PROCESSES IN FEATHERS CAUSED BY BATHING IN WATER

JOHAN G. VAN RHIJN*

Department of Zoology, University of Groningen, the Netherlands

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1. INTRODUCTION

This study had been undertaken in order to acquire more knowledge about the biological function of bathing in birds. It forms part of a project on body-care behaviour of the Herring Gull. That project is focussed on the analysis of the causal mechanisms underlying body-care. For this reason the ultimate purpose of the present study on the function of bathing, is to get ideas (no more than that) about how the system works. The underlying assumption is, that during evolution the causal mechanisms remain adapted to their biological functions by means of natural selection.

Bathing in water has been described for several groups (or species) of birds, for instance, Anatidae by McKinney (1965), penguins by Ainley (1974), and the Herring Gull by Van Rhijn (1977). McKinney distinguished three behaviour patterns associated with the wetting of the plumage: head-dipping, wing-thrashing, and somersaulting; Ainley considered only two behaviour patterns: head-dipping and body-thrashing; and Van Rhijn again three patterns: head-dipping, wing-flapping and plunging. Head-dipping is very similar in all three groups (species); wing-thrashing in Anatidae is rather similar to wing-flapping in the Herring Gull; somersaulting in Anatidae is (to some extent) comparable with the less elaborate plunging in the Herring Gull; and body-thrashing appears to be unique for penguins (it may be a combination of components of wing-flapping and plunging). The three behaviour patterns of the Herring Gull will be described in detail.

Head-dipping occurs while standing, squatting or floating in water. Occasionally it may be performed while standing or squatting on the shore-

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line of the water. It is a dipping of bill and head in the water, which is followed by a stretching of the neck upwards with the bill downwards. It is often combined with moderate tail-shaking and tilting of the wings. Wing-flapping may be performed while squatting in shallow water, or while floating. The wings are vigorously beaten against the water, which is splashed over the ruffled plumage. Wing-flapping occurs in alternation with head-dipping. Plunging is almost exclusively shown in situations when the bird is floating in water. The gull turns with ruffled plumage sideways (around its body-axis) in the water. Head and neck are turned in such a way that the back of the head makes the first contact with the water. Plunging is often combined with moderate tail-shaking and wing-tilting. It occurs in alternation with head-dipping and wing-flapping. After a plunging movement the gull resumes its original position in the water. In contrast to this, after somersaulting ducks face in a direction opposed to the original one (McKinney 1965).

Bathing is not only composed of the three wetting movements mentioned above. It may contain several bill movements in the water: snapping-water and bill-washing; some scratching movements: head-scratching and bill-scratching; some preening movements: particularly rubbing movements of the wings; and finally several shaking movements: wing-beating, tail-shaking and head-shaking (cf.: Van Rhijn 1977). The bill movements mainly occur during the early part of bathing: both before and after the actual entering of the water. The scratching movements also occur early in the bathing sequence. They are mainly performed while standing in shallow water. Most preening movements during bathing occur after the peaks of bill - and scratching movements. Preening mostly occurs in alternation with wetting movements. The peak of the shaking movements is the latest one in a bathing sequence. Shaking movements also occur in alternation with wetting movements.

Bathing may start after a wide variety of activities: eating, incubation, courtship etc. In contrast to this wide variety preceding to the start of bathing, the number of possibilities after that start is limited. The behaviour during bathing has been described already. The behaviour after bathing starts with shaking movements, and is continued with preening behaviour. A sequence of preening movements after bathing is rather well predictable in respect to both the order of the different bill and/or head movements to the plumage, and the order of the treatments of the different parts of the plumage. Preening after bathing often starts with oiling. The latter movement, which is always associated with a high frequency of preening movements, never occurs without preceding bathing. The sequence of movements after the first oiling act is highly predictable, much more than the behaviour after the start of bathing. A detailed quantitative description is given by Van Rhijn (1977).

From the above paragraphs it becomes clear that bathing must be considered as the main starting point of elaborate sequences of behaviour serving the maintenance of the feathers (at least of the sequences containing oiling). This has been noticed already by other authors, for instance: Kortlandt (1940) who distinguished between autochthonous (with a feather maintenance function, mainly after bathing) and allochthonous (out of context) preening, Van Iersel & Bol (1958) who analysed the preening in terns (*Sterna*) after bathing, and Simmons (1964). The latter author suggested that the wetting of the plumage during bathing does not primarily serve the cleansing of the feathers and skin, but that it is mainly performed in order to oil and preen more efficiently.

Although Simmons' suggestion seems to be rather plausible, it has never been experimentally tested. As far as I know, nobody studied the processes acting on the feathers during bathing and subsequent shaking or drying. It is important, however, to analyse these processes in order to make reliable suggestions about the functional significance of bathing. In this paper I shall present some data about the processes mentioned above. It must be marked that these data are not based on experiments with living birds ("in vivo"), but simply with single feathers ("in vitro"). This implies that my data are not unconditionally applicable to a natural situation.

2. THE PROCESS OF BECOMING WET

I shall start with a few simple experiments on the process of becoming wet. The underlying question is: which factors determine the amount of water absorbed by the feather? This amount may depend on the nature of the contact with water (intensity, duration, temperature, and surface tension), and on the properties of the feather (presence of oil, size, etcetera).

2.1. NATURE OF THE WATER CONTACT

A feather may be wetted by laying it carefully on the water surface for some period of time, or it may be immersed once at the start of that period (after immersing the feather floats as in the former procedure), or it may be kept under water during the whole period. Figure 1A shows that the water absorbtion by a feather strongly depends on the way the feather was put into contact with water. The hatched columns in Figures 1 and 3 refer to the average dry weights (in milligrams, vertical scales) of the feathers used for the different experiments, while the open columns refer to the average water contents of those feathers in different situations. Figure 1A shows the averages of eight secondaries of a tame goose. The water content of each of these feathers was measured once after each of three different kinds of water contacts of 4 minutes: floating on the water (F), one immersion of about one second (I), and kept under water during the whole period (U). After the

