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Chapter 2

Feather Structure and Behavioral Patterns in Seabirds

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Additional information is available at the end of the chapter

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Abstract

The structural details of the flight and contour feathers of seabirds closely match the requirements of their habitats and feeding habits. They serve a variety of functions ranging from intraspecific signaling to such physical qualities as thermal insulation, water repellency and resistance to impact. It comes as no surprise, therefore, that they are composed of an array of elements that confer these qualities to the optimal benefit of their avian bearer. In this chapter, the physical bases for these functions are provided in both mathematical and evolutionary terms. Some functions excel at the expense of others, and many species have evolved an optimal balance between functions in terms of both feather microstructure and behavioral patterns that suit their specific habitat and feeding habits. The effects of mechanical forces on feathers are presented in terms of the impact of diving, plunging and alighting, and the structural properties in seabird feathers identifiable as adaptations to these forces. Finally, the way oiling affects the water repellency and resistance of feathers is discussed. It is concluded that the flight and contour feathers exhibit morphological and mechanical features that are advantageous for specific habitats and feeding techniques.

Keywords: seabirds, feather structure, behavioral patterns, water repellency, water resistance, feather adaptations

1. Introduction

Seabirds are part of a large group of families that have made their home at open oceans, shores and estuaries inhabiting many diverse marine environments. Most of them feed in salt water, taking their prey from the surface or catching it under water by swimming, plunging and deep diving. Others exploit the skies above pursuing their prey in an unobstructed three-dimensional space without ever alighting. Among them are families that have colonized the remotest parts of our earth and have adapted to the most extremes of climatic conditions.

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Indeed, seabirds can be found foraging and often breeding at all latitudes. They can truly be said to have conquered the entire marine world.

Such widespread occurrence has exposed seabirds to a great variety of evolutionary forces that have shaped their anatomy and behavioral patterns to optimally suit their specific environment. In this chapter, we show how the feathers of seabirds, in particular the contour feathers, vary among families and exhibit a range of properties that function, among other things, to regulate body temperature, repel water, prevent water from penetrating to the skin and resist the impact forces of diving, plunging and alighting. Some of these functions excel in extreme environmental conditions or in relation to specific feeding techniques, frequently at the expense of other functions. Others represent a balance between two or more opposing functions. In consequence, many of these functions are expressed in an array of feather characters that confer these qualities to the optimal benefit of the avian bearer.

To study these functions in some detail, a closer look at the structural composition of feathers is in order. The morphology of feathers has been well described in the ornithological literature [1, 2] and is reproduced here only to the extent necessary for the purpose of this chapter. All feathers, whether flight or contour feathers, are composed of essentially the same elements, only their relative prominence is different. At the base of the spine (or rachis), we find the downy or plumulaceous feathers, only a tuft in flight and tail feathers, but extensively present alongside the proximal two-thirds of the rachis of contour feathers. These are thought to function as a means to regulate body temperature by entrapping air [3, 4]. More distally, they show a highly structured pattern with rami extending from the rachis in the plane of the feather, each sprouting barbules of which the distal ones have hooks that catch upon the curled proximal barbules of the barb next more distal. This continuous-looking, hook-and-flange arrangement provides this pennaceous part of the feather with the rigidity so critical for its mechanical properties. It also confers water repellency and resistance to water penetration to the body plumage.

In flight and tail feathers, the pennaceous part is by far the most dominant part, but in contour feathers, it occupies only the distal one-third of the length of the feather. The proximal two-third is made up of downy elements that work as structural reinforcements limiting the bending of the downy barbules. They may also function to catch other barbules and keep them from becoming entangled, thereby allowing the entrapment of more air and serve as a better thermal insulator [5]. Nodes in downy barbules, seen in some families including seabirds, may also contribute to a thick fluffy plumage resulting in even better thermal insulation [6]. Apart from conserving heat by air convection, feathers with downy texture also show adaptations for the conservation of body heat radiation emitted from the skin of all warm-blooded animals. Part of this radiation is absorbed by the feather keratin and, in turn, converted into convection heat and partially re-emitted from the keratin or lost to the surrounding environment [7].

