



## RESEARCH PAPERS

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### THE WATER PENETRATION AND REPELLENCY OF FEATHERS REVISITED

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**Abstract.** We revisit the water penetration and repellency of feathers and these factors' relation to bird behavior and habitat in the light of information that has become available since 1985. We present the physical principles of water penetration and repellency of porous surfaces and their relevance to feathers. We show that the requirements for water repellency of feathers in air and those for resistance to water penetration under water are partly in conflict with each other. Both aspects can be presented and evaluated by the same parameter, expressed in terms of the width  $2r$  and spacing  $2d$  of the barbs,  $(r + d)/r$ . This parameter is small for water birds, particularly for those that dive frequently and are concerned with water penetration. It is larger for terrestrial birds, which are concerned primarily with water repellency. In each family of water birds, with some exceptions, a balance between water repellency and resistance to penetration exists as an adaptation to their particular habitat and behavioral pattern. For example, we discuss the habit of cormorants and darters of spreading their wings after a period in the water in relation to the value of the parameter. We postulate that information on habitat and behavior and, indirectly, the family identity of water birds, including those of fossil taxa, can be inferred from this parameter.

**Key words:** *behavior, feather structure, spread-wing posture, water repellency, water penetration.*

#### Revisión de la Penetración y la Repelencia de Agua de las Plumas

**Resumen.** Revisamos las nociones existentes sobre la penetración y la repelencia de agua de las plumas y la relación de estos factores con el comportamiento y el hábitat de las aves considerando la nueva información disponible desde 1985. Presentamos los principios físicos de la penetración y la repelencia de agua de superficies porosas y su relevancia para las plumas. Mostramos que los requerimientos para la repelencia de agua de las plumas en el aire y los requerimientos de resistencia a la penetración de agua bajo el agua están parcialmente en conflicto. Ambos aspectos pueden ser presentados y evaluados por el mismo parámetro, expresados en términos de ancho  $2r$  y espaciado  $2d$  de las barbas,  $(r + d)/r$ . Este parámetro es pequeño para las aves acuáticas, particularmente para aquellas que bucean frecuentemente y están afectadas por la penetración de agua. El parámetro es mayor en las aves terrestres, a las cuales les concierne principalmente la repelencia al agua. En cada familia de aves acuáticas, con algunas excepciones, existe un balance entre repelencia al agua y resistencia a la penetración como una adaptación a su hábitat particular y al patrón de comportamiento. Por ejemplo, discutimos el hábito de los cormoranes y de las aningas de extender sus alas luego de un período en el agua, con relación al valor del parámetro. Postulamos que la información del hábitat y del comportamiento, e indirectamente la identidad de la familia, de las aves acuáticas, incluyendo aquellas de taxones fósiles, puede ser inferida a partir de este parámetro.

#### INTRODUCTION

In this paper, we revisit the water repellency and resistance to water penetration of feathers, and we show how these qualities relate to specific behavioral patterns and habitats of birds, in particular water birds. The extent of water repellency and water penetration can be determined from the substructure of

feathers by applying the general principles of interaction of water with porous surfaces, including feathers. Indeed a single parameter expressed in terms of the diameter and spacing of the barbs is capable of determining the relative degree of water repellency and penetration. The value of this parameter for water birds varies with family and reflects an adaptation that each family has made to the requirements of specific habitats

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and behavioral patterns. We examine the parameter for a number of bird families with respect to behavior such as swimming, plunge diving, surface feeding, and wing spreading.

Traditionally, ducks and other water birds have been regarded as having attained excellent water repellency, and this quality has often been ascribed to the properties of the oil from their uropygial gland. Although water birds produce relatively copious amounts of gland oil and spend much time preening, studies of the chemical and physico-chemical properties of gland oil have failed to show any unusual aspects that could explain this high water repellency (Elder 1954, Odham and Stenhagen 1971, Reneerkens 2007). Early studies on gland oil were initiated by textile industries with the aim of developing new waterproofing agents for rain garments, leading to our present understanding of how porous structures including textiles and feathers repel water and resist water penetration (Cassie and Baxter 1944, Baxter and Cassie 1945). Modern studies seeking to understand the relationship between surface morphology, wettability, and droplet sliding in plants and insects as well as electron microscopy of biological structures such as butterfly wings have confirmed and expounded the original concepts that underlie the water repellency of rough and porous surfaces (Wagner et al. 1996, Ma and Hill 2006).

The water repellency of all porous surfaces is determined by three factors. One of these is the surface energy (or surface tension) of the solid material on which the drop of water rests. This energy owes its existence to the fact that, unlike the molecules that make up the bulk of a solid material, those at the surface interact with neighboring molecules in a way that is different from way the bulk molecules interact with each other. If the interface is with air—or, strictly speaking, with a vacuum—this difference will equal the surface energy of the material. If it is with water, then the difference will be the water–solid interfacial energy. Now, if the surface of a solid is coated with another material, such as paint or preening oil, it will assume the properties of the coating material. Shafrin and Zisman (1952) showed that it may take a layer of coating only a single molecule thick to change the surface energy of a solid to that of the coating material. Such a monolayer may be extremely difficult to remove with conventional solvents. This appears to be the case for preening oil on feathers, because vigorous efforts, such as washing with alcohol, ether, or detergent solutions, do not appear to significantly alter the surface properties and specifically the water repellency of individual feathers (Stettenheim 1972). However, when the plumage of ducks whose uropygial glands have been excised is treated in this way, their feathers become brittle and lose coherence, resulting in loss of water repellency and wetting of the bird (Hou 1928). This finding suggests that preening oil also serves as a lubricant that keeps feathers smooth, coherent, and sliding easily.

