

AIR TRANSMISSIVITY OF FEATHERS

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Summary

The flight feathers and their coverts of a European kestrel *Falco tinnunculus* have been tested for their air transmissivity. The transmissivity was measured in both directions, i.e. from ventral to dorsal and *vice versa*; the mean difference between the two directions was less than 10%. However, the transmissivity of the inner *versus* outer vanes of the remiges and coverts differed significantly, with the outer vanes being more transmissive than the inner vanes. A functional interpretation of the different transmissivities of the inner and outer vanes is given, and we propose that its significance lies in the formation of a

smooth, continuous wing surface. The individual feathers are pushed firmly towards one another as a result of the different transmissivities, which cause a pressure gradient to build up from the less-transmissive inner vane towards the overlying, more-transmissive outer vane of the adjacent feather. In another test series, the transmissivity of the flight and covert feathers of 27 species was measured; the differences found between species were small.

Key words: feather, air transmissivity, kestrel, *Falco tinnunculus*, bird, flight.

Introduction

A prerequisite for flight is a relatively large ratio of surface area to body volume. All animals (and plants, i.e. seeds) that exhibit some sort of flight tend to have appendages that greatly increase their surface area with a small increase in body volume (i.e. weight). In all vertebrates except birds (i.e. fish, amphibians, various reptilian groups, mammals), the increase in surface area is accomplished through thin layers of integument spread between extendible extremities/appendages or their parts. These skin flaps are naturally impervious to air. In birds, however, the aerofoil consists largely of feathers, with the extremity itself (wing bones and muscles) and attached skin flaps (pro- and metapatagium) having a much smaller role. It has been noted frequently that the advantage of feathers over skin folds lies in the ease with which feathers can be repaired after minor damage and that they are completely replaced regularly during moulting.

Few authors have explicitly referred to the air transmissivity of feathers (Ahlborn, 1896; Mascha, 1904; Hempel, 1931; Raspet, 1960; Dyck, 1985), usually pointing out the morphological differences between flight and contour feathers. Only V. Lougheed (cited in Raspet, 1960) is reported to have measured the transmissivity of flight feathers and supposedly found it to be ten times greater in the direction from dorsal to ventral than *vice versa*. According to morphological observations, however, flight feathers (i.e. primaries, secondaries and tail feathers) are considered to be impervious to air because of the enlarged ventral margins of the barbules.

This sets them apart from the body contour feathers, which are described as being 'permeable' (Lucas and Stettenheim, 1972; Dyck, 1985) as a result of the lack of these enlarged ventral margins. A perusal of the pertinent literature leaves one with the impression that the non-transmissivity of flight feathers is simply assumed since it is the obvious expectation. Although it has not been the intention of our study to dispute this assumption, it seemed nonetheless desirable to investigate this subject quantitatively, because the aerodynamic significance of the transmissivity of feathers has been so long neglected and seems little understood.

A short introduction to wing theory

The generation of lift by an aerofoil can be visualized as described below. For a more complete introduction to aerodynamic principles, see Nachtigall (1975), Rayner (1979), Dubs (1990) and Norberg (1990). Because of the geometry of the aerofoil, air that passes over its upper surface must travel farther and, hence, have a greater velocity than air that passes over the lower surface (Fig. 1A).

According to Bernoulli's equation, an increase in velocity (kinetic energy) causes a decrease in static pressure (potential energy) in order to keep the sum of all energies constant. Thus, the change in static pressure ΔP on the upper surface is negative (i.e. pressure on the upper surface P_u is lower than pressure in the free-stream flow P_∞) and, correspondingly, ΔP on the lower surface of the aerofoil P_l is positive ($P_l > P_\infty$). (Throughout the

