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Authors: Ortega-Jiménez, Victor M., and Álvarez-Borrego, Saúl

ALCID FEATHERS WET ON ONE SIDE IMPEDE AIR OUTFLOW WITHOUT COMPROMISING RESISTANCE TO WATER PENETRATION

Víctor M. Ortega-Jiménez[1] and Saúl Álvarez-Borrego

Departamento de Ecología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada, Carretera Ensenada–Tijuana No. 3918, Fraccionamiento Zona Playitas, Ensenada, Baja California 22860, Mexico

Abstract.   While diving, small alcids appear wet, suggesting that their feathers repel water poorly. Nevertheless, once wet, their plumage resists water penetration effectively. This study's objective was to evaluate the effect of feather wetting on the critical penetration pressure of air (maximum pressure for resistance to air penetration, P_a) and water (P_w). We measured these values in breast feathers of Xantus's Murrelet (*Synthliboramphus hypoleucus*) and Cassin's Auklet (*Ptychoramphus aleuticus*) under two conditions: dry (feathers with separated barbs) and wet on one side (feathers with aggregated barbs). Dry feathers of both alcids did not resist air penetration at any pressure, but feathers wet on one side resisted 1.25 kPa. For Xantus's Murrelet P_w was 1.44 kPa, for Cassin's Auklet 1.36 kPa. These results support the hypothesis that plumages that appear wet could minimize heat loss by reducing the exchange of air within the plumage while the bird is diving.

Las Plumas Mojadas de un Lado de los Álcidos Impiden el Flujo de Aire sin Afectar la Resistencia a la Penetración del Agua

Resumen.   El plumaje de algunas aves marinas se moja aparentemente con facilidad al bucear, como en el caso de los álcidos. Sin embargo, al examinar cuidadosamente la parte interna del plumaje, ésta se encuentra seca. Con el fin de entender los efectos debidos a la adhesión superficial de agua en las plumas con relación a la resistencia a la penetración de agua (P_w) y aire (P_a), se hicieron mediciones en plumas individuales del pecho de *Synthliboramphus hypoleucus* y *Ptychoramphus aleuticus* bajo dos condiciones: mojadas de un sólo lado y secas. Se encontró que las plumas mojadas de ambos álcidos resisten una presión

máxima de aire de 1.25 kPa. Sin embargo, la resistencia máxima de penetración de agua no difirió significativamente entre plumas mojadas y plumas secas. Para *S. hypoleucus* P_w fue 1.47 kPa y para *P. aleuticus* fue 1.36 kPa. Estos resultados sugieren que en ambos álcidos el plumaje mojado impide la pérdida de aire cuando el ave sale a la superficie del agua después de sumergirse, reduciendo los costos por pérdida de calor.

Stephenson and Andrews (1997) suggested that feathers of aquatic birds must be highly water repellent to prevent the displacement of the internal air layer and to avoid excessive heat loss. Furthermore, they hypothesized that a thin film of water over the surface of the feathers could serve to minimize heat loss by reducing the loss of air from the plumage while the bird is diving. Ducks and some other aquatic birds (dippers, loons, and grebes) have feathers with high capacity to repel water (Rijke 1970). Some seabirds, however, appear wet after successive immersions, giving the observer at a distance the impression of a poor waterproofing. Nevertheless, even feathers with relatively poor water repellency can resist water penetration well if the Cassie–Baxter model of wetting applies (Rijke 1970). The Cassie–Baxter model specifies that the water repellency of a porous material is enhanced because drops sit partially on air, which remains trapped into the hollows, increasing the apparent contact angle (Cassie and Baxter 1944). Accordingly, the pressure required for water to penetrate between barbs of a feather increases as the distance between the barbs is reduced (Rijke 1970). Thus apparently wet plumage does not necessarily imply excessive heat loss, as the insulating layer of the plumage might not be compromised. However, wet birds are heavier, with wing loading and the energetic cost of flying increased. Ortega-Jiménez et al. (2010) showed that plumage wettability (6.7 % of body mass) had a negative effect on the performance of small alcids taking flight. Since some waterbirds are capable of keeping their plumage relatively dry during diving, the function of apparently wet plumage remains to be explained.