The surface energy of solids and liquids can be determined by measuring contact angles. A good approximation of the surface energy of a solid material can be attained by measuring the contact angles of liquids of different surface energies on the

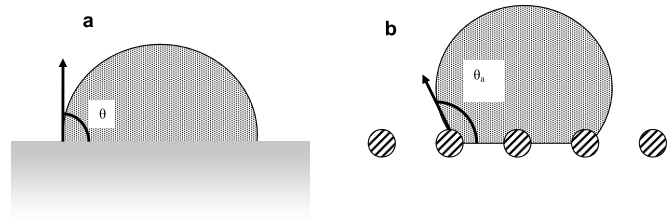


FIGURE 1. Schematic of a drop of water, small enough so as not to be perturbed by gravitational forces, on a smooth surface (a) and a porous surface (b) covered with a repellent waxy film such as preening oil. On the smooth surface a contact angle of  $90^\circ$  is measured. On the porous surface, this angle is increased to about  $115^\circ$  as a direct result of the air–water interfaces formed. Reprinted with the written approval of the Wilson Ornithological Society.

solid surface and then extrapolating to a contact angle of zero (Shafrin and Zisman 1957, 1960). Here, the contact angle that a drop of liquid makes with a solid surface is the angle between the tangent to the liquid's curved surface at the point of contact with the solid's surface, measured through the liquid. When the liquid spreads evenly on the surface, the contact angle is zero and the surface is said to be wettable or nonrepellent. When a drop "pearls" and forms part of a sphere, the surface is called repellent, the extent of which can be conveniently expressed by the value of the contact angle (Fig. 1a).

The contact angles of water drops on surfaces of various chemical compounds, such as waxes and polishes, have been extensively studied. The largest contact angles on smooth surfaces, those in the neighborhood of  $114^\circ$ , occur on surfaces consisting of carefully arrayed terminal methyl groups ( $-\text{CH}_3$ ), as seen in highly purified paraffins. Surfaces made up largely of methylene groups ( $-\text{CH}_2-$ ), as in polyethylene, measure about  $90^\circ$  (Adam and Elliot 1962). The contact angle of a water drop on the rachis of a feather or another smooth surface, such as preening oil on a prepared microscopic slide, also measures about  $90^\circ$ , and this is no coincidence: chemical analysis of preening oil of a variety of birds shows a mixture of various esters of cetyl and octadecyl alcohol and a fatty acid in all of which the methylene group is a predominant component (Elder 1954, Odham and Stenhagen 1971, Reneerkens 2007). It appears, therefore, that preening oil adds a water repellency to feathers that is far from exceptional in quality. In fact, it is on the same level as that of commercial waxes and polishes made from beeswax or from petrochemicals. It alone cannot explain the high contact angles in the vicinity of  $140^\circ$  or  $150^\circ$  observed on the contour feathers of most birds, which are responsible for the proverbial water off a duck's back.

Another factor in determining the water repellency of a surface is its porosity. It has been known for some time that surface roughness increases the contact angle of water, and this finding has been explained with a "roughness factor" that relates directly to the increase in area of the water–solid interface (Wenzel 1936, Adam 1956). If the roughness is sharp-pitched and if the contact angle is large enough so as not to

wet a smooth surface of the same material, it is possible that additional air–water interfaces are formed in the hollows and interstices of the rough surface. This process increase the contact angle markedly, well beyond what can be realized on the smooth surface (Fig. 1b). Porous surfaces, by their very nature, always involve air–water interfaces when water comes into contact with them. Provided a water drop is small enough so as not to be perturbed by gravitational forces and at the same time large enough to cover a representative area of porous surface—in other words, if the scale of the porous structure is small compared to the size of the droplet—then it is possible to determine the “apparent” contact angle of water on a porous surface by following the reasoning originally proposed by Cassie and Baxter (1944). These authors compared the energies involved in creating an interface between water and a porous surface from the separate air–water and solid–water interfaces. From these considerations follows the relationship between the apparent contact angle  $\theta_a$  as increased by the formation of air–water interfaces and the true contact angle  $\theta$  as measured on the same but smooth surface, which reads

$$\cos \theta_a = f_1 \cos \theta - f_2 \quad (1)$$

where  $f_1$  is the area of solid–water interface and  $f_2$  is that of the air–water interface per unit of macroscopic or apparent surface area. Note that equation (1) does not specify any particular structure or architecture that a porous surface must have. It requires only the input of the relative areas of solid–water and air–water interface per unit of apparent surface area to determine the increase of the contact angle from  $\theta$  to its apparent value of  $\theta_a$ . As a result, equation (1) should apply to *any* porous surface regardless of architecture or origin, whether natural or man-made. To test their premises, Cassie and Baxter constructed cages of parallel wires of carefully controlled diameters and spacing between them and coated these with a highly purified paraffin wax. For these regular arrays of wires, values for  $f_1$  and  $f_2$  could be easily controlled and calculated according to

$$f_1 = (\pi - \theta)r / (r + d) \quad (2a)$$

$$\text{and} \quad f_2 = 1 - r \sin \theta / (r + d) \quad (2b)$$

Here,  $r$  is the radius of the circular wires and  $d$  is one-half of the distance between wires. Similar expressions for  $f_1$  and  $f_2$  could be calculated if the cross-section of the wires was assumed to be elliptical, square, rectangular, etc. When put to the experimental test, excellent agreement between the measured apparent contact angles and those predicted by equations (1), (2a), and (2b) was observed for the various wire cages, proving that the principles underlying the above equations are correct. Next, Cassie and Baxter, being employed at the time by the British Council of the Wool Industries Research Association, tested their premises on wool yarn and found good agreement in view of the assumptions made to estimate values for  $2r$  and  $2(r + d)$  and the uncertainty in the fiber–water contact angle because of the fiber’s rough surface.

