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THE WATER REPELLENCY AND FEATHER STRUCTURE OF CORMORANTS, PHALACROCORACIDAE

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INTRODUCTION

A well-known characteristic of cormorants, Phalacrocoracidae, is their habit of spreading their wings to the sun or breeze after a period in the water, a feature commonly referred to as 'wing-drying'. The origin and purpose of this habit has had comparatively little investigation. Although the actual drying of the wings is the most obvious and probably also the correct interpretation of this behaviour, it leaves unexplained why this habit is entirely absent in all other water birds with the exception of the closely allied darters, Anhingidae. An alternative explanation of this behaviour was offered by an investigator who, after a study of the cormorant's skeleton and centre of gravity, suggested that the bird would be somewhat off balance in its customary upright position with the wings folded in place and that the spreading of the wings would help compensate for this shortcoming (Austin, 1963). The absence of these mechanical skeletal features in other water birds could very well support this conclusion, but Fry's observation (1957) of cormorants spreading their wings while on the water seems to disprove this theory. In what follows, support will be given for the thesis that feather drying is the function, and wetness of the feathers the proximate cause, of the wing-spreading of cormorants. It will be shown that cormorant feathers differ structurally from the feathers of ducks and that, as a consequence, the feathers of cormorants are less water-repellent than are those of ducks.

LIQUID REPELLENCY AND SURFACE STRUCTURE

Until the work of Cassie & Baxter (1944) on the wettability of porous surfaces, ducks and other water birds were generally regarded as having attained perfection in water repellency, and it was usually taken for granted that these birds use preening oil with repelling properties far superior to any known to man. Studies on the water repellency of preening oil on *smooth* surfaces have revealed that this is not the case. There exist nowadays many man-made oils and resins which are superior in this respect. However, the microscopic structure of feathers appears to conform closely to the requirements for optimal water repellency, a short outline of which is given below.

Drops of water, when placed on smooth solid surfaces, will either spread into a continuous film, or cover a limited area with the liquid taking the shape of part of

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a sphere. In this latter case, the surface is called 'water-repellent', the extent of which is conveniently expressed by the contact angle θ, this being the angle between the tangent to the curved water surface at the point of contact with the solid surface, measured through the liquid. The contact angle will be called 'advancing' when formed on addition of more water to the drop, receding when water is withdrawn. It is the receding contact angle which determines the lasting effect of repellency of a surface. The equilibrium positions of water drops on solid surfaces will be reached when the free energy involved in the air–water, solid–water and solid–air interfaces has acquired its minimum value. This is determined by the relative magnitude of the energies per unit area of each interface. A relation between the contact angle and the three interfacial energies follows from consideration of an infinitesimal displacement of the line of contact of the phases along the solid surface, which leads to

$$\cos\theta = (\gamma_{sa} - \gamma_{sl})/\gamma_{la} \tag{1}$$

where γ_{sa}, γ_{sl} and γ_{la} are the solid–air, solid–water and air–water interfacial energy per unit area, respectively (Wolf, 1957).

A similar but more useful relation is obtained by including the work of adhesion between the water and the solid, i.e. the work required to separate a unit area of solid–water interface into a solid and a water surface. Since this is (Adam, 1957)

$$W_{sl} = \gamma_{sa} + \gamma_{la} - \gamma_{sl},$$

equation (1) can be converted to

$$W_{sl} = \gamma_{la}(1 + \cos\theta). \tag{2}$$

Here only directly and easily measurable quantities appear on the right-hand side of the equation, whereas the values of γ_{sa} and γ_{sl} in equation (1) are extremely difficult or even impossible to measure.

Adam (1941) has pointed out that if the surface is not smooth, but rough or porous, large contact angles may cause the water to entrap air in the hollows and interstices, resulting in the formation of additional air–water interfaces. As the work of adhesion between water and air is negligible, an apparent contact angle will be established which is considerably larger than predicted by equation (1). These conclusions are of great importance to feathers because they imply that the structure of the feathers contributes actively to the water repellency. The formation of air–liquid surfaces will thus increase the ability of the water to pearl and roll off.

A relation between the apparent and true contact angle for drops on porous surfaces has been proposed by Cassie & Baxter (1944). If f_1 is the area of solid–water interface and f_2 that of air–water interface per unit apparent surface area, the expression for the work of adhesion between the water and the porous surface, W_{psl}, is analogous to the derivation of equation (2):

$$W_{psl} = f_1(\gamma_{sa} - \gamma_{sl}) + \gamma_{la}(1 - f_2).$$

Substitution of equations (1) and (2) then yields

$$\cos\theta_A = f_1 \cos\theta - f_2, \tag{3}$$

where θ_A is the apparent contact angle. This equation shows that θ_A will be larger than θ if f_2 is positive, i.e. when air–water interfaces are formed. The equation was tested experimentally and found to be correct by measuring the contact angles of paraffin-coated parallel wires on a wire cage, in which case (Cassie & Baxter, 1944; Rijke, 1965)

$$f_1 = [\pi r/(r+d)][1-(\theta/180^\circ)] \tag{4}$$

and

$$f_2 = 1 - r\sin\theta/(r+d),$$

r being the radius of the circular wires with their axes $2(r+d)$ apart (Fig. 1). It is seen that the contribution of the wire structure to the values of f_1 and f_2 is determined not by the absolute value of the radii of the wires and their distance apart, but by the ratios $(r+d)/r$ only. Large values of this ratio mean large f_2 and small f_1 values, increasing the apparent contact angle in the manner described by equation (3). It should be noted that the effect of relatively small values of $(r+d)/r$ on the increase of the contact angle is very pronounced. For example, when $(r+d)/r = 3$, a contact angle of 90° gives an apparent contact angle $\theta_A = 130^\circ$; if $\theta = 60^\circ$, θ_A will be 115°.