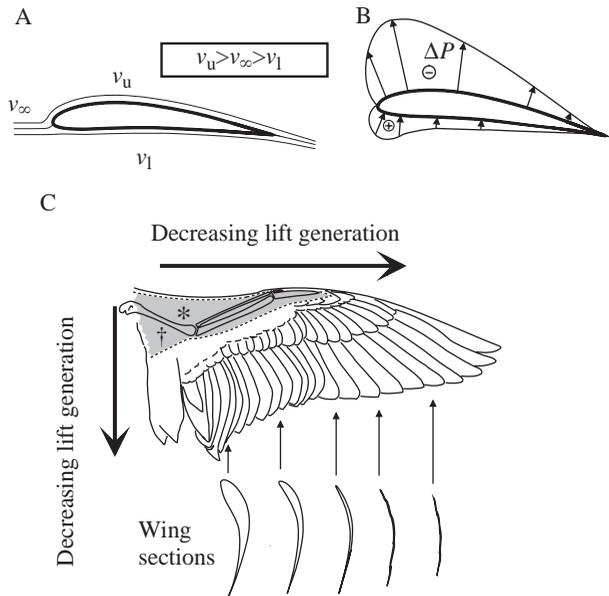


Fig. 1. (A) Flow around an aerofoil. v_∞ is the free-stream velocity, v_u is the velocity of the air on the upper surface of the wing, v_l is the velocity of the air on the lower surface of the wing. (B) Pressure distribution on an aerofoil. $\Delta P = P_u - P_\infty$ or $\Delta P = P_l - P_\infty$ (ΔP is the static pressure on the upper, P_u , or lower P_l , surface of the aerofoil minus the static pressure in the free-stream flow P_∞). The size of the arrows indicates the magnitude of ΔP . (C) Distribution of lift generation on a bird's wing. Wing sections at the locations indicated by arrows also are depicted, illustrating the decreasing camber towards the tip of the wing. The shaded area indicates the non-transmissive parts of the wing, i.e. the forelimb with propatagium (*) and metapatagium (†).

text, the terms negative or positive pressure describe ΔP). This pressure difference means that the aerofoil is both pushed up from below and pulled up from above, the latter contributing approximately two-thirds of the total lift. Integration of ΔP over the area of the aerofoil then yields the lifting forces.

However, the velocity of the air flow varies over the depth of the aerofoil, increasing sharply on the upper surface behind the leading edge and then decreasing continuously towards the trailing edge, where it is again the free-stream velocity V_∞ . Since the pressure is related directly to the velocity at any location, the pressure distribution is such that the magnitude of ΔP (which is negative or positive for the upper or lower surface, respectively) increases to reach a maximum shortly behind the leading edge and then decreases steadily towards the trailing edge (Fig. 1B).

In a bird's wing, the situation is still more complicated because three phenomena coincide (Fig. 1C). First, a bird's wing is, of course, cambered like an aerofoil (as shown in Fig. 1B), so that the pressure or lift distribution over its depth is as described above. Second, the geometry of the wing varies greatly along its length, with the arm region being highly cambered and the tip of the wing almost flat. Therefore, lift production is greatest in the arm region and decreases towards the tip of the wing. Third, an aerofoil of finite length exhibits an approximately elliptical lift distribution because of the influence of the wing tip (or trailing

vortex. This effect enhances the effect of the changing geometry of the wing. Consequently, the pressure or lift distribution on a bird's wing is such that it decreases from a maximum near the leading edge to a minimum towards the trailing edge and, at the same time, from a maximum in the arm region to a minimum towards the tip of the wing (Fig. 1C). It is interesting to note that the area of greatest lift production, and therefore the largest pressure gradient between the upper and lower surfaces, is located where non-transmissive parts (wing bones, muscles, pro- and metapatagium) make up the wing.