Finally, as reported in the same paper, the authors studied the water repellency of duck feathers by measuring the diameter and spacing of the barbs as well as the contact angle  $\theta$  on the rachis of the feather, which measured  $90^\circ$ . They observed an apparent contact angle on the vane of the feather of  $150^\circ$ , in good agreement with the values calculated from the above equations. This result implies that, for the purpose of water repellency, the structure of feathers is quite similar to that of the wire cages described above, in which the barbs of the feather play the role of the perfectly cylindrical paraffin-coated metal wires. Cassie and Baxter did not specify the species of duck, and they did not indicate from which part of the plumage their feathers came. Nor did they know at the time that the water repellency of contour feathers varies with water-bird family. However, they were the first to study the water repellency of feathers systematically and explain its mechanism. They were the first to reveal that the duck obtains its proverbial water repellency not from any exceptional or mysterious properties of its preening oil but from the structure of its feathers.

To further understand how feathers bring about a greatly enhanced apparent contact angle, a closer look at the substructure of a feather is useful. The elements that make up a feather are well described in a variety of handbooks and dictionaries (Landsborough Thomson 1964, Stettenheim 1972). The barbs, which together make up the vane on each side of the central spine or rachis, are approximately circular or elliptical in cross-section with a diameter anywhere between 20 and 70  $\mu\text{m}$  and separated from each other by a distance  $2d$  that ranges from about 100 to 400  $\mu\text{m}$  depending on bird family or species (Elowson 1984, Rijke and Burger 1985). From each barb extend barbules with a diameter of roughly 5  $\mu\text{m}$  and separated by about 15  $\mu\text{m}$ , depending somewhat on the region of origin of the feather. The distal barbules of each barb have hooks that catch upon the curled proximal barbules of the barb next more distal and thus constitute the continuous-looking vane. This hook-and-flange arrangement provides the feather the rigidity so critical for its mechanical properties. It also prevents the surface energy of water from pulling together the feather elements as it does the tips of mammalian hair. The rigid regular array of barbs, held together and at the same time kept separate by the barbules with their hooks and flanges, is a perfect example of the essential water-repelling porous surface. Such structures are relatively unusual in vertebrates but are widespread, most diverse, and most ingenious among insects. Vertebrates are generally of a larger size than insects, so that the scale effect of surface energy is much less. Thus, whereas many insects can readily be trapped by a drop of water, no vertebrate can. But the main reason for the great importance of water repellency to insects and plants is that in both these groups, air enters by small pores and is circulated through the tissues in very narrow spaces that must be kept unobstructed. It is therefore not surprising that the spiracles of insects and the stomatal apparatus of leaves are equipped with a variety of hydrophobic structures that are well adapted to keep water out (Crisp 1963).

The third and last factor that determines the water repellency of a porous surface is the surface energy of water. This factor is an inherent physical property of water somewhat dependent on temperature but otherwise constant. However, it is markedly affected by surface impurities and dissolved chemicals such as those found in polluted water. Relatively small amounts of these spreading on the surface of a drop as well as water-soluble chemicals such as detergents can drastically decrease the surface energy of water. These impurities are also a main source of discrepancy observed between the contact angles measured when a small amount of water is added or withdrawn from a water drop on a repellent surface (Moilliet 1963). The difference between the advancing and receding contact angles, as these are called, respectively, is quite small for liquids of medium to low surface energy but can be quite large for water. On the smooth surface of a rachis, the advancing contact angle, as we have seen, measures about  $90^\circ$ , whereas the receding contact angle is more like  $60^\circ$  (Cassie and Baxter 1944). Advancing angles apply when drops fall on a repellent surface or when water under pressure would penetrate through abdominal feathers, for instance, by the weight of a swimming bird on the water's surface. Receding angles, on the other hand, apply when water drops on a repelling surface coalesce, pool, and may roll off, as determined by gravitational forces and the tilting of the surface. Baxter and Cassie (1945) stated that the large advancing angle and the small receding angle may be seen in a rain drop running down a dirty window pane, a statement repeated by Elowson (1984), but this is clearly incorrect: the head and tail ends of such a drop are much dependent on the size of the drop, the angle at which the surface tilts, and the nature of the dirt on the window pane (Rijke 1987).

Yet large as the difference between an advancing and a receding angle may be, its effect on the apparent contact angle of water on a duck's back is much less pronounced. Cassie and Baxter (1944) calculated that, according to equations (1), (2a), and (2b), for a barb diameter of  $46\text{ }\mu\text{m}$  and a  $(r+d)/r$  value of 5.9, the advancing angle would be increased from  $90^\circ$  to  $146^\circ$  and the receding angle from  $60^\circ$  to  $133^\circ$ , roughly correct by experimental verification. Feather structure, therefore, not only enhances the apparent contact angle, it also markedly reduces the difference between the advancing and receding angle. This means that when a contact angle is reduced by water pollution, this reduction will result in a relatively mild decrease in apparent contact angle, suggesting that a duck may be able to cope successfully with certain levels of water contamination. In the following, we refer to the contact angle as the advancing contact angle and keep in mind, where applicable, that the receding angle will be only somewhat smaller.