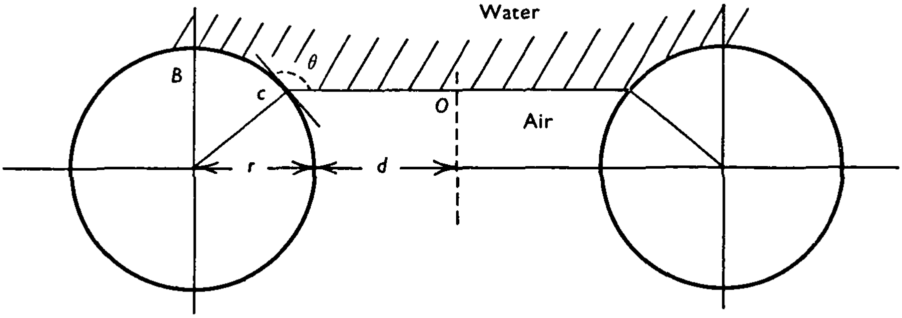

Fig. 1. Schematic of cross-section of two barbs with their axes perpendicular to the plane of the paper (barbules not shown). $f_1 = (\text{arc } BC)/(r+d)$ and $f_2 = (CO)/(r+d)$.

MEASUREMENTS ON THE FEATHERS OF CORMORANTS

Thomson (1923) has given a general description of the structure of feathers, and it is surprising how closely it conforms with the theoretical requirements of optimal water-repellency and conditions of the wire-cage experiment. From the rachis the barbs extend on either side as a system of parallel fibres, which, in the case of the mallard, *Anas platyrhynchos*, measure 46 μ diameter. Their axes are separated by a distance of 270 μ, which gives $(r+d)/r = 5{\cdot}9$. Projecting from the barbs are the barbules, fitted with rigidly interlocking hooks and notches which prevent them from being drawn together by the surface-tension forces of the water. The barbules have a diameter of 8 μ and their axes are 38 μ apart, i.e. $(r+d)/r = 4{\cdot}7$. The values of the advancing and the receding contact angle on the rachis were found to be approximately 90° and 60° respectively, which indicates quite mediocre proofing. Inserting these values in equations (3) and (4) the effective advancing and receding contact angle is calculated to be 150° and 143°, roughly correct according to experimental observation. These high contact angles cause the water to pearl off the duck's back indefinitely, and this excellent characteristic, due to the physical structure of the feathers, is preserved by elaborate and frequent preening by the bird.

The above considerations have led to the presumption that a difference in feather structure is the cause of a lesser extent of water repellency in cormorant feathers.

For this reason a microscopic study of the feathers of some species of cormorants was undertaken. Breast feathers were studied under a microscope provided with a calibrated scale ocular. The results are listed in Table 1. Remarkably lower values for $(r+d)/r$ were found for all four cormorant species, apparently due to less spacing between the barbs, which are of about the same diameter as those of the ducks. This same result was found for the darter, *Anhinga rufa*, but the larger spacing is here offset by a considerably larger barb diameter. Further assuming the contact angle on the rachis to be the same as for the mallard, an effective receding contact angle of 121° is calculated for $(r+d)/r = 4{\cdot}5$. This value of 121° is certainly too small to effect indefinite pearling off the breast feathers. It may very well force the bird to leave the water periodically before its feathers wet-out by the formation of a continuous film of water between the barbs. Subsequent drying, followed by the usual preening, will then restore the initial water-repellency again.

Table 1. *Structural dimensions of cormorant feathers compared with those of two ducks*

Species	Diameter of barb, $2r\,(\mu)$	Distance of axes of barbs, $2(r+d)\,(\mu)$	$(r+d)/r$
Mallard, *Anas platyrhynchos*	46	270	5·9
African shelduck (quill), *Tadorna cana*	57	328	5·8
Reed cormorant, *Phalacrocorax africanus*	54	231	4·3
Bank cormorant, *P. neglectus*	50	220	4·5
Cape cormorant, *P. capensis*	48	210	4·4
White-breasted cormorant, *P. carbo*	52	249	4·8
African darter, *Anhinga rufa*	87	392	4·5

The experimental data are admittedly scarce and a more comprehensive study is required for further evidence. Furthermore, a study on the feathers of other families such as Podicipedidae, Gaviidae and perhaps Alcidae and Laridae may not only provide more evidence for the cormorant's exclusive habit, but reveal as well an evolutionary pattern that governs various extents of water-repellency.

The organic origin of preening oil is likely to rule out any greatly varying levels of water-repellency as a result of different chemical composition. Therefore, the new level of water-repellency attained is a direct consequence of barb and barbule diameter and spacing only as given by the $(r+d)/r$ value. This simple structural parameter is experimentally easily accessible and can, in principle, be evaluated from fossil records as well.

At the present stage, the available results show clearly the pronounced effect of slight differences in feather structure on the water-repelling properties, the inadequacy of which in cormorants is so successfully met by their habit of wing-spreading.

It should be noted that these conclusions are not necessarily in contradiction with the earlier findings on the cormorant's skeleton and centre of gravity as reported by Austin (1963). For it could well be that the skeletal peculiarity is an evolutionary consequence rather than a cause of the habit of wing-spreading. Its function, however, is to dry the feathers and not to keep the cormorant's balance.

SUMMARY

1. The water-repellency of the feathers of ducks is greatly increased by a structural feature which can be expressed in terms of diameter and spacing of the barbs and barbules.

2. This structural parameter is smaller for cormorant's feathers and causes a lesser extent of water repellency.

3. The resulting wetness of the feathers is the proximate cause of the cormorant's characteristic habit of wing-spreading.

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