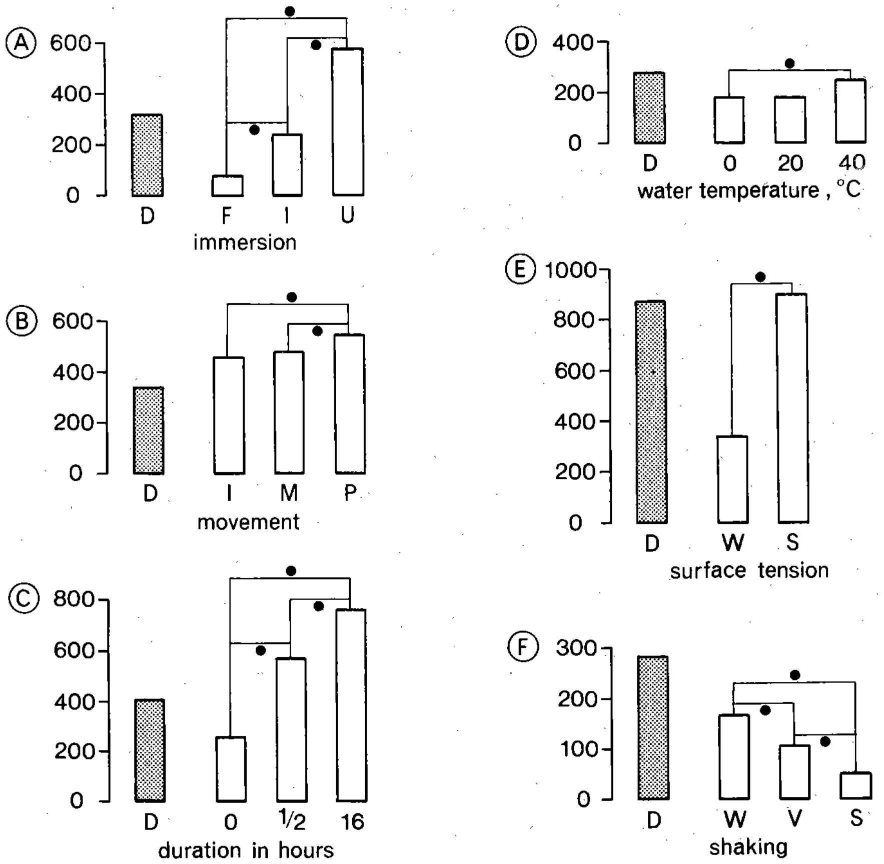

Fig. 1. Average dry weight (D, hatched columns) and average water content of feathers after different treatments. Vertical scales are in milligrams. Solid dots indicate significant differences.

A: eight secondaries of a tame goose; F = floating, I = one immersion, U = whole period under water. B: seven primaries of a tame duck; I = immobile, M = slowly moving under water, P = plunging in and out of the water. C: four primaries of a tame duck; O = one immersion, ½ = one immersion + ½ hour floating, 16 = one immersion + 16 hours floating. D: six secondaries of a Herring Gull at a water temperature of 0, 20, and 40°C. E: six primaries of a Herring Gull; W = clean water, S = soap solution. F: six secondaries of a Herring Gull; W = wet, V = 30 seconds in a vertical position after wetting, S = five vigorous shaking movements after wetting.

contacts the feathers were held vertically for 30 seconds to remove the large water drops attached to the feather's surface, and again 30 seconds later the weights of the feathers were determined. All differences in Figure 1A are significant (indicated by solid dots; sign test, one sided, $p < 0.01$).

Figure 1B shows how the movement with the feather influences the amount of water absorbed by the feather. This Figure refers to seven primaries of a tame domestic duck. The water content of each of these feathers was measured once after each of three different kinds of water contacts of 5 minutes: immobile under water (I), slowly moving under water (M), and plunging in and out of the water (P) with a frequency of 1 per 10 seconds (30 immersions of about 9 seconds). After the contacts the feathers were held vertically for 30 seconds, and again 30 seconds later the weights of the feathers were determined. It appears from this Figure that there are no large differences between the three situations. Nevertheless, the differences between I and P, and between M and P are significant (sign test, two sided, $p < 0.05$).

The influence of the duration of the water contact is shown in Figure 1C. This Figure refers to four primaries of the tame duck. Three replicates were made of the determination of the water content of each of these feathers after each of three different water contact durations: one single immersion (O), one immersion + ½ hour in the water (½), and one immersion + 16 hours in the water (16). After the contacts the feathers were held vertically for 30 seconds, and 90 seconds later the weights of the feathers were determined. All differences in Figure 1C are significant (sign test, one sided, $p < 0.01$). It can be concluded from this Figure that the process of becoming wet may last several hours.

The influence of the water temperature is shown in Figure 1D. This Figure refers to six secondaries of a Herring Gull. The water content of each of these feathers was measured once after each of the three situations: one immersion + 5 minutes in water of 0°C. (O), the same at a water temperature of 20°C. (20), and the same at 40°C. (40). After the contacts the feathers were held vertically for 30 seconds, and again 30 seconds later the weights of the feathers were determined. The difference between 0° and 40° is significant (sign test, two sided, $p < 0.05$); the other differences are not significant. From these findings it could be concluded that only a considerable rise of the temperature of the water causes a perceptible acceleration of the process of becoming wet. However, during the 30 seconds in a vertical position after a contact with water of 0°C. only part of the drops of the water on the feather's surface falls off, whereas after contacts with water of 20° or 40° almost all drops of water fall off. Since water drops from the feather's surface can easily be removed by the bird (by shaking movements; see section 3), the net effect of the water temperature on the wetting of a bird's plumage may be stronger than shown in Figure 1D.

The effects of the surface tension have been studied by adding a few drops of a soap solution to the water. Rutschke (1960) demonstrated that the waterproofing of a bird's plumage can be destroyed by lowering the surface tension. It can be seen from Figure 1E and Table 1 (third column) that the amount of water absorbed by the feather increases strongly as the surface tension decreases. Figure 1E refers to six primaries of a Herring Gull. Two replicates were made of the determination of the water content of each of these feathers after each of the two situations: one immersion + 5 minutes in clean water (W), and one immersion + 5 minutes in soap water (S). After the contacts the feathers were vigorously shaken, and next (1 minute after the contacts) the weights of the feathers were determined. The difference between both situations in Figure 1E is significant (sign test, one sided, $p < 0.01$). Table 1 refers to hundred-twenty feathers (six feathers from each of twenty regions) of the tame duck. The water content of each of these feathers was measured once after each of the two situations: one immersion + 5 minutes in clean water (second column), and one immersion + 5 minutes in soap water (third column). After the contacts the feathers were held vertically for 30 seconds, and again 30 seconds later the weights of the feathers were determined. The average water contents in the second column are expressed as percentages of the dry weights (first column). The average water contents in the third column are expressed as percentages of the water absorbtion in the control experiment, viz. in clean water (second column). All percentages in the third column are larger than 100. Thus, in soap water

Table 1. Wettability of different duck feathers in different situations

		water absorbtion as a percentage of		
		dry weight	absorbtion in clean water	absorbtion while oil on feather
	dry weight in mg.	clean water + oil	soap solution + oil	clean water — oil
wing feathers:				
primaries	354	127	127	98
their upper greater coverts	72	149	174*	89
their under greater coverts	26	330	137	127
secondaries	148	157	206*	81
their upper coverts: large	30	247	193*	73
the same: middle and small	11	256	268*	113
their under coverts: large	40	270	158*	109
the same: middle and small	7	347	171*	123
marginal coverts	3	331	242*	91
tail feathers:				
rectrices	76	180	169	99
upper coverts	22	314	424*	88
under coverts	13	258	393*	138
body feathers:				
head	1	800	206*	72
back	10	417	238*	134
surroundings of oil gland	20	160	597*	195*
shoulder	60	156	286*	109
throat	6	238	535*	242*
breast	28	218	232*	158*
flank	35	160	278*	169
belly	5	586	265*	141

a feather is wetted more intensively than in clean water. In 17 (out of 20) feather regions the difference is significant (indicated by asterisks; Wilcoxon's test, one sided, $p < 0.05$).