#### WATER REPELLENCY, WATER RESISTANCE, AND WATER-BIRD FAMILY

Water repellency, as we have seen, is a surface phenomenon that occurs at the interface between a (porous) surface and water. Those parts of the feather and other biological surfaces

(Byun et al. 2009) that have the structure to repel water do so according to the above principles outlined by Cassie and Baxter (1944). However, the ability of the feather coat to keep water away from the skin—in other words, how wet a bird gets—is determined by another factor: its resistance to water penetration. While rigid, open structures primed with a waxy coating may be ideal for repelling water, they are also vulnerable to water penetration. Attempts to explain how the feather coat keeps water out should include considerations of water penetration in addition to those of water repellency of the individual feathers as well as the entire feather coat (Fabricius 1959, Elowson 1984, Mahoney 1984). Resistance to water penetration can be defined as the pressure  $P$  required to force water between the barbs and barbules. This pressure for the case of the above wire cages and by extension for feathers can be calculated from premises very similar to those used to derive equations (2a) and (2b) and reads (Cassie and Baxter 1944, Moilliet 1963)

$$P = \gamma / r \left\{ \cos \theta + \sqrt{[(r+d)/r]^2 - \sin^2 \theta} \right\} \quad (3)$$

where  $\gamma$  denotes the surface energy of water. Note that whereas the water repellency is determined by the ratio  $(r+d)/r$  only and not by the separate values for  $r$  and  $d$ , the expression for the resistance to water penetration includes both the parameter  $(r+d)/r$  and  $r$ , indicating that the *scale* of the structure contributes to this resistance. Also note that water repellency increases with larger values of  $(r+d)/r$ , whereas smaller values of this parameter favor good resistance to water penetration. Therefore, the need to attain good water repellency is opposed by the requirement of relatively small values for  $(r+d)/r$  to provide sufficient resistance to water penetration. As a result, the structural characteristics compatible with optimal water repellency are in part in conflict with the requirements of resistance to water penetration. This conflict has important implications for water birds, which must realize a balance between water repellency and resistance to water penetration to cope with their respective habitats and behavioral patterns. No such demands are made on the feathers of terrestrial birds, which are concerned with water repellency only.

Experimental evidence to verify the validity of equation (3) is sparse and for good reasons. Whereas the water repellency of feathers can be determined simply and reliably by measuring contact angles on the vane of feathers, the resistance to water penetration involves a dynamic test in which water is forced through the vane. To this end, the samples must be structurally perfect with the hooks and flanges of all barbules latched together. Any irregularity or void in the feather will cause water to penetrate it at a lower pressure than is representative for its structure. In addition, water must not only penetrate between the barbs, it must by necessity also penetrate between the barbules, and these structures will therefore also contribute to the observed pressure on their own account. Contact angles, on the other hand, are determined only by the



diameter and spacing of the barbs and do not involve the barbules, as can be observed directly with a magnifying glass.

To our knowledge, only the feathers of the Double-crested Cormorant (*Phalacrocorax auritus*) and the African Darter (*Anhinga melanogaster*) have experimentally been tested for their resistance to water penetration (Rijke et al. 1989). The results can be summarized as follows: for wing and tail feathers, the measured values for  $P$  are larger than those calculated for water penetration between the barbs but smaller than those calculated for penetration between the barbules. This suggests that the contribution of the barbules to water resistance is real but not based on the same mechanism as applies to the barbs. The barbules may provide an interlocking mechanism by preventing the barbs from separating under the increasing water pressure while increasing their own separation by their hooks sliding in the flanges. Such a process would also explain why penetration pressures were measured to be smaller than the calculated pressures for the contour feathers of the African Darter, which show a pattern of barbules without interlocking hooks and flanges (Kennedy 1972, Casler 1973). Unlike those of darters, however, the contour feathers of the Double-crested Cormorant have barbules with a full set of hooks and flanges, and their resistance to water penetration is about the same as that of their tail and wing feathers. Also, for both contour and flight feathers, the measured pressures were found to be inversely proportional to  $(r + d)/r$ , in agreement with equation (3).

The actual resistance to water penetration of the entire plumage cannot, of course, be determined from measurements of  $P$  on single feathers alone. The way in which multiple feathers are stacked and positioned should also be expected to contribute to the overall resistance to water penetration in an as yet unknown manner. Preliminary measurements of a stack of two or three identical feathers have indicated that multiple layers of feathers increase the resistance to water penetration by approximately 50% over that of a single feather for each layer added.

As part of determining the apparent contact angle and values for  $r$  and  $d$ , Rijke et al. (1989) also measured the contact angle  $\theta$  of water drops on a microscopic slide covered with preening oil. In agreement with the results of other authors, they found the value of  $\theta$  to be consistently about  $90^\circ$ , as it was indeed observed on all smooth feather surfaces (Cassie and Baxter 1944). Accordingly,  $\cos \theta = 0$  and  $\sin \theta = 1$  in the above equations. In the equation (1), this means that the apparent contact angle  $\theta_a$  is determined only by the value of  $f_2$ , the relative area of air–water interface. It also means that the air–water interface lies in the plane of the long axes of the barbs and, as a result, the noncircular cross-sectional shape of barbs is of no consequence for calculating the values for  $f_1$  and  $f_2$  because  $2r$  then equals the width of the barbs with their axes  $2(r + d)$  apart, as measured in this plane (Moilliet 1963). These fortuitous circumstances allow the investigator to measure  $2r$  and  $2d$  by transmission light microscopy and determine the apparent contact angle as well as the balance between water repellency and resistance to water penetration