Contour feathers are arranged in an overlapping fashion like shingles on a roof having their distal dorsal aspect exposed to air or water. It is at this interface that the physical interaction with the external world occurs and where adaptations to environmental factors can be found.

2. Water repellency and resistance to water penetration

One of the major functions of feathers is to prevent water from reaching the skin or weighing down the remiges and tail feathers in flight. With very few exceptions, all birds benefit from a plumage that optimally repels and resists the penetration of water. However, the manner in which this optimum is realized for each seabird family is closely associated with its behavior and interaction with its habitat and, as a result, the feather characters responsible for water repellency and resistance vary accordingly. To understand the way, a water-repellent/resistant structure functions, certain aspects of surface physics should be made clear.

The water repellency of feathers and other biological porous structures, such as the stomatal apparatus of leaves and the spiracles of insects, is governed by the fundamental principles of surface physics that apply to *all* porous surfaces whether natural or manmade. It is determined by the relative areas of solid-water and air-water interface and their respective interfacial energies regardless of the actual architecture of the repellent structure itself [8]. If the surface of the solid is coated with another material, such as paint or preening oil, it will assume the properties of the coating material. For feathers coated with uropygial gland oil, the feather-water interface is, in fact, an interface between gland oil and water.

When a drop of water is placed on a smooth feather surface such as the rachis, it will pearl up and roll off easily. The surface is then said to be water repellent, the actual extent of which is determined by the contact angle θ, defined as the angle between the tangent to the curved water surface at the point of contact with the solid surface and the plane of the surface on which the drop is resting, measured through the water. When the drop is placed on the porous vane of the feather, it will entrap air in the hollows and interstices, forming additional air-water interfaces, which will cause considerable increase in the contact angle, according to

$$\cos\theta_a = f_1 \cos\theta - f_2 \tag{1}$$

where f_1 is the area of solid-water interface and f_2 is the area of the air-water interface per unit of apparent surface area. For water drops on barbs, f_1 and f_2 can be expressed as

$$f_1 = (\pi - \theta) r/(r + d) \tag{2a}$$

and

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

where $2r$ represents the diameter of the rami measured in the plane of the long axes of the rami separated by distance $2d$ [8, 9].

Note that the increase in apparent contact angle is ascertained only by the parameter $(r + d)/r$ and not by the separate values of r and d. Thus, θ_a for values of this parameter ranging between 2.4 (penguins, *Spheniscidae*) and 10 (land birds) would vary between about 126° and

154°, roughly correct by experimental verification [10]. These values are significantly higher than those attained for the most repellent of smooth surfaces which equal about 114° [9].

Eq. (1) has been derived solely from basic physicochemical principles without reference to parameters pertaining to any specific dimensions of the porous surface. In addition, the values of f_1 and f_2 are determined only by the areas of solid–liquid and air-liquid interface per unit of macroscopic surface areas without dictating the shape, curvature or configuration of these interfaces. Therefore, the relationship between the dimensions of a porous surface provided in terms of f_1 and f_2 and its ensuing contact angle as represented by Eq. (1) is a rigorous one, not an empirical one, and is of general validity. Eq. (1) has been tested experimentally and was found to be correct by Cassie and Baxter and Rijke using paraffinated stainless steel wire cages and grids [8, 11]. For these particular models, calculations for the values of f_1 and f_2 could be made according to Eqs. (2a) and (2b). Many other studies including recent ones have reported contact angle measurements on porous substrates including feathers and consistently confirmed the correctness of the above premises [9, 11–13].

In order to measure contact angles on smooth or porous surfaces correctly, certain experimental conditions have to be met, such as: the drop has to be small enough so as not to be perturbed by gravitational forces, but large enough to cover a representative area of the porous surface. The drop should be prevented from evaporation which would turn the advancing contact angle into a receding one. Feather specimens should be covered with fresh preening oil, not rinsed with an ethanol wash [12]. When these conditions are met, the correct contact angle is usually found to be within one degree error as observed by multiple authors [8, 11, 14–17]. These results have shown conclusively that contact angles can be reliably calculated from and represented by the dimensions of the porous surface alone.

