

## COMMENTARIES

### The Water Repellency of Water-bird Feathers

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Elowson (1984) analyzed the physico-chemical principles involved in the water repellency of textile fabrics. Based partly on measurements of the feather structure of 14 water-bird species, she concluded that the "textile model" cannot be applied reliably to feathers, and does not account for the spread-wing behavioral differences among water birds. I present a rebuttal to Elowson's critique centering on three main issues.

First, the physical principles of the water repellency of porous surfaces, originally applied to treated textile fabrics to explain the mechanism of water repellency, generally have been accepted in the ornithological and textile-processing literature (Moilliet 1963; Clark 1969; Kennedy 1969, 1972; Siegfried et al. 1975; Mahoney 1984). Elowson argued that textile fabrics and feather substructure are too dissimilar to justify comparison. More specifically, Elowson considered the condition of parallel, perfectly cylindrical rows of rami and barbules essential for the validity of the "textile model" to predict the water repellency of feathers. Because the rami and barbules are not circular in cross section, Elowson implicitly rejected the applicability of the physics of porous surfaces to feather structures, and, indeed, stopped just short of stating that feather structure is not a relevant factor in the water repellency of the feather coat.

When a drop of liquid is placed on a smooth, solid surface, the liquid either spreads into a continuous film or covers a limited area, with the liquid taking the shape of part of a sphere. In the latter case, the equilibrium position of drops is determined by:

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

where  $\theta$  is the contact angle between the tangent to the curved water surface at the point of contact with the solid surface, measured through the liquid.  $\gamma_{sa}$ ,  $\gamma_{sl}$ , and  $\gamma_{la}$  are the solid-air, solid-liquid, and liquid-air interfacial energies per unit area (Moilliet 1963).

Alternatively, the work of adhesion ( $W$ ), i.e. the work required to separate a unit area of solid-liquid interface into a solid-air and a liquid-air interface, can be expressed as:

$$W_{sl} = \gamma_{sa} + \gamma_{la} - \gamma_{sl}, \quad (2)$$

or, by incorporating Eq. 1:

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

Adam (1956) pointed out that if a surface is rough or porous, large contact angles may cause drops to entrap air in the hollows and interstices, thereby forming additional air-liquid interfaces. This will cause a considerable increase in contact angle because the work of adhesion between liquid and air is essentially negligible. The work of adhesion between a liquid and a porous surface,  $W_{psl}$ , is analogous to Eq. 2:

$$W_{psl} = f_1(\gamma_{sa} - \gamma_{sl}) + (1 - f_2)\gamma_{la}, \quad (3)$$

where  $f_1$  is the area of solid-liquid interface and  $f_2$  that of liquid-air interface per unit macroscopic surface area. Substitution of Eqs. 1 and 2a then yields (Cassie and Baxter 1944):

$$\cos \theta_A = f_1 \cos \theta - f_2, \quad (4)$$

where  $\theta_A$  is now the apparent contact angle as increased by the formation of air-liquid interfaces. Equation 4 has been derived solely from basic physico-chemical principles without reference to parameters pertaining specifically to textile fabrics or feather structure. In addition, the values of  $f_1$  and  $f_2$  are determined only by the solid-liquid and liquid-air interfaces per unit of macroscopic surface areas, without dictating the shape, curvature, or configuration of these interfaces. The validity of Eq. 4, therefore, extends to *any* porous surface that is covered by liquid for finite values of  $\theta$ , i.e. larger than about  $10^\circ$ . These premises have been tested experimentally and found to be correct by Cassie and Baxter (1944) and by Rijke (1965) using paraffinated ( $\theta = 114^\circ$ ) and uncoated ( $\theta = 0$ ) stainless steel wire cages and grids. For these specific models, composed of parallel rows of perfectly cylindrical wires, a simple calculation for the values of  $f_1$  and  $f_2$  can be made:

$$\begin{aligned} f_1 &= [\pi r / (r + d)] [1 - (\theta / 180^\circ)] \\ f_2 &= 1 - r \sin \theta / (r + d), \end{aligned} \quad (5)$$

where  $r$  is the radius of the circular wires with their axes  $2(r + d)$  apart. Similar expressions can be calculated if the cross section of the wires are assumed to be elliptical, square, rectangular, etc. without affecting the validity of Eq. 4.