for a variety of bird species and families from the parameter  $(r + d)/r$  alone. For instance, Cassie and Baxter's duck measured a  $(r + d)/r$  value of 5.9. According to equation (2b), this means that  $f_2$  equals 0.83 and therefore, according to equation (1),  $\theta_a$  is  $147^\circ$ , in good agreement with the experimental observation of  $150^\circ$ . In addition, this value of 5.9, when compared with 4.8 for the White-breasted Cormorant (*P. carbo*) (Rijke and Burger 1985) and 7.1 for the European Starling (*Sturnus vulgaris*) (Rijke and Jesser 2010), suggests that the duck, and probably all dabblers, are more water repellent than cormorants but less so than starlings. On the other hand, cormorants show a superior resistance to water penetration, particularly when compared with starlings.

Measurements on more than 160 species of about 45 bird families (Rijke 1970, Bernstein and Maxson 1982, Elowson 1984, Rijke and Burger 1985) have shown that  $(r + d)/r$  values vary from about 2.3 for penguins (Spheniscidae) to about 7 or more for most terrestrial birds (Table 1). This range in values for this parameter suggests that each water-bird family has evolved a balance between water repellency and resistance to water penetration that suits its particular habitat and behavioral pattern.

The data on barb diameter, spacing, and  $(r + d)/r$  values published in the peer-reviewed literature are far from a complete inventory of bird plumage, but on the basis of what is available, the following observations had been made and tentative conclusions reached.

First, the distal one-third of breast, abdominal, and back feathers shows the patterned structure that confers the water repellency and resistance to penetration. The proximal and medial parts show no such structure. The patterned parts overlap like shingles on a roof and protect the bird from water reaching the skin. The tail feathers and remiges, on the other hand, are structured over essentially the entire length of the feather and have values of  $(r + d)/r$  that are generally small, which prevent these feathers from becoming waterlogged. Among water-bird families, contour feathers vary more in values of  $(r + d)/r$ , which range from 2 to 10, than rectrices and remiges, both of which vary little and range from 2 to 4 (Rijke 1970, Elowson 1984, Mahoney 1984).

Second, within most families, the contour feathers that protect the skin from coming in contact with water have, on the whole, very similar values for  $(r + d)/r$ . Exceptions are only observed when a species within a family behaves differently from its relatives (Rijke 1970, Rijke and Burger 1985).

Third, these data sets on feather structure have produced a relationship between barb diameter  $2r$  and  $(r + d)/r$  values that is linear and particularly strong for true water-bird families (Fig. 2). Families such as the penguins and other diving water-birds, with wide barb diameters, have small values for  $(r + d)/r$ , whereas the opposite holds true for terrestrial families such as the starlings and nightjars (Caprimulgidae). Birds that come into occasional contact with open water such as the Ardeidae and Laridae show intermediate values. Penguin

TABLE 1. Summary of families and species, barb diameter ( $2r$ ), and  $(r + d)/r$  values of contour feathers, habitat/behavior, and literature sources. SD is the standard deviation.

Family/species	$2r$ ( $\mu\text{m}$ )	SD	$(r + d)/r$	SD	Behavior/habitat	Reference
Cormorants (Phalacrocoracidae):	~50		4.3–4.9		wing-spreader/diver	Rijke and Burger 1985,
Double-crested, White-breasted, Reed						Rijke 1968
Flightless	36	2	7.2	0.1	wing-spreader/diver	Rijke and Burger 1985
Blue-eyed Shag	?		3.8		wing-spreader in	Rasmussen and
					Chilean population	Humphrey 1988
Darters (Anhingidae): African Darter	28	1	9.1	1.0	wing-spreader/ underwater stalker	Mahoney 1984, Rijke et al. 1989
Ducks (Anatidae)	~47	1	4.5–6.0	0.1		Rijke and Burger 1985
Mallard	46	1	5.9	0.1	dabbler	Rijke 1970, Elowson 1984
Penguins (Spheniscidae)	70	2	2.3	0.1	swimmer/diver	Rijke and Burger 1985
Auks (Alcidae)	61	1	3.4	0.1	swimmer/diver	Rijke and Burger 1985
Loons (Gaviidae)	58	1	3.9	0.1	swimmer/diver	Rijke and Burger 1985
Gannets (Sulidae)	50	1	3.8	0.1	plunge-diver	Rijke and Burger 1985
Shearwaters (Procellariidae)	51	1	4.6	0.1	surface feeder/ swimmer	Rijke and Burger 1985
Pelicans (Pelecanidae)	~53		4.9–5.4		swimmer	Rijke and Burger 1985
Brown Pelican	37	1	5.9	0.1	surface feeder	Rijke and Burger 1985
Rails (Rallidae)	~50		5.4–5.9		wader	Rijke and Burger 1985
Galapagos Rail	30	1	10	0.1	terrestrial	Rijke 1986
Hérons (Ardeidae)	~54		6.8–7.4		wader	Rijke and Burger 1985
Gulls (Laridae)	~53		6.5–6.9		occasional swimmer/ surface feeder	Rijke and Burger 1985
Storm-Petrels (Hydrobatidae)	~35		6.9–7.4		surface feeder	Rijke and Burger 1985
Cranes (Gruidae): Common, Wattled, Demoiselle, and Blue	~44		4.4–5.8		wader	Rijke and Jesser 1993
Black Crowned	40	1	9.2	0.1	terrestrial	Tarboton 1990
Gray Crowned	40	1	8.0	0.1	terrestrial/arboreal	Tarboton 1990
Starlings (Sturnidae): European Starling	34	1	7.1	0.1	terrestrial	Rijke and Jesser 2010
Nightjars (Caprimulgidae)	26	1	7.9	0.1	terrestrial	Rijke and Burger 1985
Swifts (Apodidae)	27	1	7.8	0.1	terrestrial	Rijke and Burger 1985
Dippers (Cinclidae)						
White-throated	24	1	7.1	0.2	plunger	Rijke and Jesser 2010
American	24	1	8.7	0.1	plunger	Rijke and Jesser 2010
Brown	24	1	10.1	0.2	plunger	Rijke and Jesser 2010
Rufous-throated	24	1	7.8	0.1	non-plunger	Rijke and Jesser 2010
White-capped	27	1	7.9	0.4	non-plunger	Rijke and Jesser 2010