2.2. PROPERTIES OF THE FEATHER

One might imagine that preen oil protects a feather against the ill-effects of water. However, the exact function of oiling is rather uncertain, despite much speculation and experiment. Elder (1954) showed that ducks of several species, which had been surgically deprived of their oil glands before reaching the age of ten days, became water logged when entering the water, and were subject to a high mortality rate before reaching maturity. The feathers of these birds appeared unusually dry, and the bills and feet tended to become scaly. Fabricius (1959) could not confirm these findings in a similar experiment, although of a much shorter duration: about one week, whereas Elder was able to follow some birds for several years. Fabricius found that the appearance and the water repellent quality of the feathers was strongly associated with the amount of time spent preening by the bird (irrespective of the application of oil). Rutschke (1960) showed that (complete?) experimental removal of the oil on the belly feathers of ducklings and adult ducks, does not affect the buoyancy of the birds. From these experiments it seems that there is no direct relation between preen oil and waterproofing of a bird. The finding that preen oil quickly penetrates into the medulla cells of the shaft and the barbs of feathers (Rutschke 1960), may indicate that it plays a role in maintaining the elasticity of the different parts of the feathers. Thus, indirectly (via the structural properties of the feather) preen oil may (in the long run) be important in keeping the bird waterproof.

In the fourth column of Table 1 some information is given about the effect of removing oil from the feathers (with benzol and ethanol) on water absorbtion. The water content of each of the hundred-twenty feathers was measured once after one immersion + 5 minutes in clean water. The average water contents in the fourth column are expressed as percentages of the water absorbtion of the same feathers in a control experiment, viz. before the removal of oil (second column). In only 12 (out of 20) cases water absorbtion is increased after removal of oil (percentage in the fourth column larger than 100); 3 of these cases are significant (indicated by asterisks; Wilcoxon's test, two sided, $p < 0.05$). The effect of removing oil is much lower than the effect of lowering the surface tension of the water: all percentages in the fourth column are smaller than the percentages in the third column.

It is interesting to see which feathers seem to be more or less protected by oil (percentages above 100), namely: all under coverts, the whole ventral side of the bird (throat, breast, flank, and belly), and part of the dorsal side of the bird (back and surroundings of oil gland). Thus, it seems that there is a correlation between the degree of protection by oil and the probability of being exposed to water for swimming (ventral side of the bird). It is strange that there is no clear correlation between the orientation of the preening movements of a bird during oiling and the degree of protection by oil of the different regions. A considerable number of movements during oiling (cf.: Van Rhijn 1977) is directed towards the pinions (primaries and secondaries), the wingbow (marginal coverts), and the outside of the wing (upper secondary coverts). The amount of fat in the feathers of the different regions was estimated by means of Sudan III stain (intensity of the colour and the number of droplets per surface unit). This method failed to show a relation between the amount of oil present in the feather and the degree of protection by oil.

The size of the feather may be important too in the process of becoming wet. This can also be seen from Table 1: the percentage of water absorbed after a contact with clean water, while oil is still present on the feather, may be different for feathers from different regions (second column). The dry weight of the feather (first column) and the percentage of absorbed water seem to be negatively correlated: the primaries are heaviest and absorb the lowest percentage, while the head feathers are lightest and absorb the highest percentage. A comparison between the first two columns yields a Spearman's rank coefficient $r = -0.81$, which is highly significant for $n = 20$ (two sided, $p < 0.001$). This negative correlation may be due to the fact that in large (heavy) feathers the feather-surface per milligram feather weight is much smaller than in small feathers. The size of the feather-surface must be one of the factors determining the amount of water to be absorbed. Besides, morphological features like ratio between length and width of the feather, distance between barbs, solidity of the shaft, etcetera, may play important roles.

3. THE PROCESS OF BECOMING DRY

A considerable part of the water absorbed by a bird's plumage during bathing will be removed by the bird by means of vigorous wing-beats, head-, tail- and body-shakes. The remaining part of the water disappears by evaporation. For single feathers in the plumage a third factor may have an influence on drying, namely the water absorbtion by neighbouring dry feathers. The former two factors will be further analysed.

Figure 1F shows to what extent the shaking movements may play a role. This simulation refers to six secondaries of a Herring Gull. The water content (after one immersion + 5 minutes in water) of each of these feathers was measured once after each of the three situations: no shaking or vertical position (Wet), 30 seconds in a vertical position (Vertical), and five vigorous shaking movements by hand (Shaking). Weights were determined 1 minute after the last contact with water. All differences in Figure 1F are significant

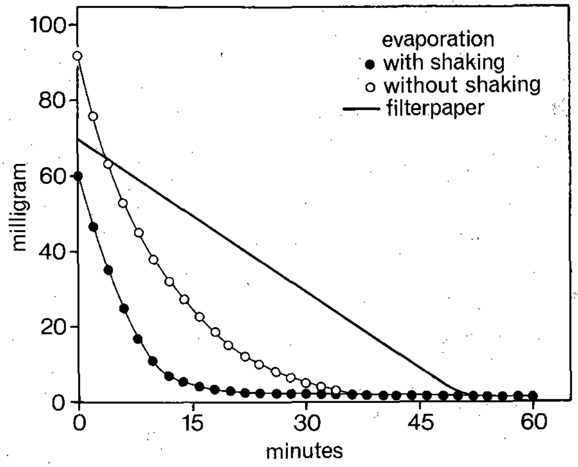

Fig. 2. Decrement of the water content of a secondary of a Herring Gull after 5 minutes in water with subsequently 30 seconds in a vertical position (open circles), and with five vigorous shaking movements (solid dots). The decrement of a piece of filter paper is indicated by the third curve.

(sign test, one sided, $p < 0.05$). The effect of the five vigorous shaking movements in particular, is very strong: about 70% of the water of a wet feather was removed by shaking.