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 distances apart, but

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by the ratio  $(r + d)/r$  only. Large values of this ratio imply large  $f_2$  and small  $f_1$  values, which increase the apparent contact angle in the manner described by Eq. 4 and are independent of the cross-sectional shape of the wires.

In the case of feathers, there is an additional reason why conformity to a circular cross section of the rami and barbules is not critical. When a drop of water is placed on a smooth surface covered with a thin film of preening oil such as a rachis or a prepared microscopic slide, a contact angle of approximately  $90^\circ$  is obtained. Inserting this value for the contact angle in Eq. 4 reduces the first term on the right-hand side to zero or nearly so. As a result, the apparent contact angle  $\theta_a$  is essentially determined by the value of  $f_2$  alone. This conclusion is reached without specifying the dimensions of the ramus-water or air-water interfaces. Its validity, therefore, extends to any such interfaces irrespective of the cross-sectional shape. As in the case of circular cross sections, it is easy to show that if the cross section of the rami would be both continuous and elliptical, or square, or any intermediate shape, the air-water interfaces under zero hydrostatic pressure would lie in the plane of the long axes of the rami when  $\theta$  is  $90^\circ$ . The term  $f_2$  is then equal to  $d/(r + d)$ , where  $2r$  is the width of the ramus as measured in the plane of the air-water interface. The values of  $(r + d)/r$  range between 2.1 (penguins) and 6.0 (ducks). This means the apparent contact angle would vary between about  $120^\circ$  and  $150^\circ$ . This difference has been advanced as the proximate cause of a penguin's wet appearance on the one hand and the proverbial behavior of water drops on a duck's back on the other (Rijke 1970).

I submit that Eq. 4 represents an expression for the behavior of water drops on porous surfaces, determined by contact angle and the relative areas of solid-liquid and liquid-air interfaces, and based on general physico-chemical principles. When these principles subsequently are applied to specific models, such as feathers, certain simplifying assumptions may be helpful in estimating the values for  $f_1$  and  $f_2$ , but these do not detract from the general validity of Eq. 4.

Second, in her discussion of water penetration and water repellency of the porous feather structure, Elowson chose to distinguish between advancing and receding contact angles as two different entities, but there is no physical basis for this. When a small quantity of water is added to a drop on a repellent surface, the water-solid interface will expand slightly and advance with a contact angle that is larger than the receding contact angle observed when the water is withdrawn. This difference reflects any changes in surface energies from selective absorption and contamination of the water surface by selective dissolution. It is usually small and unimportant in the absence of absorption or contamination, as for mercury drops on a glass slide. Elowson claimed that the advancing and receding contact angles can be visual-

ized in raindrops trickling down a dirty window pane, but this is incorrect as gravitational force disproportionately increases the advancing front and decreases the following tail of the drop. An advancing angle is established in the initial contact of water with the feather surface and also when water penetrates between the rami and barbules and, therefore, determines the water repellency and resistance to water penetration. The receding angle determines the beading and eventual shedding of water drops.