An expression for the pressure (P), required to force water between the rami and barbules, can be derived from similar premises and reads

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

here, γ represents the surface tension of the water. This equation shows P to be inversely proportional to r and $(r + d)/r$. As a result, the requirement of relatively large values for $(r + d)/r$ to provide sufficient water repellency is opposed by the need for small values for this parameter to attain good resistance to water penetration. Thus, the structural characteristics compatible with optimal water repellency are, at least in part, in conflict with the requirements of resistance to water penetration. This conflict has important implications for seabirds, which must realize a balance between these two opposing functions to cope with their respective habitats and behavioral patterns as indeed they do [10].

Experimental data on water repellency and resistance to water penetration for Double-crested cormorants (*Phalacrocorax auritus*) and Anhingas (*Anhingidae*) have shown that results can be satisfactorily interpreted in terms of ramus diameter and spacing only without recourse to barbules. Their $(r + d)/r$ values for barbules are in the approximate range of 4.5–5.5 as found for almost all bird families regardless of their feeding habits or interaction with open water [10]. This suggests that the contribution of barbules to water resistance is real, but not based

on the same mechanism as applies to rami. Barbules provide an interlocking mechanism by preventing the rami from separating under the increasing water pressure while increasing their own separation by their hooks sliding in the flanges, a process that can be verified under a low-powered light microscope. Similarly, water drops being repelled by the rami and not involving the barbules can be observed with a magnifying glass.

The contact angle θ of water drops on smooth feather surfaces, such as the rachis or on a microscopic slide covered with preening oil, measures about 90° as established by various authors [8, 9, 17]. The same value was found for water drops on polyethylene foil [14] and this is no coincidence: polyethylene almost exclusively consists of methylene groups (-CH_2-) which are the predominant chemical component of preening oil [18, 19].

Note that when θ is 90°, cosθ equals zero and sinθ equals one, which reduces Eq. (1) to $\cos\theta_a = -f_2$ and Eq. (2b) to $f_2 = 1 - r/(r + d)$. These fortuitous circumstances allow the investigator to determine the apparent contact angle from the value of $(r + d)/r$ alone. For instance, Cassie and Baxter [8] found $(r + d)/r$ for their duck feathers to be 5.9, which corresponds to a θ_a of 147° in good agreement with their experimental value of 150°. These results, corroborated by other workers [20], have shown that for feathers coated with fresh preening oil, both the water repellency in terms of the apparent contact angle θ_a and the balance between water repellency and resistance expressed by the value of $(r + d)/r$, can be correctly predicted from the micro-structure of the feather alone. Furthermore, the value of 5.9 for duck feathers, when compared with 4.8 for the White-breasted Cormorant (*Phalacrocorax carbo*) [21] and 7.1 for the European Starling (*Sturnus vulgaris*) [22], 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 [20, 21, 23–25] have shown that $(r + d)/r$ values vary from about 2.3 for penguins to about 6.5 for gulls (*Laridae*) and up to 10 for most terrestrial birds (**Table 1**). This range in values for this parameter suggests that each seabird family, and indeed 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 can 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 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 [20, 24, 26].

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 seen only when

Family/species	2*r* (μm)	(*r* + *d*)/*r*	Behavior/habitat
Penguins (*Spheniscidae*)	70	2.3	Swimmer/diver
Diving Petrel (*Pelecanoididae*)			Swimmer/diver
Common	42	5.0	
Cormorants (*Phalacrocoracidae*)			
Double-crested, White-breasted, Reed	~50	4.3–4.9	Wing-spreader/diver
Flightless	36	7.2	Wing-spreader/diver
Blue-eyed Shag	?	3.8	Wing-spreader in Chilean population
Darters (*Anhingidae*) African Darter	28	9.1	Wing-spreader/Under water stalker
Auks (*Alcidae*)	61	3.4	Swimmer/diver
Gannets (*Sulidae*)	50	3.8	Plunge-diver
Petrels (*Procellariidae*)	51	4.6	Surface feeder
Storm Petrels (*Hydrobatidae*)	~35	6.9–7.4	Swimmer
Pelicans (*Pelecanidae*)	~53	4.9–5.4	Swimmer
Brown Pelican	37	5.9	Surface feeder
Frigatebirds (*Fregatidae*)	54	5.7	Surface feeder
Gulls (*Laridae*)	~53	6.5–6.9	Occasional swimmer/Surface feeder
Skuas (*Stercorariidae*)	51	5.8	Occasional swimmer
Terns (*Sternidae*)	36	6.0	Surface feeder
Albatrosses (*Diomedeidae*)			
Yellow-nosed	61	4.3	Surface feeder/swimmer

Table 1. Summary of seabird families and species, barb diameter (2***r***) and (***r*** + ***d***)/***r*** values of contour feathers, habitat/behavior.