feathers have excellent resistance to water penetration but poor water repellency. The breast feathers of nightjars, on the other hand, are very water repellent but promise little resistance to water penetration. Those of the Ardeidae and Laridae fall somewhere in between.

#### WATER REPELLENCY, WATER RESISTANCE, AND SPREAD-WING POSTURES

The first effort to correlate the value of the parameter  $(r + d)/r$ —that is, the balance between water repellency and resistance to water penetration—with behavioral patterns was made more than 40 years ago (Rijke 1968). In that paper, the well-known habit of cormorants of spreading their wings to the sun or breeze after a period in the water, a feature commonly referred to as “wing-drying,” was proposed to follow

from the poor water repellency of their breast feathers, as evidenced by their low value for  $(r + d)/r$  in comparison to that for the Mallard (*Anas platyrhynchos*), and presumably other dabblers, that do not spread their wings. Only four species of cormorants and one species of anhinga (Anhingidae) had been examined with little attention paid to the important differences in the water-repellent structures between contour feathers and flight feathers. In addition, no systematic comparison was made with other water-bird species that do not show spread-wing behavior, such as the penguins and loons (Gaviidae). In spite of these limitations, the conclusion that the poor water repellency of the cormorant’s breast feathers is the proximate cause of its characteristic habit of wing-spreading has been generally accepted in the ornithological literature (Clark 1969, Kennedy 1970, 1971, Kahl 1971, George and

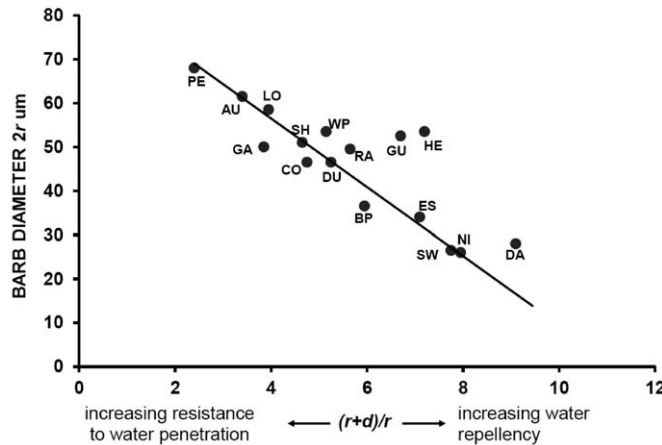


FIGURE 2. Plot of averaged barb diameter  $2r$  in  $\mu\text{m}$  against  $(r + d)/r$  of the breast feathers of 16 families and species. A best-fitting straight line is drawn for the truly aquatic and truly terrestrial families (PE, AU, LO, SH, DU and ES, SW, NI) and is expressed by the equation  $2r = 87.8 - 7.83(r + d)/r$ . PE, penguins; AU, auks; LO, loons; GA, gannets; SH, shearwaters; WP, American White Pelican; CO, cormorants; DU, ducks; RA, rails; GU, gulls; HE, herons; BP, Brown Pelican; ES, European Starling; SW, swifts (Apodidae); NI, nightjars; DA, darters.

Casler 1972, Stettenheim 1972, 1976, Siegfried et al. 1975, van Rhijn 1977, Schreiber 1977, Jones 1978, Winkler 1983, Bernstein and Maxson 1982, Hennemann 1982). Since then, further studies on the “wing-drying” of cormorants have overwhelmingly supported the notion that its function is the drying of contour feathers and not thermoregulation, balancing, intraspecific signaling, or an aid to swallowing fish (Sellers 1995). Yet the relation between the cormorant’s feather structure, specifically its parameter  $(r + d)/r$ , and this behavior has remained elusive and has been criticized by Elowson (1984). It is one of the purposes of this paper to address the controversy raised by Elowson’s critique (Elowson 1987, Rijke 1987) and resolve the underlying issues in the light of new information that has become available since 1985.

Elowson questioned the applicability of Cassie and Baxter’s expressions for the water repellency of porous surfaces to feathers and has dubbed their equations “the textile model.” This misnomer has erroneously suggested that equation (1) had been derived specifically for textiles and, therefore, is not valid for feathers, as the two materials are obviously very different from one another. However, as mentioned earlier, the only premises relating to the interface between water and a porous surface that enter into equation (1) are the relative areas of solid–water and air–water interface  $f_1$  and  $f_2$ , respectively, which do not specify the geometric nature or origin of the porous interface. Therefore, this equation applies to all porous surfaces. It is equally valid for water drops on porous surfaces such as pumice, leaves, and butterfly wings as it is for feathers and, yes, textiles.