The decrement of the water content of a feather by evaporation is shown in Figure 2. Two series of measurements were carried out on one secondary of a Herring Gull. This secondary was for the two treatments exposed to one immersion + 5 minutes in water; after that is was either held in a vertical position for 30 seconds (open circles), or it was 5 times vigorously shaken (solid dots). Finally the feather was placed (with its calamus) in a stand on a balance, in such a way, that the feather-vance and the rhachis were in contact with air only. In this position the water content of the feather was measured every two minutes during 1 hour, the first measurement about 1 minute after the last contact with water.

To understand the shapes of both graphs a comparison has been made with another evaporation process, referring to the water absorbed by a piece of filter paper. This piece was moderately and evenly wetted, and placed on a slide on the balance. The decrement of its water content is indicated with the smooth line in Figure 2. This decrement appears to be almost linear, while in both series of measurements on the feather the decrement is obviously non-linear. The linearity in the case of the piece of filter paper is due to the fact that the surface of evaporation is constant during the process: the water remains evenly distributed over the piece of paper. The non-linearity in the case of the feather is (at least partly) due to the fact that the surface of evaporation becomes smaller during the process: the water is not evenly distributed, some parts of the feather dry quicker than other parts.

A comparison between evaporation after shaking (solid dots) and evaporation after 30 seconds in a vertical position (open circles) reveals that the process is more rapid in the former (steeper angle of inclination). This phenomenon is probably due to the fact that the water which is not removed by shaking, is (by the same shaking movement) distributed in very tiny droplets over the whole feather (large surface of evaporation), whereas without shaking the water remains in rather large drops (small surface of evaporation). We may thus conclude that for the process of becoming dry shaking is important in two respects: (1) the direct removal of a considerable part of the absorbed water, and (2) the acceleration of the evaporation of the remaining part of the water by means of an enlargement of the surface of evaporation.

4. INTERACTION BETWEEN WETTING AND DRYING

Bathing is frequently interrupted by shaking- and preening movements. Such interruptions last from a few seconds up to several minutes. It often occurs that the bird leaves the water during these interruptions, and thus, that the process of becoming dry is set in action. It may be questioned now to what extent the partial drying during interruptions of bathing influences the wetting during subsequent water contact.

To find an answer to the above question I designed an experiment in which the feathers were exposed to the following wetting and drying regimes: (A) 1 minute under water, 2 minutes out of the water, and again 1 minute under water, (B) as A but all durations doubled, (C) as A but all durations quadrupled, (D) 8 minutes under water, and (E), (F) and (G) as A, B and C, but per 2 minutes out of the water five vigorous shaking movements. After the contacts the feathers were held vertically for 30 seconds (except after the first contacts of regimes (E), (F) and (G), and again 30 seconds later the weights of the feathers were determined. The experiment was done with seven primaries of the tame duck, each of which was exposed once to the seven regimes.

The results are shown in Figure 3. The solid dots refer to the situations without shaking, the open circles to situations with shaking (here the weights were only determined after the second contact). The two measurements in each of the situations (A), (B) and (C) are connected with lines. Points referring to similar total durations of water contacts (either the first contact, or the sum of both contacts) are drawn on the same vertical. The moments of weight determinations are indicated with arrows in the wetting and drying schemes in Figure 3.

The following conclusions can be drawn from this Figure: (a) in situations (A), (B) and (C) the water content after the second contact is higher than

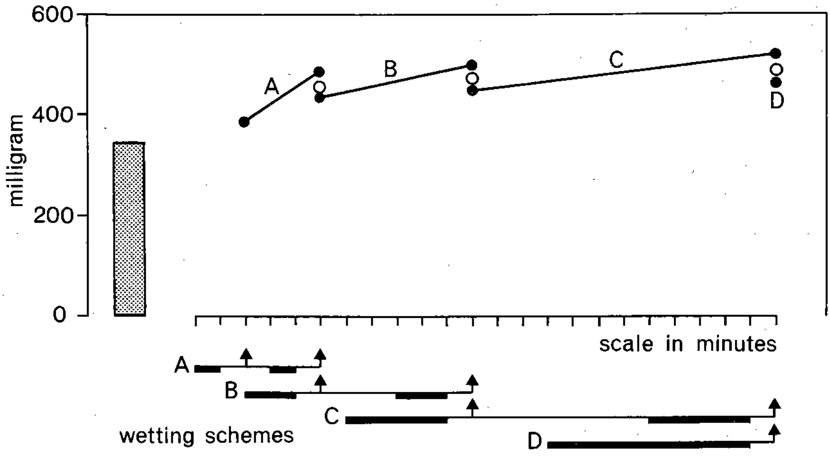

Fig. 3. Average dry weight (hatched column) and average water content of seven primaries of a tame duck after different treatments. Wetting schemes are given below: black bars refer to water contacts, arrows to measurements. Schemes and corresponding data are indicated by the same letters. Open circles refer to experiments with shaking during the pause between the water contacts. Measurements after water contacts of similar total durations are given on the same vertical.

after the first contact (sign test, one sided, $p < 0.01$), (b) the water content after the second contact is higher in situations without shaking than in situations with shaking between the first and the second contact (sign test, one sided, $p < 0.01$), (c) the water content after two contacts separated by a pause is higher than the water content after one uninterrupted contact with a similar total duration (sign test, two sided, $p < 0.01$), and (d) even the water content after two contacts separated by shaking seems to be higher than the water content after one uninterrupted contact with a similar total duration (not significant). The first and the second conclusion (a and b) are not very surprising, the third and the fourth conclusion, however, are quite unexpected.

One might imagine that the increased water absorbtion in situations of interrupted water contact was due to the fact that the feather was immersed twice instead of once at uninterrupted contact. It was shown in Figure 1B that water absorbtion can be enlarged by more immersions (column I with one immersion versus column P with thirty immersions). However, the increase by one extra immersion is certainly too small to give a satisfactory explanation for the difference between interrupted and uninterrupted water contacts. A more elegant hypothesis is based on the assumption that water absorbtion by the feather is the result of two processes: (1) the attachment of water to the feather's surface (an instantaneous process taking place when the feather contacts water), and (2) the penetration of the water into the feather (a long lasting process continuing as long as water adheres to the feather's surface). Thus, immediately after bathing, the water content of the interior of a feather is supposed to increase by penetration from the outer surface, whereas the quantity of the water attached to the feather's surface decreases by penetration into the feather and drying (shaking, evaporation, and absorbtion by neighbouring feathers).