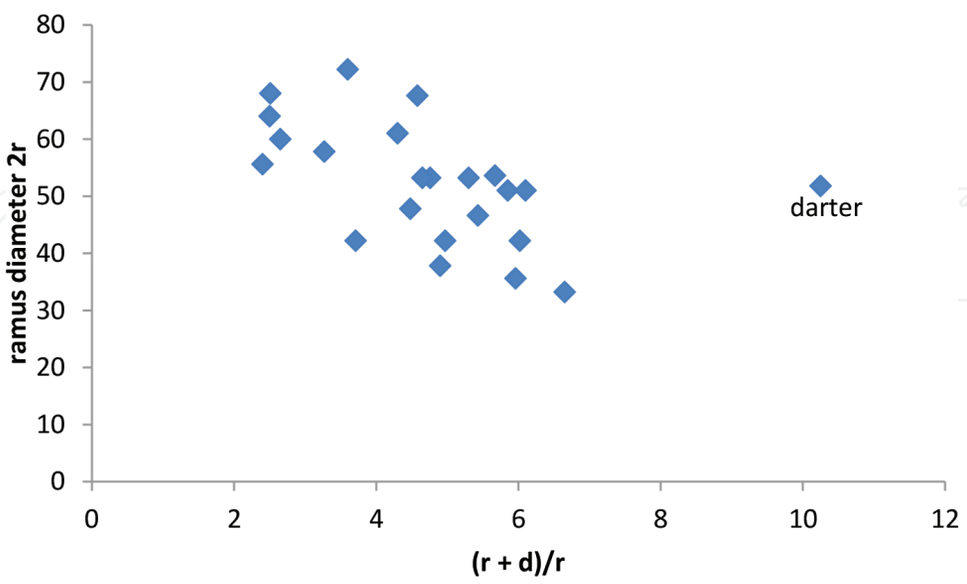


Figure 1. Plot of ramus diameter against wettability parameter (*r* + *d*)/*r* for 23 species of seabirds showing barb width decreases with decreasing resistance to water penetration. The values for the darter, which benefits from water penetration, are shown for comparison.

a species within a family behaves differently from its relatives. A typical example is the Brown Pelican (*Pelecanus occidentalis*), which, unlike its congeners, dives for its prey from the air.

Third, these data sets on feather structure suggest a relationship between barb diameter 2*r* and $(r + d)/r$ values (**Figure 1**). Families such as the penguins and other diving water birds have wide barb diameters and 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 herons (*Ardeidae*) and gulls have intermediate values. Penguins have excellent resistance to water penetration but poor water repellency as shown by their 'wet' appearance when they exit the water. The breast feathers of terrestrial birds, on the other hand, are very water repellent but promise little in the way of resistance to water penetration. Those of herons and gulls fall somewhere in between.

3. 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 almost 50 years ago [27]. 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 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 divers (*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 [2, 23, 28–39]. 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 [25]. However, 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 [24]. However, the underlying issues have since been resolved in the light of new information that has become available since 1985. One of these issues was the necessity to select samples with only perfectly latched barbules with rami parallel. Damaged regions will yield values for 2*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.

Seabirds that regularly spread their wings include several species of cormorants, such as the Reed Cormorant (*P. africanus*), Bank Cormorant (*P. neglectus*), Cape Cormorant (*P. capensis*),

White-breasted Cormorant 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 divers (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*) (4.9–5.4), including the Brown Pelican (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 [40, 41] 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 [25] 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 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 [23], but common in birds of this species breeding in Chile [42]. 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 μm and $(r + d)/r$ values between 4.3 and 4.9, those for the Flightless Cormorant are 31–41 μm and 7.1–7.4, respectively

[21]. 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 N m^{-2}, whereas only 550–590 N m^{-2} pressure is required to force water between the barbs [43, 44]. For other cormorants, the maximum weight for no water penetration between the barbs lies well above the bird's weight range [20]. 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.