Elowson’s other criticism is that the values for  $(r + d)/r$  do not correlate with spread-wing behavior. Her scanning

electron microscopic images show barb diameters of contour feathers that correspond, on the whole, well with the values from transmission light microscopy of Rijke et al. (1985, 1989), except for the Mallard. In this species, she measured a barb diameter of  $20\ \mu\text{m}$  as opposed to the  $46\ \mu\text{m}$  found by Rijke (1968) and Rutschke (1960) and, incidentally, also by Cassie and Baxter (1944) on their unidentified duck. In addition, Rijke and Burger (1985) found nine other species in the family Anatidae to have diameters ranging between  $43$  and  $50\ \mu\text{m}$ . Later studies using modern imaging software have provided further evidence that Elowson’s diameter for the Mallard is not correct. Typically, diameters in the  $20\text{--}\mu\text{m}$  range are found for small terrestrial birds, not for water birds (Rijke and Jesser 2010).

Elowson published SEM micrographs of the back and breast feathers of three species including the Reed Cormorant (*Phalacrocorax africanus*). These show barbules in disarray with hooks and flanges unlatched and barbs splayed. As mentioned above, such samples are not suitable for evaluation. Only perfectly latched barbules with barbs parallel should be selected, as damaged regions will yield values for  $d$  that are too large and, consequently, values for  $(r + d)/r$  that are too large. Unfortunately, these inaccuracies in the  $(r + d)/r$  values have introduced uncertainties large enough to negate a meaningful correlation between this parameter and species that do and do not wing-spread. It is still possible, though, to draw a number of conclusions if only uncontested data are considered and if more recent data recorded with modern imaging software are included.

Water birds that regularly spread their wings include several species of cormorants, such as the Reed Cormorant, Bank Cormorant (*P. neglectus*), Cape Cormorant (*P. capensis*), White-breasted Cormorant (*P. carbo*), and the Double-crested Cormorant, most of which have  $(r + d)/r$  values for their contour feathers between  $4.3$  and  $4.9$  (Table 1). Families and species with parameters under about  $4.2$ , such as the loons ( $4.0$ ), gannets (Sulidae) ( $3.8$ ), auks (Alcidae) ( $3.4$ ), penguins ( $2.3$ ), and the Antarctic Blue-eyed Shag (*P. atriceps*) ( $3.8$ ) never show wing-spreading behavior. Pelicans (Pelecanidae) ( $4.9$  to  $5.4$ ), including the Brown Pelican (*Pelecanus occidentalis*;  $5.9$ ), do so only very occasionally, but all other water birds do not with the notable exception of the darters ( $10$  to  $11$ ). Darters have contour feathers that promote water to penetrate to the skin in order to reduce their buoyancy (Owry 1967, Mahoney 1981) so their very large  $(r + d)/r$  value comes as no surprise. It is reasonable to assume that, with the exception of the darters, all water birds benefit from a plumage with good water repellency and equally good resistance to water penetration. However, as we have seen, the structural requirements for these two qualities are partly opposed, so it is to be expected that each family or species will have struck a balance that suits its specific demands of habitat and behavior. Spread-wing postures can then be explained as being part of a behavioral pattern in those birds that dive frequently and

therefore require good resistance to water penetration, but this resistance comes at the expense of a measure of water repellency, which is compensated for by “wing-drying.”

The question as to whether it is the wings or the body plumage that is being dried by wing spreading was raised by Sellers (1995) and can be addressed by considering the difference in  $(r + d)/r$  values between flight and contour feathers. Values for flight feathers, in particular the outer coverts, measure 2 to 4 for both water and terrestrial birds, and these are therefore well protected from becoming waterlogged. Those for contour feathers, on the other hand, show much difference between these two groups of birds, with those of water birds that spend much time in the water and dive frequently ranging from about 2 to 4 and those of terrestrial birds ranging from about 7 to 10. Other water birds, including cormorants, have values that fall somewhere in between (Table 1). Contour feathers with  $(r + d)/r$  values higher than about 4 are at risk of becoming waterlogged, which suggests that it is the exposed contour feathers rather than the flight feathers that need drying in cormorants and in darters.

Apart from  $(r + d)/r$  values, weather may also influence wing-spreading behavior. Cormorants reduce the extent to which their wings are spread with increasing wind speed, and at speeds of 4 on the Beaufort scale Sellers (1995) never saw birds to extend their wings more than about 50%. Wind speeds may also be the reason why spread-wing postures are unknown in the Antarctic populations of the Blue-eyed Shag (Bernstein and Maxson 1982) but common in birds of this species breeding in Chile (Rasmussen and Humphrey 1988). The persistent strong winds at high latitudes may well be the cause for the absence of wing-spreading behavior in the Antarctic populations.