In order to evaluate the hypothesis that apparent wet plumage of alcids impedes water penetration and loss of warm air during diving, we used feathers of Xantus's Murrelet (*Synthliboramphus hypoleucus*) and Cassin's Auklet (*Ptychoramphus aleuticus*) to measure the maximum penetration pressure of air and water on feathers wet on one side.

METHODS

WATER-PRESSURE RESISTANCE

We collected feathers from the breast of the carcasses of a single specimen each of Xantus's Murrelet and Cassin's Auklet at the San Benito Islands, Baja California. The afterfeathers were removed before the experiment was run. We defined critical penetration pressure (P_w) as the hydrostatic pressure required for water to start penetrating through a single feather and measured it by following Stephenson and Andrews (1997). The external side of each single feather was fixed downward with Loctite on a test tube (3 mm internal diameter, 4 cm long). The test tube was connected to the lower part of a large J-shaped plastic tube. Using a syringe, we then progressively filled the upper part of the J tube (6 mm internal diameter) with water, so that the pressure on the external side surface of the feather increased (at a rate of approximately 70 Pa sec^{-1}) until the water started penetrating through the feather.

This procedure was performed in two ways. In one, the feather was originally dry and fixed to the test tube. This method
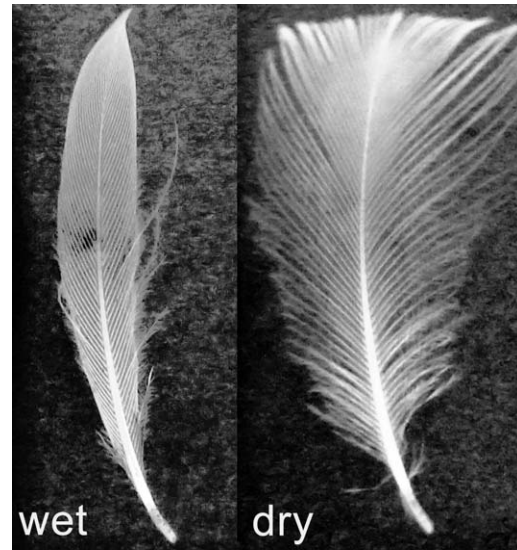

FIGURE 1.   Breast feathers of Xantus's Murrelet dry and wet on one side.

enabled comparison with other studies (Stephenson and Andrews 1997, Grémillet et al. 2005). In the second, we placed the external side of the feather on water, holding it at the calamus with the fingers and pushing it lightly into the liquid's surface without submerging it completely. The result of this procedure was a feather with aggregated barbs, whose internal side was dry and external side was wet (Fig. 1). To remove excess water, we placed the external side of the feather on a paper napkin for ~2 sec. Taking care that the barbs remained aggregated, we then fixed the feather to the test tube.

AIR-PRESSURE RESISTANCE

To measure resistance to maximal air pressure (P_a), we devised an air manometer. The apparatus used the principle of communicating vessels. A single feather was fixed between two plastic tubes (3 mm internal diameter) with a mechanical press, and this arrangement was connected to a bottle half filled with water and so to the air in the bottle. To allow the air pressure in the bottle to be changed, we connected a manual air pump to the air in the bottle. We then inserted a tube vertically into the bottle, down into the water. If the pressure of air within the bottle increased, both the level of the water in the vertical tube and the air pressure resisted by the internal side of the feather increased (Fig. 2). With the air pump, we increased the air pressure within the bottle until the water level of the vertical tube reached its maximal height, then dropped off rapidly. We assumed that this happened when air penetrated through the feather.