4. 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 as reflected in the value of the parameter $(r + d)/r$. Therefore, it is 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 μm), but gannets have a value for $(r + d)/r$ of 3.8, which lies at the low end of the range (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 benefit mostly from an increased resistance to water penetration, whereas surface feeders, such as the Brown Pelican, gulls and storm petrels (*Hydrobatidae*), profit from an increased water repellency (**Table 1**). Similar findings were recorded for the five species of Dippers (*Cinclidae*), which among them show a slightly different water repellency and resistance in their contour feathers as an adaptation to their different feeding habits and river habitats [22]. Certain species of cranes (*Gruidae*) and rails (*Rallidae*) can also be regarded as having attained structural characters in their plumage that relate to their specific interaction with their watery feeding grounds [44–46].

It is likely that many more examples of contour feather structure correlating with specific behavior/habitat will be found once more data have been gathered. However, the abovementioned 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.

5. Do seabird feathers show adaptations to the impact forces of diving, plunging and alighting?

Unlike terrestrial birds, seabirds and other birds that have access to open water physically interact with water at the interface between feather coat and water. Water is about 800 times denser than air and, as a result, the impact forces of diving, plunging and alighting are so much more severe than when operating in air. Therefore, it is no surprise that seabird feathers are composed of stiffer elements to cope with these conditions. However, since each family interacts with water in its own specific way, variations in feather stiffness among families are to be expected for this reason alone.

All feathers are built from beta-keratin the elastic modulus of which is an inherent property of the keratin material itself. However, the actual stiffness of the various feather elements, rachis, rami and barbules, is determined by the respective shapes and sizes of these elements. The mechanical forces involved in diving, plunging and alighting are not accessible to direct measurement in any reliable or representative way. Any such data would not be meaningfully correlated to the resulting yield or flexure of barbs and vanes during forceful interaction with water. However, the bending and flexing of materials of different shapes and sizes have been well described in engineering physics and it is from these considerations that a number of conclusions can be drawn.

When a force F is applied over the length of a single barb, the barb will bend in the direction of the applied force with its tip flexing over a distance S. This relates to the barb length l and barb radius r as

$$S = F \cdot l^3 / 2\pi \cdot r^4 \cdot E \tag{4}$$

where E stands for the Young's elastic modulus of the feather keratin. When the force is applied to the vane, the flexural displacement of the tips of the vane per repeating unit $2(r + d)$ can be written as

$$S_v = F_v . l^3 \cdot 2(r + d) / 2\pi \cdot r^4 \cdot E \tag{5}$$

where the subscript v refers to the repeating unit of the vane. Rearrangement of Eq. (5) then yields

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$$\pi.E.S_v/F_v = (l/r)^3 \cdot (r+d)/r \quad (5a)$$

Apart from π and the elastic modulus E, the left-hand side of Eq. (5a) represents the extent of flexing of the tips of barbs per unit of force applied over the lengths of the barbs and measured over a distance $2(r + d)$. For the bending of the entire vane, F_v needs to be considered for the number of repeating units per vane. Note that the right-hand side of the equation is made up of the feather variables l, r and d, which, unlike S_v and F_v, are easily and directly accessible to measurement. These considerations allow us to semi-quantitatively predict the bending of the vane under an applied force from the dimensions and spacing of the barbs alone.

The role of the barbules in resisting bending of the vane has been considered in the light of their primary function, that is, keeping the barbs from separating under an applied force and doing so by their hooks sliding in the flanges of the barbule next more distal. Therefore, as well as for their small size, they are assumed to make only a minimal, if any, contribution to the overall resistance to bending.

To test the above premises, the contour feathers of 23 species belonging to 15 families of seabirds were examined (**Table 1**). The values for r and d of these contour feathers had been measured for the purpose of a 1970 study using a transmission light microscope equipped with a calibrated scale ocular. However, there is no reason to suspect the accuracy and precision of these data to be anything less than of those collected with electronic imaging techniques such as used in more recent studies [22, 47]. Values for l of the closed pennaceous portion of the contour feather were measured at the mid-part of the vane to the nearest half millimeter using a traveling microscope. At least three feather specimens of each species were examined.

