of several species lost their water-proofing on a diet consisting of raw-crushed fish, and regained it on a diet of insects.

Even in specimens that had lost their water-proofing there were indications that the gland was functioning.

The oil gland was removed from 14 young Tufted Ducks just after hatching, while their down feathers were still enclosed in their isolating horny sheaths. After the bursting of these sheaths and the full development of the down the plumage was as repellent to water as that of normal control birds, indicating that it is not the secretion of the oil gland which makes the plumage waterproof.

Operated and normal control birds alike lost their water-proofing when subjected to contact with smearing substances. In this condition the barbules of the down feathers were disarranged, sticking together in groups, between which there were irregular spaces. The normal waterproofing was gradually restored if the bird was allowed to preen. Plumage remains water-repellent when the birds feed on insects because insects are dry and clean. Plumage even remains water-repellent on a diet of fish, provided that the pieces of fish are only given to the birds while these are swimming in clean water. In rearing waterfowl, smearing food and crowding should be avoided.

The preening consists of a number of stereotyped movements which are described. The nibbling type of preening movements in particular aid in maintaining the barbules in a state which makes the plumage repellent to water.

These findings confirm the view of Madsen (1941), that the large amount of finely distributed air among the ramifications of the fethers is the principal factor in the water-repellency of plumage.

There is a discussion of a paper by Hou (1928), who showed that the secretion of the oil gland contains ergosterol, which changes into vitamin D when subjected to sunlight on the feathers, and is then swallowed by the birds during preening.

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