We estimated the exerted pressure P_a ($P_a = \rho g h$, where ρ is water density, g is the acceleration of gravity, and h is the water's maximal height) on the basis of the water's maximal height. Before using the pump to increase the internal pressure, we corrected h for capillarity by subtracting 2.6 mm, which corresponds to the height of water in the tube (3 mm internal diameter) with relation to the water surface in the bottle Measurements were made with feathers dry and wet on one side. The procedure for wetting the feathers was similar to that for measurement of P_w, except the excess water was not removed with a napkin.
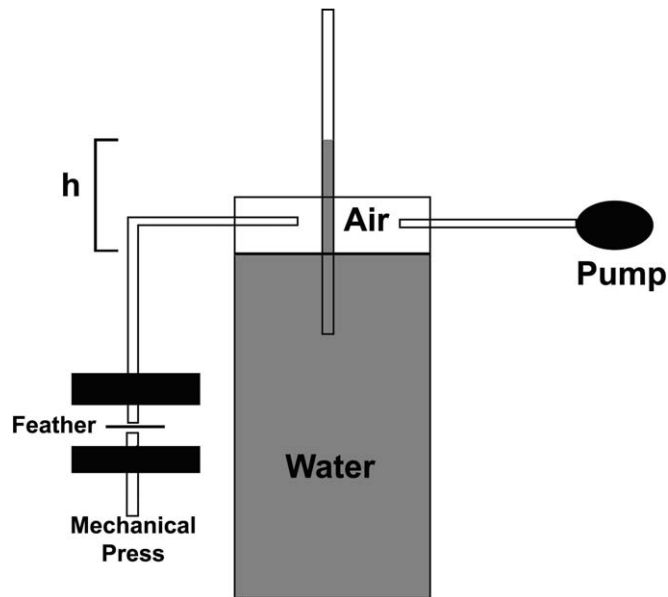
FIGURE 2. Manometer used to measure the critical pressure of air (P_a) through a single feather.

STATISTICAL ANALYSES

We used 30 feathers of each species to measure the two variables (P_w and P_a), 15 for each condition (dry and wet on one side), and independent-samples t-tests (SPSS v.12) to compare means of variables by condition. In all statistical analyses, the probability level at which the null hypotheses of "no difference" were rejected was $P > 0.05$. In what follows, data are shown as mean ± standard error.

RESULTS

FEATHER MORPHOLOGY

In the central part of the feather, barbules run perpendicular to the barbs. Basally, their structure is bladelike, but distally they are plumulaceous. Images from a scanning electron microscope show that, after being wetted on one side, the plumulaceous part of the barbs aggregates and compacts more than the bladelike structure (Fig. 3).

PRESSURE MEASUREMENTS

The mean P_w for dry feathers did not differ significantly from that for feathers wet on one side (murrelet: $t_{14} = 0.938$, $P = 0.356$; auklet: $t_{14} = 0.253$, $P = 0.802$). Mean values of P_w for feathers dry and wet on one side were 1.47 ± 0.025 kPa and 1.44 ± 0.027 kPa for Xantus's Murrelet, respectively, and 1.37 ± 0.022 kPa and 1.36 ± 0.028 kPa for Cassin's Auklet, respectively.

Results of the P_a experiments indicate that dry feathers are totally permeable to air (P_a is atmospheric pressure). But when feathers were wet on one side, they resisted air pressure effectively up to 1.27 ± 0.042 kPa for the murrelet and 1.23 ± 0.037 kPa for the auklet.