Apart from feather stiffness, the resistance to impact forces is also determined by the extent of contour feather overlap and body feather density. To estimate the former, the length of the rachis L_f was measured to the nearest millimeter. The extent of overlapping can be approximated by the product of L_f and the square root of the number of feathers per surface area. To estimate the latter, we made use of the data on number of feathers and body weights as reported by several authors [48–54]. By fitting a second-order polynomial to these data, an estimate of the number of contour feathers as a function of the mass of the bird could be obtained. For the relationship between body surface area and body mass, expressions proposed by Perez et al. [55] and by Mitchell [56] were used to estimate surface area as a function of body weight. Combining the results of these two sets of calculations, contour feather densities expressed in number of feathers per surface area were found to be about 100,000 to 150,000 per m^2 for seabirds weighing less than 1.2 kg for all families studied. This number increases with weight to 200,000/m^2 at about 7 kg. The extent of feather overlaps, according to these calculations, yields about 10–15 feathers in a stack for families in the lower weight range with twice that number for heavier birds. Apparently, feather overlapping is the same for seabirds in the lower weight range regardless of family identity and, as a result, the restriction that stacking provides to bending is also the same. Only for birds weighing more than 1.2 kg do we find an increase in feather density and overlap with weight up to 250,000 per m^2

Cat.	Description	Stiffness parameter range	Deflection parameter (avg.)	Standard deviation
		l/r	$(l/r)^3$ $(r + d)/r$ (10^6)	(10^6)
1	**Deep divers**	59–108	1.6	0.92
	Dive/pursue prey under water			59%
	Penguins			
2	**Swim and dive**	188–237	49	24.5
	Pursue prey under water, extended time swimmers			50%
	Common diving petrel, cormorants			
3	**True plungers**	301–381	194	71
	Petrels, gannets, auks,			37%
4	**Large surface feeders**	377–410	387	14
	Pelicans, frigatebirds, skimmers			4%
5	**Shorebirds**	539–1009	839	260
	Skuas, gulls, terns			31%
6	**Large birds of open ocean**	689	1403	—
	Yellow-nosed albatross			

Table 2. Stiffness and deflection parameters for six seabird categories.

and stacks of 18 for a pink-backed Pelican (*P. rufescens*) weighing 9.6 kg. This is in line with expectation as impact forces are directly proportional to mass [57].

The above findings may be explained by any of two or both possibilities: (1) the feather density and number of feathers in a stack for the lower-weight families are sufficiently large to prevent feather bending regardless of behavioral pattern and (2) barb stiffness and resistance to water penetration of the contour feathers of each of these families are large enough to prevent water from reaching the skin on their own account and do not benefit from a further increase in feather density or stacking. Other than preventing water from reaching the skin, thermoregulatory adaptations can also be expected to affect feather density. Lowe [53] counted 48/cm^2 on a young Gentoo penguin (*Pygoscelis papua*).

According to Eq. (5a), the bending of the vane of a contour feather under the impact of forces associated with diving or landing on water surfaces consists of two factors: (1) the ratio of the length to the thickness of the barbs expressed as l/r and (2) the wettability parameter $(r + d)/r$. The first factor indicates that short and thick barbs make the vane stiff resisting bending, whereas long and thin barbs favor flexibility that promotes bending. The appearance of the wettability parameter in the equation shows that feathers resistant to water penetration also help prevent their bending, whereas highly water repellent feathers do not. Note that l/r enters the equation in the form of a third power which markedly enhances its contribution in the equation and dwarfs that of the other factor: over its range of 2.5 to about 7, $(r + d)/r$ increases by only a factor of 3, whereas $(l/r)^3$ does so by about three orders of magnitude.