5. CONSEQUENCES OF WETTING

Simmons (1964) states that "drenching could seriously damage the feathers by rendering them brittle and weak, rob the bird of flight, and in the case of water birds, destroy waterproofing and buoyancy" (p. 279). To measure the slackness of feathers, I examined how far they were bending if exposed to a certain force. To this end the rhachis was put in a clip, in such a way, that its proximal 5 centimeters (+ the proximal 5 centimeters of the vane) and the calamus were kept about horizontally with the convex side below, and were in contact with air only. The bending was defined as the vertical displacement of the top of the calamus after attaching a weight of 50 grams on the boundary between calamus and rhachis. It turned out that a considerable number of feathers cracked when this weight was attached after wetting, although the same weight could be borne in a dry condition. The slackness (in arbitrary units) of six primaries of the tame duck before and 2, 10, and 50 minutes after 1, 5, or 25 minutes under water is indicated in Figure 4. After the contacts the feathers were held vertically for 30 seconds. This Figure shows that (1) there is a positive relation between the duration of water contact and the degree of slackness, and (2) particularly for short durations of water contacts the degree of slackness seems to increase during the first 10 minutes after wetting. These findings may be associated with the two-stage process sketched earlier. It is plausible that the degree of bending is a function of the water content of the interior of the feather.

The effect of wetting on waterproofing of a bird has been studied by attaching pieces of feather-vane with some vaseline across the lower opening of a transparant tube. This tube was slowly pushed vertically into the water. At the moment that the water penetrated the piece of vane, the distance between water surface and lower opening of the tube was measured. Dry pieces of vane could be immersed several (2-6) centimeters before starting to become pervious to water, on the other hand, pieces of vane which were wet on the inside (within the tube) could not be immersed without leaking.

Wetting is an expedient to change the setting of hair (water wave). It is plausible that wetting in combination with pressure also influences the shape of a feather. To investigate this phenomenon four primaries and four secondaries of a tame goose were exposed to the following treatments: (1) 5 hours under pressure, than 19 hours rest, followed by 1 hour wetting and 5 hours drying; and (2) 1 hour wetting and than as (1). The pressure was used to

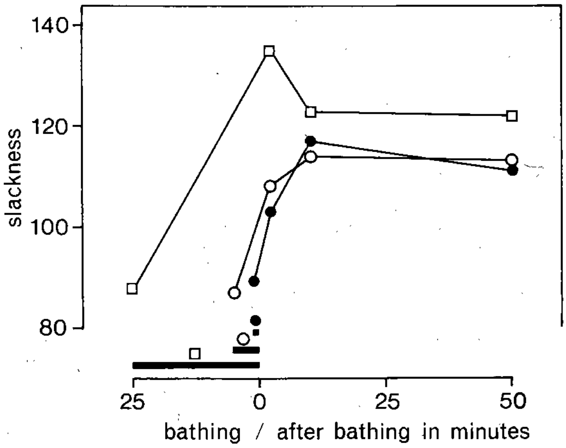

Fig. 4. Slackness (in arbitrary units) before, and 2, 10 and 50 minutes after water contacts of 1 (dots), 5 (circles), and 25 minutes (squares) of six primaries of a tame duck.

enlarge the bend of the shaft in the case of the primaries, and to enlarge the bend of the vane (and thus of the barbs) in the case of the secondaries. The bend of a primary was measured by means of the perpendicular from the top of the feather to the straight line through the calamus. The bend of the vane of a secondary was defined as the reciprocal of the distance between the margins of the vane, 5 centimeters from the top of the feather. Measurements were executed (1) before the pressure, respectively the first wetting in the second treatment, (2) immediately after the pressure, (3) 1 hour later, (4) 18 hours later, and (5) after wetting + drying. The results (in arbitrary units) are shown in Figure 5. The first treatment (pressure without wetting) is indicated with circles, the second (pressure with preceding wetting) with dots. It turns out that the second treatment causes a stronger and more permanent bend than the first treatment. Additionally, it is obvious that the original shape is restored after wetting and drying without pressure.

Finally something can be said on the cleansing effect of wetting. Measurements on the feathers of Table 1 revealed that (1) after the first wetting in clean water the dry weight decreased by 2.6% (sign test, two sided, $p < 0.01$), (2) after subsequent wetting in clean water no further decrease could be noticed, but (3) after the following wetting in soap water and after extraction of fat, a decrease of 3.6% was observed (sign test, two sided, $p < 0.01$). It is unlikely that this decrease was only due to the extraction of lipids. Bollinger & Varga (1961) found that feathers contain approximately 2% of lipids which are extractable with ether or chloroform. If the decrease of 3.6% was not only due to the loss of fat and to corrosion of the feather by soap and/or benzol + ethanol, we may conclude that simply wetting in clean water is not sufficient to remove all dirt from a feather. Thus, a bird has to perform „cleansing behaviour", additional to simply wetting.

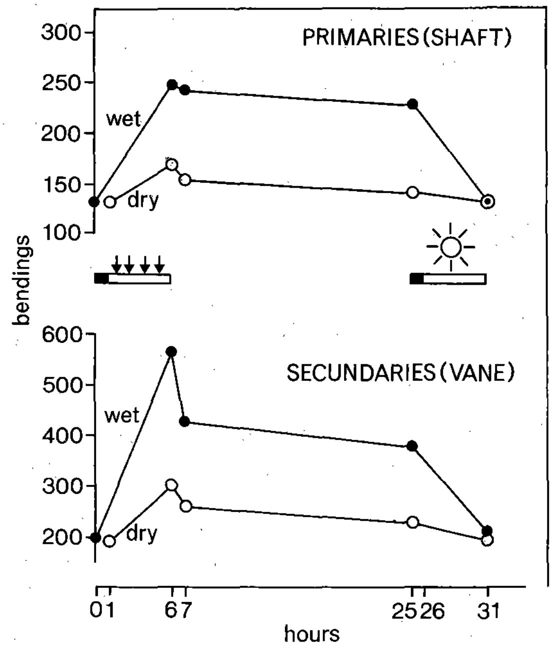

Fig. 5. Influence of pressure (white bars with arrows) on the bending (in arbitrary units) of wet (solid dots) and dry (open circles) feathers of a tame goose, and influence of wetting (black bar) + subsequent drying (white bar with sun) on bended feathers.

6. EFFECTS OF BATHING

6.1. COMPARISON BETWEEN SIMULATED AND NATURAL WETTING

The amount of water absorbed by a feather, as measured in the experiments described above, ranges between 25% and 800% of the dry weight of that feather. Since the data were mainly based on samples of large feathers (primaries and secondaries), which absorb a relatively small amount of water (section 2.2.), the average water absorbtion by a feather certainly exceeds the average dry weight of a feather. If the water absorbtion of the whole plumage of a bird during natural wetting would be in the same range, it should lead to a considerable rise of the body weight of the bathing bird, and to a gradual drenching during a prolonged water contact. Water birds, however, do not seem to lie deeper in the water after bathing than before, and they do not look wetter after a long stay in the water than after a short. On the contrary, with a few exceptions (e.g. cormorants), water birds do not look wet at all after a normal water contact; after intensive bathing a water bird may even look drier than before (Swennen 1977). This strongly contrasts with the appearance of the experimental feathers after wetting: they normally seemed to be rather soaked.