Materials and methods

Feathers of 27 species from 15 families (Table 1) were tested for their air transmissivity. Specimens obtained from Zoologische Schausammlung der Universität Tübingen (ZSUT) had been treated with Eulan SPA (Bayer) to protect them from pests. In a separate test, it was verified that treatment with Eulan did not alter the air transmissivity of the feathers. Most of the specimens had been stored temporarily in a freezer prior to their preparation. All specimens were less than 10

Table 1. *Species used in this study*

Species	Taxonomic name	Source of specimen
Great crested grebe	<i>Podiceps cristatus</i>	SWM
Goosander	<i>Mergus merganser</i>	SWM
Eider	<i>Somateria mollissima</i>	SWM
Tufted duck	<i>Aythya fuligula</i>	SWM
Pochard	<i>Aythya ferina</i>	SWM
Imperial eagle	<i>Aquila heliaca</i>	ZSUT
Red-tailed hawk	<i>Buteo jamaicensis</i>	ZSUT
European buzzard	<i>Buteo buteo</i>	ZSUT
Goshawk	<i>Accipiter gentilis</i>	SWM
Sparrowhawk	<i>Accipiter nisus</i>	ZSUT and SWM
Peregrine falcon	<i>Falco peregrinus</i>	ZSUT
Kestrel	<i>Falco tinnunculus</i>	ZSUT and SWM
Water rail	<i>Rallus aquaticus</i>	SWM
Curlew	<i>Numenius arquata</i>	ZSUT
Swift	<i>Apus apus</i>	SWM
Alpine swift	<i>Apus melba</i>	SWM
Great spotted woodpecker	<i>Dendrocopos major</i>	ZSUT and SWM
Nuthatch	<i>Sitta europaea</i>	SWM
Song thrush	<i>Turdus philomelos</i>	ZSUT
Golden oriole	<i>Oriolus oriolus</i>	ZSUT
Skylark	<i>Alauda arvensis</i>	SWM
Blackbird	<i>Turdus merula</i>	SWM
Brambling	<i>Fringilla montifringilla</i>	SWM
Jay	<i>Garrulus glandaris</i>	ZSUT and SWM
Nutcracker	<i>Nucifraga caryocatactes</i>	SWM
Magpie	<i>Pica pica</i>	ZSUT
Rook	<i>Corvus frugilegus</i>	ZSUT

ZSUT, Zoologische Schausammlung der Universität Tübingen; SWM, personal collection of W. Müller; one specimen of each species was used, except for the four species for which one specimen each from ZSUT and SWM is indicated.

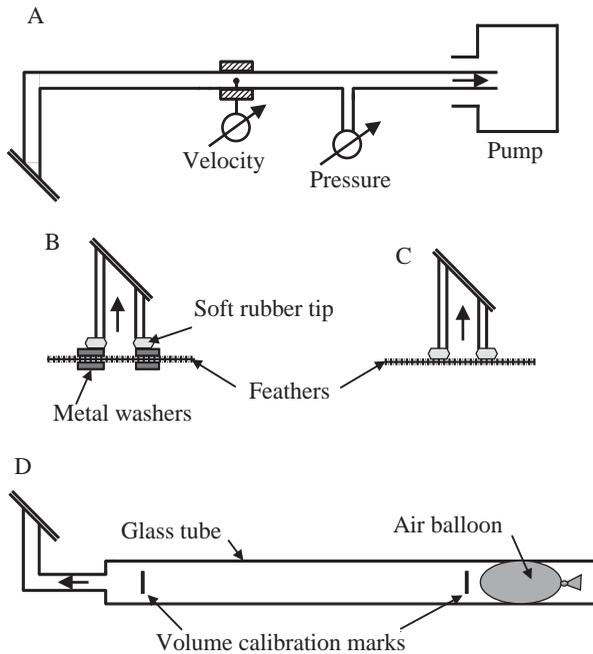


Fig. 2. (A) Experimental arrangement for measuring the air transmissivity of feathers. Suction is produced by a pump, and the pressure and velocity in the tube are measured. (B) In the first method, metal washers were glued onto the feathers, and a measuring tip with a soft rubber tip was placed onto the washers. Measurements were possible in both directions, i.e. from dorsal to ventral and from ventral to dorsal. (C) In the second method, the soft rubber tip was placed directly onto the dorsal surface of the feathers. (D) The glass tube in which a lubricated balloon can glide almost frictionlessly used to measure the dependence of volume flow on flow velocity and pressure. Arrows indicate the direction of air flow.

years old, but the age of the individuals at their death was unknown. The time that had elapsed since the last moult, i.e. the age of the individual feathers, was unknown, although excessive wear of feathers was recorded. All experiments were conducted at room temperature (approximately 22 °C).

