

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 θ , established by preening oil or intrinsic feather lipids (Stettenheim 1972) or both, are required to increase significantly the apparent contact angle θ_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 θ , 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 θ 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

A. MARGARET ELOWSON¹

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-

¹ Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA.

mentary ends the first issue by reaffirming the validity of Eq. 4, which is geometry-free (with respect to surface structure). This equation—which is Eq. 1 in Elowson (1984)—predicts that feathers of water-repellent birds such as the Mallard (*Anas platyrhynchos*), which does not assume spread-wing postures, should have larger contact angles than nonrepellent species such as the Reed Cormorant (*Phalacrocorax africanus*), which does engage in wing spreading. Direct tests are difficult to carry out, but my empirical data (Elowson 1984: 380, table 5) show results just opposite of the predictions. In sum, whatever the theoretical arguments, it is difficult to retain faith in a model that has been tested empirically by two different methods and failed to predict empirical measurements correctly.

(2) *Contact angles, gravity, and hydrostatic pressure.*—Rijke makes three points under the second issue. First, Rijke claims that the distinction between advancing and receding contact angles is irrelevant. However, Cassie and Baxter (1944) treated them separately, Cassie (1948, 1958) maintained the distinction in subsequent papers, other authors (e.g. Moilliet 1963) treated the two angles as well established, and the commentary notes that the two types differ in their interaction with porous surfaces. In any case, the point is irrelevant because the results of both angles reject the textile model (Elowson 1984: 380, table 5). Second, Rijke objects to the analogy between water droplets trickling down a dirty window pane and those on a bird's feather coat because gravity affects only the former. The analogy is appropriate, however, because shedding water from a bird's plumage obviously involves gravity in just the same way. Third, he claims that hydrostatic pressure acting on diving birds is irrelevant because "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." This assertion assumes that the plumage is a closed system like the lungs and air sacs, so that no air escapes, but that assumption is unlikely to be true. In fact, most diving birds probably must lose some trapped air to reduce their buoyancy and permit diving.

(3) *Sample sizes.*—The commentary asserts that sample sizes are actually much larger than published figures (Rijke 1968, 1970), and that 426 specimens of 133 different species actually were measured. If one does the arithmetic (426 specimens, 3 breast feathers each, both r and d at each of 9 different locations, on both dorsal and ventral feather surfaces), this totals 46,008 measurements—certainly an impressive achievement. The fact remains that the methodology of using light microscopy virtually restricts measurements to breast feathers (e.g. vanes of most primaries are thick, densely covered with barbules, and darkly pigmented) and entails large errors in measurement. As ornithologists know, and electron micrographs confirm (Elowson 1984), feathers differ structurally

on various parts of the body, so we should not base a general theory of water repellency on breast feathers alone. Only attempts to replicate by other investigators can finally resolve which data set is the more accurate: light-microscope viewing of breast feathers from many unnamed species, or electron micrographs of feathers from various regions of the bodies of identified species, with statistical analyses of variation.

Rijke is incorrect in stating that "Elowson implicitly rejected the applicability of the physics of porous surfaces to feather structure, and, indeed, stopped just short of stating that feather structure is not a relevant factor in the water repellency of the feather coat." I actually wrote, "This is not to say, however, that feather structure is not a relevant factor in the water repellency of the feather coat—Rijke's approach is useful in promoting this issue, but his hypothesis does not provide the mechanism" (Elowson 1984: 381). Nothing in the commentary dissuades me from reaffirming that conclusion.

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