One of the factors responsible for the large amount of water absorbed by the experimental feathers may be connected with pollution in the water and/or on the feather's surface. Pollution decreases the surface tension of the water. It has been shown by Swennen (1977) that the water repellent properties of a bird's plumage are strongly dependent on the quality of the water. In my experiments this water quality may be negatively influenced by (1) the use of containers which were not very clean, (2) by leaving the water for several days in these containers, and (3) by using this water for several feathers which were manipulated by hand. This, however, cannot be the whole story, since ducks and gulls do not look soaked at all after bathing in water, the quality of which is comparable to that in my experiments.

The low water absorbtion during natural wetting may also be associated to the fact that a considerable part of the plumage never comes into direct contact with water during bathing. Water transfer from the contour feathers towards the underlaying down packet is prohibited by an infinite number of air cavities between the feathers. By these cavities two-sided wetting of a feather (and thus leaking: section 5) is minimal. On the other hand, all experimental feathers were directly exposed to the water, most of them even with the two sides of their vanes, resulting in an easy penetration of water between barbs and barbules.

6.2. EFFECTS OF THE SEPARATE BATHING MOVEMENTS

To conclude this paper, I shall try to connect some of the previous results with the processes occurring during the bathing movements of a Herring Gull. To this end I shall consider the consequences of both the three wetting movements (head-dipping, wing-flapping, and plunging) and the other movements occurring during bathing (bill-, scratching-, preening-, and shaking movements). Before entering into the details of the separate movements, some data will be presented about the general properties of

Table 2. Occurrence of wetting movements after deprivation of bathing

type of wetting behaviour	number of observations (% of total)	frequencies (averages and extremes) of the three wetting movements		
		head-dipping	wing-flapping	plunging
no wetting	62 (31%)	—	—	—
only head-dipping	72 (35%)	51 (1—151)	—	—
head-dipping + wing-flapping	61 (30%)	79 (37—149)	5 (1—15)	—
head-dipping + wing-flapping + plunging	8 (4%)	89 (50—140)	11 (5—14)	16 (1—46)

bathing sequences. The occurrence of the three wetting movements is indicated in Table 2, which is based upon two-hundred-and-three ½-hour bath presentations after two hours deprivation of bathing. From this Table it becomes evident that the mean frequency of wing-flapping is higher during sequences with plunging than during sequences without plunging. Similarly, the mean frequency of head-dipping is highest during sequences with wing-flapping and plunging, and lowest in sequences without other wetting movements. The temporal distributions of the different bathing activities over a bathing sequence are shown in Figure 6, which is based on twelve bathing sequences followed by oiling (cf.: Van Rhijn 1977). These sequences (starting with the first entering of the bath after deprivation, and ending with the last leaving of the bath before oiling) were subdivided into three parts of equal durations. The histograms represent the mean frequencies (per 5 minutes) of the different bathing activities in the three parts of a bathing sequence.

Immersions by head-dipping are restricted to head and bill. Because of the stretching of the neck immediately after the dipping movement, shoulders, and (during intensive head-dipping) back and outside of the wings are rinsed. Each immersion lasts a few tenths of a second. During bursts of head-dipping the frequency of immersing is about one per second. A bathing sequence may contain up to 150 head-dipping movements (Table 2). The frequency of head-dipping gradually increases during a bathing sequence (Fig. 6). The movements of the bird during head-dipping force the water to flow according to the feather arrangement (from proximal to distal). Because the plumage is kept rather sleek during head-dipping, the water cannot penetrate between the feathers. The nature of the water contact by head-dipping is therefore comparable with the simulation presented in columm F in Figure 1A. Consequently head-dipping causes a rather poor wetting of the plumage.

Immersions by wing-flapping involve the wrists and the distal parts of the wings. Because of the splashing by wing-flapping almost the whole outer plumage is rinsed. Each immersion lasts less than one tenth of a second. During bursts of such immersions the frequency of immersing is about 4 per second. Each burst, which is mostly followed and preceded by head-dipping, contains about 5 immersions. A bathing sequence may contain up to 16 wing-flapping bursts (Table 2). Wing-flapping occurs in about 50% of the sequences with wetting movements (Table 2); its frequency is very low in the early part of bathing (Fig. 6). The movements of the bird during wing-flapping often force the water to flow opposite to the feather arrangement (from distal to proximal). Because of the ruffled plumage during wing-flapping, the splashing water penetrates between the feathers. The nature of the water contact by wing-flapping is comparable with simulations presented in columns I and U in Figure 1A, and in column P in Figure 1B. It is therefore obvious that wing-flapping causes an intensive wetting, in parti-

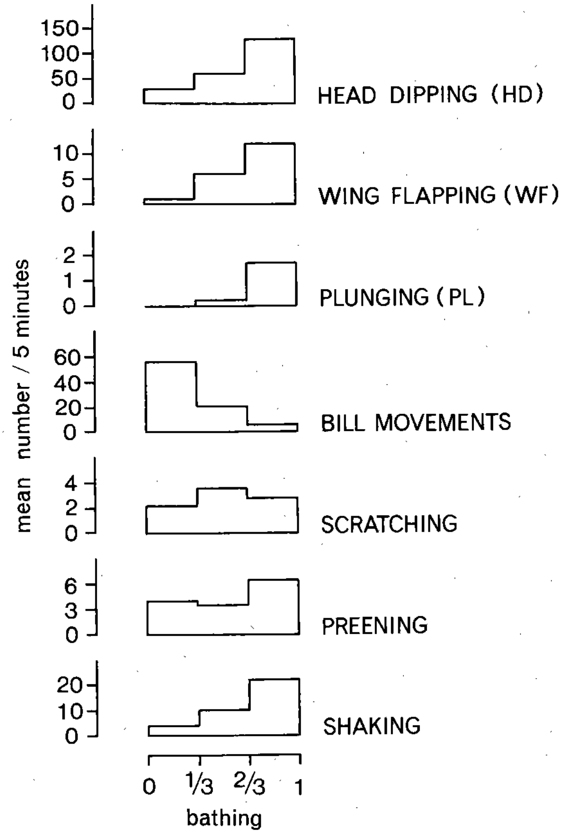

Fig. 6. Average frequencies (per 5 minutes) of seven behaviour categories during bathing divided into three parts of equal durations.