DISCUSSION

In order to understand the morphological changes of feathers wet on one side and their capacity to resist water penetration and air outflow, it may be helpful to refer to theories of water repellency of textiles. The Cassie–Baxter model indicates that air can remain trapped below a drop of water, strengthening water repellency of porous material (Bormashenko et al. 2007). This is because the drop sits partially on air, increasing the apparent contact angle in agreement with the Young equation (Cassie and Baxter 1944). Water repellency could also be explained with the Wenzel model, which uses a geometrical argument based on the ratio between the actual surface area and the apparent surface area of a rough surface. The Wenzel model assumes that water droplets penetrate
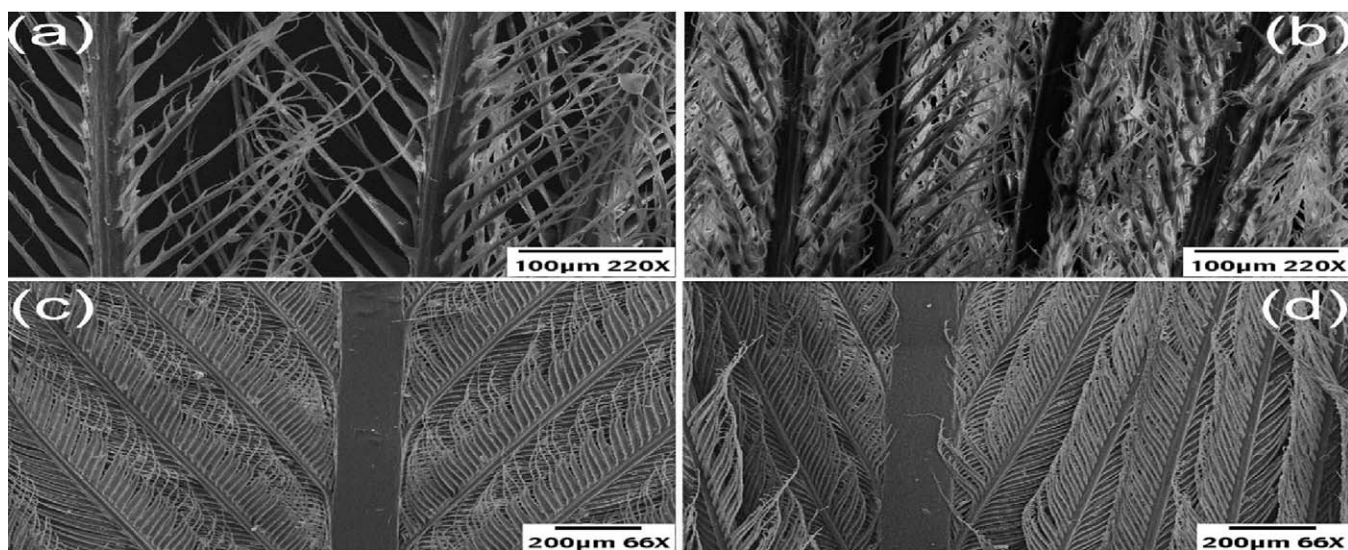

FIGURE 3. Scanning electron microscope images of Xantus's Murrelet's feathers. Pennaceous part: dry (a); wet on one side wet (b). Central part: dry (c); wet on one side (d).

fully into the surface gaps, increasing the available surface area of the solid, which geometrically increases the apparent contact angle and so enhances hydrophobicity. Application of this model requires that the material of the feather be hydrophobic. If the porous material is hydrophilic, however, the Wenzel model predicts an increase of hydrophilicity (Quéré 2008). It is generally agreed that hydrophobicity of feathers emerges from the coating of the keratin with the uropygial secretions of waxes and esters (Stephenson and Andrews 1997). Rijke (1970), however, suggested that feathers' water repellency is more complicated, partially supported by their microstructure. Furthermore, on the basis of the contact angle of a drop sitting on a rachis cleaned of traces of preening oil, Bormashenko et al. (2007) found that the tissue forming the feather is hydrophilic. Therefore, a Cassie–Wenzel transition on bird feathers is to be expected. It may occur on pigeon feathers and rough materials when the radius of an evaporating drop decreases or when external pressure on the drop increases (Lafuma and Quéré 2003, Bormashenko et al. 2007). A distinction of the Wenzel regime is that it produces a stronger adhesion of a drop on the surface of rough materials than does the Cassie regime (Lafuma and Quéré 2003). Therefore, transition from one regime to another could explain the loss of repellency experienced by the external side of feathers of both alcids we sampled.

The structure of the feathers of the two alcids we studied is similar to that of cormorants. Grémillet et al. (2005) suggested that the plumage of cormorants is only partly wettable, maintaining a thin inner layer of air, because cormorants' body feathers have a loose distal section, wetted quickly, and a highly waterproof inner part. In the case of alcids, wetting reduces the gaps between barbs of the distal part of the feather, clumping them together (Fig. 3). In this case, the loosely structured and highly flexible distal barbs could improve the resistance of the entire plumage to water penetration, filling gaps between adjacent feathers and forming a waterproof mesh. The aggregation of barbs due to wetting could be explained as a consequence of a balance between adhesion and repulsion forces acting between neighboring barbs of a single feather. Studies of the coalescence of wet hair indicate that pairs of hairs aggregate as a result of capillary and elastic forces (Bico et al. 2004). Therefore, these forces could possibly explain the morphological change observed on a feather wet on one side in comparison to a dry feather.