To measure transmissivity, air can be blown through or drawn through a feather. The latter method is preferable because it is easier to seal off a particular area of the feather if it is drawn towards a tube rather than pushed away from it by the air current. By drawing air through the feather from ventral to dorsal, one can simulate the air pressure on the ventral surface of the feather that occurs during the downstroke or during soaring flight; air drawn through the feather in the opposite direction simulates the pressure during the fast upstroke that occurs in some birds.

A constant negative pressure (suction) was obtained by placing the open end of a tube into the opening of a suction pump (a commercial vacuum cleaner) (Fig. 2A). Pressure in the tube could be varied by changing the size of the opening of the suction pump and was measured using a Betz manometer (resolution 0.1 mmH₂O, which converts to 0.98 Pa). Velocity in the tube was measured using a thermo-anemometer (Alnor GGA-65; resolution 0.01 m s⁻¹, precision ±0.05 m s⁻¹ in the

range 0.1–0.49 m s⁻¹; not usable below 0.1 m s⁻¹). The anemometer switched off automatically below 0.1 m s⁻¹, so that no data were available for that range.

The opposite end of the tube was applied to the feather, using two methods. In the first method, metal washers were glued onto the ventral and dorsal surfaces of the feathers opposite to each other (Fig. 2B). Uhu plus Sofortfest, a two-component fast-polymerizing epoxy glue, was chosen for its viscosity, so that it would fill in all the gaps under the washers (e.g. between the barbs on the ventral surface) but would not flow appreciably beyond their margins. In this way, the inner diameter of the washers (4.2 mm) defined the area through which air could be drawn. After the washers had been glued onto the feathers, they were checked under a dissecting microscope to ensure that the barbules were still arranged correctly without any disruptions caused by the gluing process and that no excess glue had flowed beyond the margins of the metal washers. The soft rubber tip of the suction tube could be placed tightly onto the washers so that the transmissivity in either direction could be measured accurately and values compared directly. Because gluing of the washers onto the feathers is irreversible and, in addition, very time-consuming, this method was used extensively only for one specimen of a kestrel *Falco tinnunculus*. For this individual, all remiges and coverts were removed and labelled separately to ease handling and to allow checks under the dissecting microscope. This method was also used for control measurements in some other species to establish the reliability of the second method of determining transmissivity (see below).

In the second method, the soft rubber tip of the tube was pushed gently directly onto the dorsal surface of the feathers (Fig. 2C). The ability of the soft rubber tip (inner diameter 4.4 mm²) to seal off the measured area tightly depended on the smoothness of the surface of the feather. In areas (and species) with large friction barbules, or in species with long pennulae (owls, Strigidae), the method proved to be unapplicable. The soft rubber tip also failed to provide a tight seal on the ventral side of the feathers, where the surface is formed by lamellae-like ventral ridges of barbs between which there are large gaps that allow air to be drawn in from the side. The ability of the soft rubber tip to seal off the measuring area also depended on the way in which the tip was placed onto the feather. For this reason, air transmissivity at each location was measured three times. For each individual specimen, the air transmissivity of six feathers was measured: the outermost primary, RP 10 or RP 9 (see Table 2 for nomenclature of feathers); the fifth primary, RP 5; the first secondary, RS 1; the sixth secondary, RS 6; the first upper major secondary covert, TSMaS 1; and the sixth upper major secondary covert, TSMaS 6. In several specimens, some of these feathers were missing or damaged so that no measurements could be taken. For all feathers, the measuring location was situated in the distal third of the inner vane.