cular of the wing feathers. An intensive wetting of the wings, however, is disadvantageous because a softening of pinions may prevent the bird from flight (Simmons 1964). Hence, bursts of wing-flapping are mostly succeeded by vigorous wing-beating, lowering the wetting by wing-flapping. The relation between wing-flapping and wing-beating is shown in Figure 7. It can be deduced from this Figure that for sequences without plunging 50% of the wing-flapping bursts is followed within 12 seconds by wing-beating; the great majority of wing-flapping bursts is followed within 30 seconds by wing-beating (87%). It may thus be questioned, whether the actual function of wing-flapping is a wetting of the wings. I shall consider two alternative functions of wing-flapping, namely (1) the removal of dirt from the pinions by means of the vigorous movements through the water, and (2) the restoration of the fine structure of the pinions. The latter suggestion is not very likely, because water currents from distal to proximal seem to be unsuitable for this purpose, and because during bathing after handling of the

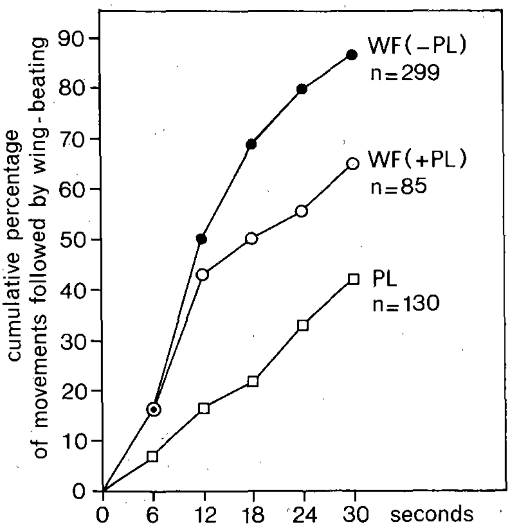

Fig. 7. Percentage of movements (ordinate) followed within a certain time interval (abscissa) by wing-beating. WF — PL (dots) = wing-flapping in sequences without plunging; WF + PL (circles) = wing-flapping in sequences with plunging; PL = plunging.

bird (destruction of the fine structure of the feathers) the occurrence of wing-flapping is extremely low. Thus, by means of elimination, the former suggestion (removal of dirt) seems to be the most plausible hypothesis. This suggestion is supported by the finding that the frequency of wing-flapping is unusually high if the soil of the bird's cage is very slushy.

During plunging head, neck, part of the breast, and one flank + wing of the bird are immersed. Because of the quick rotations of the body during plunging, almost the whole outer plumage is rinsed. Each immersion lasts about half a second. During bursts of plunging the frequency of immersing is about 5 per 10 seconds. Bursts of plunging are mostly followed and preceded by wing-flapping or head-dipping. A bathing sequence may contain up to 50 plunging movements (Table 2). Plunging occurs in less than 10% of the sequences with wetting movements (Table 2); its occurrence is mainly confined to the final part of bathing (Fig. 6). The movements of the bird during plunging force the water to flow according to the feather arrangement (Fig. 1B, column M). Plunging is associated with a ruffled plumage, which implies that the water penetrates between the feathers. The duration of water contact during a burst of plunging is roughly the same as during a burst of head-dipping: plunging immersions last about twice head-dipping immersions, but the frequencies of immersing is for plunging about half that of head-dipping. The main differences between plunging and head-dipping involve (1) the extent of the plumage to be immersed, and (2) the position of the feathers (sleek versus ruffled). On the basis of these differences it can be concluded that plunging causes a more intensive wetting than head-dipping. Plunging is not closely associated with wing-beating (Fig. 7) or shaking, movements reducing the effect of wetting. Even the wing-flapping bursts occurring during sequences with plunging are less often followed by wing-beating, than wing-flapping bursts during sequences without plunging (Fig. 7). It is therefore possible that the actual function of plunging concerns the wetting of the plumage. Besides, because of water currents according to the feather arrangement, plunging may play a role in the restoration of the fine structure of the feathers.

The effects of the bill movements on the wetting of the plumage can be neglected. In respect to body-care their function seems to be restricted to the wetting and cleansing of the bill. This applies in particular to bill washing, a sideways shaking with the bill through the water. That movement, which normally occurs in the early part of a bathing sequence (Fig. 6), appears most often among the eating of sticky food. Occasionally bill-washing precedes preening. In that case it may be performed in order to prevent dirtying of the plumage by the bill, and/or it may possibly play a role in the wetting of the plumage.

The direct effect of scratching movements on the wetting of the plumage is limited. A wet foot brings a tiny amount of water to the head. The indirect effect of head-scratching may be more important. About one third of the scratching movements is immediately followed by head-dipping. As a consequence of dislocations of the feathers by scratching, water absorbtion by the head feathers may be increased.

The effects of the preening movements during bathing on wetting may be important too. By rubbing (the most common preening movement during bathing) dislocations of the feathers may be achieved, resulting in an enlarged water absorbtion during subsequent water contact. About one third of the rubbing movements is immediately followed by head-dipping. However, the direct transfer of water from the head to breast, shoulder, or outside of the wing may be even more important. About 75% of the rubbing movements is immediately preceded by head-dipping! Besides, the temporal distributions of preening movements and scratching movements are fairly similar (Fig. 6). The only difference is that the peak in the preening activity during bathing occurs somewhat later than the peak in the scratching activity. It is therefore possible that scratching + subsequent head-dipping (wetting of the head) is performed as a mean to wet other parts of the body by rubbing.

The shaking movements all result in a removal of water if performed in a wet condition. The function of wing-beating (the most common shaking movement during bathing) after wing-flapping has been discussed earlier. The other shaking movements (head-shaking, tail-shaking, etcetera) seldom occur during bathing.

The bathing movements of the Herring Gull are rather similar to those of most other water birds. In land birds bathing in water may be very different: the feather tracks are opened and closed to expose bare spaces of skin to the water, to attrap this water, and to squeeze it through the feathers (Slessers 1970). Consequently land birds often look very wet after bathing, whereas in water birds the effects of wetting are almost invisible. The bathing methods of land birds seem to be more effective for the cleansing of the feathers than the methods of water birds. Many properties of water birds can be brought in relation with the problem: how to maintain buoyancy and insulation. The thickness of the layer of belly feathers in water birds (Rutschke 1960) is certainly associated with this problem. Other examples are: the size of the radius of and the distance between barbs of a feather (Rijke 1968, 1970), the presence of flexules on the tip of body feathers (Kennedy 1972), and probably, the larger oil glands (Kennedy 1971). It is very likely that the bathing methods of water birds can also be considered as an adaptation to the problem of waterproofing. The loss of waterproofing may have serious consequences for the bird. Victims to fuel-oil or stomach-oil of the Fulmar (Swennen 1974) are usually doomed to death. Two-sided wetting of feathers (like land birds often do) interferes with the waterproofing of those feathers (section 5). In water birds two-sided wetting would lead to a decrease of buoyancy and insulation, and hence, this method can only be applied in a very restricted way.