The *l*/*r* values for the 15 families of the 23 seabird species have been assorted into six more or less distinct ranges listed in **Table 2** as categories. As shown, 'deep divers,' represented here by four species of penguins and characterized by their habit of diving and pursuing prey under water, fall in the lowest range (59–108) and therefore have the highest vane stiffness. The next range is made up of birds that 'swim and dive' in pursuit of their prey and spend much time in and on the water. This range includes the Common Diving Petrel (*Pelecanoididae*) with an *l*/*r* value of 237 and the cormorants (188). Category 3 covers the range 301–381, into which fit the 'true plungers' such as petrels (*Procellariidae*), gannets and auks. Large surface feeders, such as pelicans, frigatebirds (*Fregatidae*) and skimmers (*Rhynchopidae*), form the next category with a range of 377–410. Category 5, the 'shore birds,' includes skuas (*Stercorariidae*), gulls, and terns (*Sternidae*) that have the lowest vane stiffness with a range of 450–550. These birds are not extended time swimmers, do not pursue their prey under water and spend much time in flight or on shore. Albatrosses (689) are mostly airborne and alight only to take food from the surface or slightly below. In this respect, they behave much like category 5 families. Not listed are the Flightless Cormorant in category 2 and the Brown Pelican in category 4, because, as mentioned above, these species behave in a different way from their congeners, a feature expressed in the dimensions of their feather structure (**Table 1**).

The large differences in contour feather stiffness for the six categories of seabirds are borne out by a wide range in deflection parameter $(l/r)^3 \cdot (r + d)/r$. Averaged for each category, this parameter runs from 1.6×10^6 for penguins in category 1 to 1403×10^6 for albatrosses in category 6. By averaging the deflection parameters for each category, a large 'standard deviation' is introduced, but since the range of parameter values is very large, this does not affect the conclusions.

From these data, it can be concluded that the contour feathers of penguins, the most aquatic of families, are about 30 times stiffer than those of diving petrels and cormorants, and 120 times more so than those of plungers like gannets. Similarly, penguin feathers are 250 times more resistant to bending than those of surface feeders like pelicans, over 500 times more so than those of shorebirds such as skuas, gulls and terns and almost three orders of magnitude stiffer than albatross feathers. These large differences are directly related to feeding habits and interaction with water. Penguins find their prey exclusively under water and dive to great depths to catch it. Diving petrels and cormorants also dive, but spend more time on the surface and in the air. Plungers dive from the air with associated high pressure on impact, but catch their prey at lesser depths. Surface feeders do not dive and do not pursue their prey under water (brown pelicans dive from the air, but do not pursue under water). Shore birds feed from the water surface and are not extended time swimmers. Albatrosses, one of the most aerial of seabirds, alight only to feed from the surface and may occasionally dive at feeding frenzies.

5.1. The following pattern of feather structure in relation to feeding habits/behavior emerges

Barb width and spacing determine the relative water repellency and resistance to water penetration of feathers. Diving birds, and in particular deep diving birds, benefit from a mostly water resistant plumage with little in the way of water repellency. Less aquatic families, such as gannets and to a greater extent cormorants, show more repellency, but at the expense of

some of their water resistance. Some cormorants compensate for this by their habit of wing spreading. Swimming and hovering birds that catch their prey from the surface, shore birds and those operating mostly in the skies show a predominantly water repellent plumage.

The length and diameter of the rami of contour feathers vary widely among seabirds. Barb stiffness varies with barb length and width and is the largest for deep diving birds, less so plungers and very much less so for surface feeders ranging over three orders of magnitude. These structural differences in the feather plumage are believed to represent evolutionary adaptations to feeding habits and, in some cases, environmental conditions.

One of the greatest threats to the lives of seabirds is oil spills. In spite of heroic rescue operations, it is clear that the vast majority of seabirds perish at sea. In the context of this chapter, it may be useful to consider the potential role of the feather micro-structure in the demise of the victim. All components of petroleum, including the residues, are inherently hydrophobic and as such could be considered water repellent and perhaps even helpful in shedding water from the feather coat. However, it is the fine microstructure with its regular array of parallel rami and barbules latched together that is destroyed by the stickiness of the oil residues. This renders the resistance to water penetration nil, allowing seawater to reach the skin with the bird exposed to hypothermia. This mechanism is somewhat analogous to the infamous experiment in which the uropygial gland of ducks was extirpated whereupon the feathers did not so much lose their water repellency as their water resistance as a result of brittleness and lack of coherence [58]. Bird rescuers have long realized that removing the oil is only the first step in the recovery of the victim to be followed by restoration of the normal feather microstructure. This is eventually achieved by the bird's preening habits if the oil gland is functional, a very time-consuming process.

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