To convert the air-speed measurements from the anemometer into a measure of volume flow, a known volume of air was drawn through the apparatus at different air speeds. This was done by attaching the suction tube to a glass tube in which a lightly expanded sealed balloon, lubricated by water

Table 2. *Nomenclature of feathers*

Common name	Scientific name	Abbreviation
Primaries	Remiges primariae	RP 1– <i>n</i>
Secondaries	Remiges secundarii	RS 1– <i>n</i>
Alular remiges	Remiges alulae	RA 1– <i>n</i>
Shoulder feathers	Pterylya humeralis	Pter. hum.
Tail feathers	Rectrices	Rec 1– <i>n</i>
Coverts	Tectrices	T
Coverts of primaries	Prim.	P
Coverts of secondaries	Secund.	S
Major	Maj.	Ma
Median	Med.	Me
Minor	Min.	Mi
Upper	Superiores	S
under	Inferiores	I

As an example, the abbreviation for the sixth upper major primary covert would be TPMaS 6.

The numbering of the feathers follows Lucas & Stettenheim (1972): the primaries are numbered distally (outwards) from the carpal region, the secondaries proximally (inwards) from the carpal region, the alular remiges inwards from the most anterior, the coverts according to their corresponding remiges and the tail feathers from medial to lateral.

and dish-washing detergent, could glide almost frictionlessly (Fig. 2D). On the tube were two markings which delimited a certain volume. By measuring the time taken by the balloon to pass between the two markings in the suction tube at different flow velocities (and at two different pressures), a linear least-squares regression ($y=19.8x-1.9$, $r^2=0.997$, $N=40$) of volume flow *versus* flow velocity was obtained; this regression was used to convert the experimental flow velocity measurements into a measure of volume flow.

In another separate test, we confirmed that (within the pressure range we applied to the bird's feathers, i.e. below 2000 Pa) volume flow Q is proportional to the decrease in pressure ΔP at the resistive element (Fig. 3). Thus, by analogy with Ohm's law for electrical conduction, we can express resistance R as the quotient of pressure drop and volume flow (see Vogel, 1994, p. 290f):

$$R = \Delta P / Q. \quad (1)$$

However, the reciprocal of resistance, i.e. conductance C ,

$$C = Q / \Delta P, \quad (2)$$

characterizes better the quality of interest of the feathers, namely the volume of air passing through at a given pressure. Since conductance is dependent on the cross-sectional area of the resistive element, it seems desirable to divide conductance by the area, which then yields conductivity, or transmissivity T ($\text{m}^3 \text{s}^{-1} \text{N}^{-1}$), as we propose it should be preferably called:

$$C/A = T = Q / (\Delta P \times A). \quad (3)$$

Transmissivity is therefore a variable describing the quality of the feather independently of the test area.

Measurements with the kestrel feathers were performed at two different suction pressures, 390 and 1880 Pa, and transmissivity was calculated from both data sets to increase accuracy. Measurements for the species series could only be performed at the higher pressure (1880 Pa). These pressures were chosen for several reasons. The pressure difference between the ventral and dorsal side of the flight feathers during steady soaring flight is proportional to the wing loading (i.e. the weight of the bird/the area of both outstretched wings). Wing loadings were obtained from various sources (Poole, 1938; Warham, 1977; Rüppell, 1980), and for the birds in the present study wing loadings range from approximately 50 N m^{-2} for buzzards to 150 N m^{-2} for ducks and grebes. However, the pressure acting on the wing during a rapid downstroke can exceed that during soaring flight by several-fold. Taking this into account, a pressure of 390 Pa was taken as an approximation of the physiologically relevant pressure. Measurements were also performed at 1800 Pa to increase the accuracy with which the transmissivity could be calculated. This higher pressure pulled the soft rubber tip of the measuring device more strongly towards the feather and thereby sealed off the area to be measured more efficiently. At the lower pressure of 390 Pa, especially for birds with large friction barbules or long pennulae (see above), the rubber tip often failed to seal tightly and therefore no measurements could be obtained. Although 1880 Pa certainly exceeds the naturally