Rijke's (1970) theoretical results suggest that feathers of aquatic birds, like those of alcids, may be only marginally resistant to water penetration. However, empirical evidence indicates that dry feathers of diving birds resist water pressure higher than that predicted by Rijke (a maximum of ~0.6 kPa for ducks). Measurements of P_w in other aquatic birds range from 1.69 kPa for scaups (Stephenson 1997, Stephenson and Andrews 1997) to ~6 kPa for cormorants (Grémillet et al. 2005). Note that our P_w of ~1.4 kPa for alcids is smaller than that reported for the Lesser Scaup (*Aythya affinis*), but higher than that predicted theoretically for ducks and also higher than that reported for the down coat of Mallard (*Anas platyrhynchos*) ducklings. The penetration pressure of a clean coat of down of Mallard ducklings is ~0.8 kPa (Bakken et al. 2006). It is enough to allow static immersion to a depth up to 8 cm before water saturates the duckling's down. According to the value of P_w we report, feathers of Xantus's Murrelet and Cassin's Auklet resist the passage of water at depths up to ~14 cm. This value is sufficient for the plumage to resist water penetration when birds are floating on the water surface because they submerge their body ~4 cm (Ortega-Jiménez, pers. obs.). However, P_w values of a single feather are not enough to explain why the inner layer of the plumage remains dry during diving. This is because the feathers' density, their size, and the way each feather is arranged and

oriented with respect to the other feathers affect plumage permeability (Ribak et al. 2005). Also, with depth, the plumage is compressed, reducing the spaces between adjacent barbs/barbules in direct contact with water, increasing their resistance to water penetration (Stephenson 1997). As noted by Grémillet et al. (2005), values of P_w may be taken as indices that permit interspecific comparisons, but they are inadequate to estimate accurately the permeability of the entire plumage of diving birds.

We did not take into account the effect of time on P_w. However, Stephenson (1997) did not find differences in water-pressure resistance between feathers in contact with water briefly and those held in prolonged contact with water at a pressure similar to that exerted on the underparts of a floating Lesser Scaup.

The capacity of wet feathers to resist air penetration agrees with observations made on wet porous materials. For example, in wet paper with ~85% water content or more, at low air pressures no air intrudes (Van de Ven 2008). The critical air pressure of 1.25 kPa, measured for both alcids' feathers, is possibly enough to resist air outflow from wet plumage when a small alcid is floating on the sea surface. However, this result must be applied with caution in explanation of air losses observed in diving auklets and murrelets. Our measurements of P_a were made under a static situation, but diving is a hydrodynamic process. When a wing-propelled diving bird descends in the water column, both the active downstroke and upstroke accelerate the body. Air pressure within the plumage depends not only on depth but also on speed and the gradient between the body's front and back during active strokes. If this pressure gradient is larger than the dynamic critical pressure resistance to air outflow, a loss of bubbles from plumage is expected.

When water repellency is low and water penetration is high, the water increases the birds' body mass significantly (Mahoney 1984). Aerodynamic theory predicts that induced power requirements, which are greatest at low flight speeds, increase with mass (Pennycuick 1975). Ortega-Jiménez et al. (2010) showed that wettability (6.7% of body mass) reduces the aerodynamic performance of small alcids as they take off from the water. The fact that feathers wet on one side resist water penetration helps the birds avoid a mass increment that they have to lift during flight and therefore eliminates the increase in energetic cost. Furthermore, water penetration could reduce the air content of plumage, negatively affecting insulation and maintenance of body heat. The thermal conductance and heat loss of the Anhinga (*Anhinga anhinga*), a wettable bird, increases 32% when the bird is wet (Mahoney 1984). Saturation with water increases the thermal conductance of the down coat of Mallard ducklings tenfold over that of a dry down coat (Bakken 2006).