Other than wind speed, the relative temperatures of water and air may be a factor in wing-spreading. A case in point is the Flightless Cormorant (*P. harrisi*) of the Galapagos, which is known to spread its stubby wings after a dive in the cool waters of the archipelago and, in this respect, behaves no different from other cormorants. However, whereas most other cormorants have contour feather with barb diameters between 48 and 54  $\mu\text{m}$  and  $(r + d)/r$  values between 4.3 and 4.9, those for the Flightless Cormorant are 31–41  $\mu\text{m}$  and 7.1–7.4, respectively (Rijke and Burger 1985). These numbers suggest that the Flightless Cormorant suffers a measure of water penetration through the barbs of its contour feathers, a feature that is more reminiscent of darters than of cormorants. As with darters, increased water penetration is thought to assist the underwater bottom-feeding habits of *P. harrisi* for which too much buoyancy would prove to be a disadvantage. Simple calculations appear to support this notion: the pressure that a surface-swimming Flightless Cormorant exerts on the water ranges between 630 and 780  $\text{N m}^{-2}$  (Brudis and Bass 1979), whereas only 550 to 590  $\text{N m}^{-2}$  pressure is required to force water between the barbs (Rijke 1986). For other cormorants, the maximum weight for no water penetration between the barbs lies

well above the bird's weight range (Rijke 1970). So, unlike those of other cormorants, the Flightless Cormorant's contour feathers are waterlogged after a dive in cold water, but the bird can then proceed to dry its plumage in the warm tropical breezes on the lava rocks, an advantage denied to cormorants inhabiting high latitudes.

#### WATER REPELLENCY, WATER RESISTANCE, AND OTHER BEHAVIORAL PATTERNS

In the previous section, we attributed the occurrence or absence of spread-wing postures to the need for a balance between water repellency and resistance to water penetration as reflected in the value of the parameter  $(r + d)/r$ . It is therefore to be expected that other behavioral patterns, directly or indirectly, relate to this parameter in a similar manner.

As an example of the relationship between  $2r$ ,  $(r + d)/r$ , and behavioral pattern, gannets, cormorants, and shearwaters (Procellariidae) all have about the same barb diameter (50–51  $\mu\text{m}$ ), but gannets have a value for  $(r + d)/r$  of 3.8, which lies at the low end of the range of values (3.8–4.9), indicating a greater resistance to water penetration. This may well be an adaptation to the gannet's habit of diving from the air (with associated high pressure at impact) and then pursuing prey under water, as seen in the 1998 BBC documentary *The Life of Birds*. Brown Pelicans also dive from the air but unlike gannets do not pursue their prey under water. Their breast feathers have smaller barb diameters and higher  $(r + d)/r$  values than those of gannets, producing an increased water repellency. American White Pelicans (*Pelecanus erythrorhynchos*), on the other hand, find their prey while swimming on the surface and have smaller values for  $(r + d)/r$ . Apparently, plunge-divers and birds that swim underwater frequently benefit from an increased resistance to water penetration, whereas surface feeders, such as the Brown Pelican, gulls (Laridae), and storm-petrels (Hydrobatidae), profit from an increased water repellency (Table 1).

Dippers (Cinclidae) are the only passerines that find their food almost exclusively under water. Their contour feathers are predominantly water repellent as is typical for passerines and other terrestrial birds. However, adaptations to their aquatic lifestyle are apparent in the White-throated Dipper (*Cinclus cinclus*), the American Dipper (*C. mexicanus*), and the Brown Dipper (*C. pallasi*), which habitually plunge into shallow streams and lakes to search for food among rocks and vegetation. Of these three, the first has contour feathers with a slightly increased resistance to water penetration and occurs at low altitudes where currents are slow and the water is deep. The other two show an increased water repellency and are found at high altitudes where the currents are fast and the water is shallow. No such adaptations are found in the Rufous-throated Dipper (*C. schulzi*) and the White-capped Dipper (*C. leucocephalus*), which only dip their heads under water to catch prey detected from their rocky perch (Rijke and Jesser 2010).



Of the six species of cranes occurring in Africa, the Common (*Grus grus*), Wattled (*Bugeranus carunculatus*), Demoiselle (*Anthropoides virgo*), and Blue (*A. paradisea*) Cranes have  $(r + d)/r$  values in the same range as typical water and marsh birds such as ducks, gulls, and rails (Rallidae), but the Black Crowned (*Balearica pavonina*) and the Gray Crowned (*B. regulorum*) Cranes have values in the range of 8 to 9, comparable with truly terrestrial birds (Table 1). These findings support the observation that the crowned cranes are more terrestrial in their habits than the others, with the Gray Crowned also being rather arboreal (Rijke and Jesser 1993). DNA-sequence analysis provides genetic support for classification of the Black and Gray Crowned Cranes as a subfamily in their own right (Tarboton 1990).

Rails, like most marsh and shore birds, have contour feathers with barb diameters of about 50  $\mu\text{m}$  and  $(r + d)/r$  values near 5.7. However, the Galapagos Rail (*Laterallus spilonotus*) has barbs that are approximately 20  $\mu\text{m}$  narrower and a spacing that is about 35  $\mu\text{m}$  wider, increasing the value of  $(r + d)/r$  to about 10 (Table 1). This particular feather structure may have evolved in the damp, high-altitude habitat of the Galapagos Rail under the selective pressure of a need for water repellency alone without the necessity to prevent water penetration, as faced by other rails in their more typical marshy habitats elsewhere in the world (Rijke 1986).

It is likely that many more examples of contour-feather structure correlating with specific behavior or habitat will be found once more data have been gathered. However, the above examples suffice to suggest that each feather substructure represents an evolutionary adaptation to a specific set of behavioral patterns and habitat conditions. It should be borne in mind that feather structure relates in the first place to behavior and habitat and secondarily to family identity and then only to the extent that family members behave in essentially the same way and inhabit similar habitats. As we have shown, congeners with different behavior/habitat patterns show a correspondingly different value for the structural parameter. That this behavior difference occurs in conjunction with a structural difference supports the existence of a correlation between feather structure and the habitat and behavior of its avian bearer.

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