The ability of feathers to prevent water from penetrating to the skin is at least as important as water repellency alone. A mathematical expression for the pressure required to force water between the rami and barbules has been derived on premises similar to the ones referred to above (Baxter and Cassie 1945, Rijke 1970). Here, the absolute value of  $2r$  and, therefore, the *scale* of the feather substructure come into effect, in addition to the ratio  $(r + d)/r$  and contact angle  $\theta$ . Elowson claimed that the inherent assumption of a zero pressure gradient across the feather surface at depth  $h$  is flawed because it ignores the considerable hydrostatic pressure,  $P = h \times D \times G$  ( $D$  is the density of water and  $G$  is the gravitational constant), to which the diving bird is exposed. This argument, however, fails to take into account that the air between the feather coat and skin, as well as air in the air sacs and respiratory tract, will be compressed so as to balance the hydrostatic pressures surrounding the diving bird. Elowson's case would be valid if the air would communicate and the hydrostatic pressures equilibrate, by means of a tube for instance, with the atmospheric pressure above the water surface. The difference between Elowson's presentation and a diving water bird is exactly why snorkelers cannot submerge much deeper than 60 cm below the water surface (provided the length of snorkeling tube would permit this) without severe respiratory problems, whereas pearl divers are known to function well at a depth of 20 m or more.

Finally, Elowson considered my 1968 and 1970 sample sizes too small and without sufficient elaboration on methods and measurements to permit a meaningful conclusion. In fact, as reported in the 1970 paper, feathers of at least one species of 45 different aquatic families were examined and compared with those of another specimen or species of the same family to ascertain that the observed values were representative of the family. I included a total of 133 different species and 426 different specimens. Of each specimen, the dorsal and ventral aspects of at least three breast feathers were examined for the dimensions of the rami and their distances apart, each at nine different locations on the vane. The results were compared with those of terrestrial birds. The data recently were analyzed statistically, and the differences between the two groups were statistically significant.

The contribution of liquid-air interfaces to the in-

crease of the contact angle of water drops on porous structures, such as feathers, is based on general physical principles. Feather structure alone cannot confer water repellency. Sufficiently large values for the contact angle  $\theta$ , established by preening oil or intrinsic feather lipids (Stettenheim 1972) or both, are required to increase significantly the apparent contact angle  $\theta_a$  to where water drops will bead up and roll off. Chemical analysis of preening oil has shown high species specificity (Odham and Stenhagen 1971), but this is not reflected in the values of  $\theta$ , which are in the neighborhood of 90°. The highest contact angle measured for water on a continuous smooth surface is 114°, using chemically pure, highly crystallized paraffin waxes (Moilliet 1963). Water drops on breast feathers of ducks, on the other hand, measure 140–150°.

The resistance to water penetration through the feather structure of a diving water bird is determined by a zero hydrostatic pressure gradient across the feather surface, the values of  $\theta$  and  $(r + d)/r$ , and the absolute values of the diameters of rami and barbules. Because of their relatively small size, barbules probably make the most significant contribution to the resistance to water penetration. Values of  $(r + d)/r$  for barbules are about 4.7 and vary little among species. Breast feathers of cormorants show smaller values for  $(r + d)/r$  than those of ducks. This difference has been proposed as the proximate cause of the cormorants' wing-spreading behavior (Rijke 1968). This habit of cormorants is likely to contribute significantly to an optimal feather condition that suits their behavior both in the air and in the water.

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#### Response to A. M. Rijke

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Elowson (1984) tested empirically Rijke's model of water repellency, and Rijke's (1986) commentary fails completely to address the core finding: that the values of the ratio  $(r + d)/r$  of neither rami nor barbules separate those species that do and do not assume spread-wing postures. I here reply to the three ancillary issues of the commentary.

(1) *Feather structure and the textile model*.—Rijke's first point is the contention that the model is a phys-

ico-chemical one that is not dependent on surface geometry. Yet Cassie and Baxter (1944), as well as subsequent authors (e.g. Warburton 1963; Rijke 1967, 1968, 1970) developed the measurable variables  $f_1$  and  $f_2$  based on circular cross sections (see Eq. 5 in Rijke's commentary). Lucas and Stettenheim (1972) depicted cross sections of rami (i.e. barbs without the barbules) as irregular, not even approximating a known regular geometric shape. Rijke implies that the textile model should not be rejected because "certain simplifying assumptions" are not met by feather structure, but in that case we need a new model that will withstand empirical tests. Geometry aside, the com-

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