In diving cormorants, plumage wettability increases with time (Ribak et al. 2005). Our results suggest that feathers wet on one side promote a superficial plumage wetting. Thus, in agreement with our P_a results, it may be expected that when the water overlays the entire plumage and the alcid floats on the sea surface, there should be no air outflow.

Seabirds in cold water face unique challenges with respect to body-heat maintenance. Subdermal fat, plumage air, and possibly vasoconstriction of peripheral tissues serve to reduce heat loss during diving (Wilson et al. 1992). The positive effect of wetting of feathers on one side on retention of air in the plumage should benefit auklets and murrelets that forage in cold waters, like those of the California Current, because this mechanism should reduce loss of plumage air when the bird is diving, maintaining its insulation and reducing heat loss.

LITERATURE CITED

BAKKEN, G. S., M. R. BANTA, C. M. HIGGINBOTHAM, AND A. J. LYNOTT. 2006. It's just ducky to be clean: the water repellency and water penetration resistance of swimming Mallard ducklings. Journal of Avian Biology 37: 561–571.

BICO, J., B. ROMAN, L. MOULIN, AND A. BOUDAOUD. 2004. Adhesion: elastocapillary coalescence in wet hair. Nature 462:690.

BORMASHENKO, E., Y. BORMASHENKO, T. STEIN, G. WHYMAN, AND E. BORMASHENKO. 2007. Why do pigeon feathers repel water? Hydrophobicity of pennae, Cassie–Baxter wetting hypothesis and Cassie–Wenzel capillarity-induced wetting transition. Journal of Colloid and Interface Science 311:212–216.

CASSIE, A. B. D., AND S. BAXTER. 1944. Wettability of porous surfaces. Transactions of the Faraday Society 40:546–551.

GRÉMILLET, D., C. CHAUVIN, R. P. WILSON, Y. LE MAHO, AND S. WANLESS. 2005 Unusual feather structure allows partial plumage wettability in diving Great Cormorants. Journal of Avian Biology 36:1–7.

LAFUMA, A., AND D. QUÉRÉ. 2003. Superhydrophobic states. Nature Materials 2:457–460.

MAHONEY, S. A. 1984. Plumage wettability of aquatic birds. Auk 101:181–185.

ORTEGA-JIMÉNEZ, V. M., S. ÁLVAREZ-BORREGO, S. ARRIAGA-RAMÍREZ, M. RENNER, AND E. S. BRIDGE. 2010. Takeoff flight performance and plumage wettability in Cassin's Auklet *Ptychoramphus aleuticus*, Xantus's Murrelet *Synthliboramphus hypoleucus* and Leach's Storm-Petrel *Oceanodroma leucorhoa*. Journal of Ornithology 151:169–177.

PENNYCUICK, C. J. 1975. Mechanics of flight, p. 1–75. *In* D. S. FARNER AND J. R. KING [EDS.]. Avian biology. Vol. 5. Academic Press, London.

QUÉRÉ, D. 2008. Wetting and roughness. Annual Review of Materials Research 38:71–99.

RIBAK, G., D. WEIHS, AND Z. ARAD. 2005. Water retention in the plumage of diving Great Cormorants *Phalacrocorax carbo sinensis*. Journal of Avian Biology 36:89–95.

RIJKE, A. M. 1970. Wettability and phylogenetic development of feather structure in water birds. Journal of Experimental Biology 52:469–479.

STEPHENSON, R. 1997. Effects of oil and other surface-active organic pollutants on aquatic birds. Environmental Conservation 24: 121–129.

STEPHENSON, R., AND C. A. ANDREWS. 1997. The effect of water surface tension on feather wettability in aquatic birds. Canadian Journal of Zoology 75:288–294.

VAN DE VEN, T. G. M. 2008. Capillary forces in wet paper. Industrial and Engineering Chemistry Research 47:7250–7256.

WILSON, R. P., K. HUSTLER, P. G. RYAN, A. E. BURGER, AND E. C. NOLDEKE. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? American Naturalist 140:179–200.