7. ACKNOWLEDGEMENTS

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8. SUMMARY

This paper describes how bathing may influence the water content and the quality of a bird's plumage in particular of some Anatidae and the Herring Gull.

The water absorbtion by a feather depends on the intensity of the water contact (Fig. 1A), the movement of the feather in the water (Fig. 1B), and the duration of the water contact (Fig. 1C). It is accelerated by high temperatures of the water (Fig. 1D) and by a low surface tension of the water (Fig. 1E and Table 1). Preenoil seemed to play a minor role in the protection against water absorbtion (Table 1). Only the feathers from the ventral side and from the surroundings of the oil gland absorbed slightly more water after removal of oil. Water absorbtion seems to be a function of the size of the feather's surface (Table 1).

Drying of a feather is strongly accelerated by shaking movements (Fig. 1F). Apart from the direct removal of water, shaking may play a role in the dispersion of tiny water droplets over the feather, resulting in an acceleration of the evaporation of water (Fig. 2).

Water absorbtion of a feather is higher after wetting with an interruption of a few minutes, than after the same amount of wetting without interruption (Fig. 3). This phenomenon is probably due to the fact that the water slowly penetrates into the feather as long as some water adheres to the feather's surface.

Wetting results in a decrease of the stiffness of the shaft of a feather (Fig. 4). This decrease is probably a function of the amount of water penetrated into the feather. Feathers become pervious to water if they are wet on both sides. Shapes of wet feathers can be changed by means of pressure (Fig. 5). The original shape can be restored by wetting. It is likely that wetting results in a partial removal of dirt.

At the end of this paper I have drawn some connections between the results on simulated bathing, and on data of real bathing of a Herring Gull. Firstly, some comments have been made to explain the large water absorbtion by the experimental feathers. Secondly, the effects and the patterning (Table 2 and Fig. 6) of the separate bathing movements have been discussed. The most common wetting movement (head-dipping) causes a rather poor wetting of the outer plumage. The movement „wing-flapping" is probably not primarily serving the wetting of the plumage. It is mostly followed by „wing-beating" (Fig. 7), a drying movement. „Wing-flapping" may play a role in the removal of dirt from the wings. The movement „plunging" causes an intensive wetting of the plumage. It is not clearly associated with drying movements. Bill movements during bathing play a minor role in the wetting of the plumage. „Head-scratching" may indirectly (via head-dipping) cause an intensive wetting of the head. „Rubbing" may be performed in order to carry water from the head towards other parts of the plumage. The bathing methods of the Herring Gull seem to be rather well comparable with those of other water birds. A comparison has been made with the bathing of land birds.

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10. SAMENVATTING

In dit artikel wordt beschreven hoe baden het watergehalte en de kwaliteit van het verenkleed van een vogel (in dit geval tamme eend, tamme gans en Zilvermeeuw) zou kunnen beïnvloeden.

De wateropname door een veer hangt af van de intensiteit van het watercontact (figuur 1A), van de beweging van de veer in het water (figuur 1B), en van de duur van het watercontact (figuur 1C). De opname wordt versneld door hoge watertemperaturen (figuur 1D) en door een verlaging van de oppervlaktespanning van het water (figuur 1E en tabel 1). De wateropname hangt slechts in zeer geringe mate samen met de aanwezigheid van stuitvet (tabel 1). Alleen de veren van de buikzijde van een vogel en van de omgeving van de stuitklier namen iets meer water op na ontvetting. De wateropname hangt ook in belangrijke mate samen met de grootte van het veer-oppervlak (tabel 1).

Het droog worden van een veer wordt aanmerkelijk versneld door schud-bewegingen (figuur 1F). Schudden veroorzaakt, naast de directe verwijdering van water, waarschijnlijk een tamelijk egale verdeling van zeer kleine waterdruppeltjes over de veer. Hierdoor wordt de verdamping van het resterende water versneld (figuur 2).

De wateropname door een veer is groter na een watercontact met een onderbreking van enkele minuten dan na een ononderbroken contact van dezelfde totale duur (figuur 3). De oorzaak van dit verschijnsel ligt waarschijnlijk in het feit dat water langzaam in een veer binnendringt zolang er water aan het oppervlak van de veer hangt.

Een gevolg van nat worden is dat de stijfheid van de schacht afneemt (figuur 4). De grootte van die afname hangt waarschijnlijk samen met de hoeveelheid water die in de veer is gedrongen. Een veer wordt doorlatend voor water wanneer beide zijden nat zijn. De vorm van een natte veer kan onder invloed van druk veranderd worden (figuur 5). De oorspronkelijke vorm kan weer hersteld worden door de veer opnieuw nat te maken. Nat maken heeft waarschijnlijk tot gevolg dat een deel van het vuil uit de veren verdwijnt.

Aan het eind van dit artikel heb ik verbanden gelegd tussen de resultaten over gesimuleerd baden (gecontroleerd nat maken van afzonderlijke veren) en gegevens over werkelijk baden van een Zilvermeeuw. Daarbij is eerst behandeld waarom de wateropname van de experimentele veren zo hoog was. Daarna ben ik ingegaan op de effecten en de plaatsing in het complete baadpatroon (tabel 2 en figuur 6) van de afzonderlijke baadbewegingen. De meest voorkomende baadbeweging (duiken) veroorzaakt waarschijnlijk een betrekkelijk geringe bevochtiging van de buitenkant van het verenkleed. De beweging „vleugel-flapperen" dient waarschijnlijk niet in de eerste plaats voor het nat maken van het verenkleed. Deze beweging wordt meestal gevolgd door „vleugel-slaan" (figuur 7), een droogbeweging. Vleugel-flapperen zou wel eens kunnen dienen voor de verwijdering van vuil uit de vleugels. De beweging „dompelen" veroorzaakt wel een intensieve bevochtiging van het verenkleed. Deze handeling hangt niet duidelijk samen met droogbewegingen. De snavel-bewegingen die voorkomen tijdens baden spelen nauwelijks een rol bij de bevochtiging van het verenkleed. „Kopkrabben" zou indirect (via duiken) wel eens belangrijk kunnen zijn bij het nat maken van de kop. „Wrijven" met de kop over de veren zou de functie kunnen hebben van wateroverdracht van de kop naar andere delen van het verenkleed. De baadmethoden van de Zilvermeeuw lijken tamelijk veel op die van andere watervogels. Deze methoden zijn vergeleken met het baadgedrag van landvogels.

Dr. J. G. van Rhijn

Zoölogisch Laboratorium, Kerklaan 30, Haren (Gr.), The Netherlands.