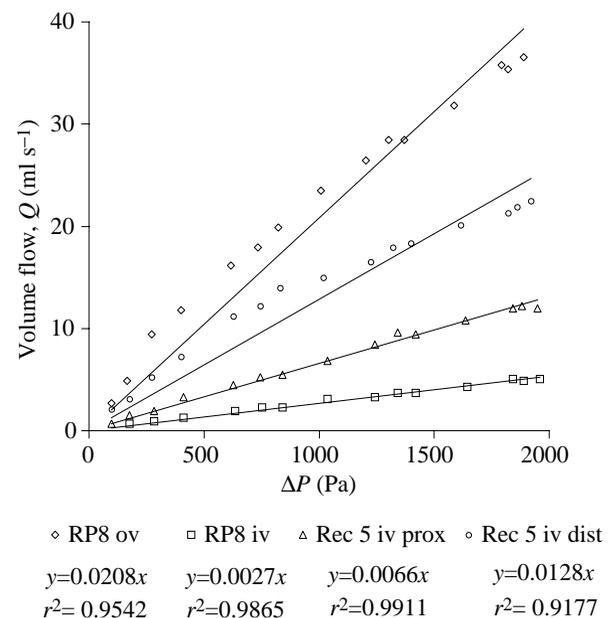


Fig. 3. Relationship between volume flow Q and the pressure difference at the resistive element ΔP . The air transmissivity of four feathers (see Table 2 for abbreviations) was measured using the apparatus shown in Fig. 2. Suction pressure produced by the pump was varied and flow velocity was measured. Volume flow Q was then calculated using the formula obtained in the previous experiment (see Materials and methods). The slope of the least-squares regression lines gives the conductance C of the objects. iv, inner vane; ov, outer vane; prox, proximal; dist, distal.

occurring pressure, the structural stiffness of the feather parts was able to withstand even this excessive force.

Results

Transmissivity of different feathers of a kestrel

The results of the measurements on different feathers of a kestrel are shown in Fig. 4. The transmissivity from dorsal to ventral differs only slightly from that in the opposite direction in all the locations measured. On average, the transmissivity from dorsal to ventral is 10% higher than in the opposite direction. This small difference was nonetheless statistically significant ($P=0.001$, t -test with dependent variables). However, when discussing the functional relevance of this difference, it should be noted that the transmissivities at different locations can vary by an order of magnitude.

The coverts (prefix T, see Table 2) show transmissivities comparable to those of the remiges (prefix R). This holds true for both the inner and outer vanes. This was also true for the median and minor upper coverts and the major under coverts, for which results are not shown because only the inner vanes could be tested for these feathers.

The outer vanes of the remiges and coverts exhibit a significantly higher transmissivity than the corresponding inner

vanes. To illustrate this better, data for the inner and outer vanes of the primaries (RP), the secondaries (RS) and the upper major secondary coverts (TSMaS) were grouped (Fig. 5). There was a highly significant difference in transmissivity between the outer and inner vanes (two-way analysis of variance ANOVA; $P=1.07\times 10^{-10}$). This high significance reflects the fact that, for every single location, the transmissivity of the outer vane exceeded that of the inner vane (see Fig. 4). There was no significant difference in transmissivity among the three groups of feathers, i.e. the primaries, the secondaries and the coverts (Fig. 5).

Transmissivity of feathers of different species

The transmissivity of the inner vanes of feathers from 27 different species were obtained using the second method (see Fig. 2C) with the soft rubber tip of the measuring device applied directly onto the dorsal surface of the feathers. Values ranged from 0.0001 to 0.0005 $\text{m}^3 \text{s}^{-1} \text{N}^{-1}$ and were similar to the values obtained using the more detailed first method for the inner vanes of the kestrel feathers (Fig. 5).

Morphological observations on different feathers of a kestrel

The transmissivity results are supported by the morphological observations on kestrel feathers. The structures

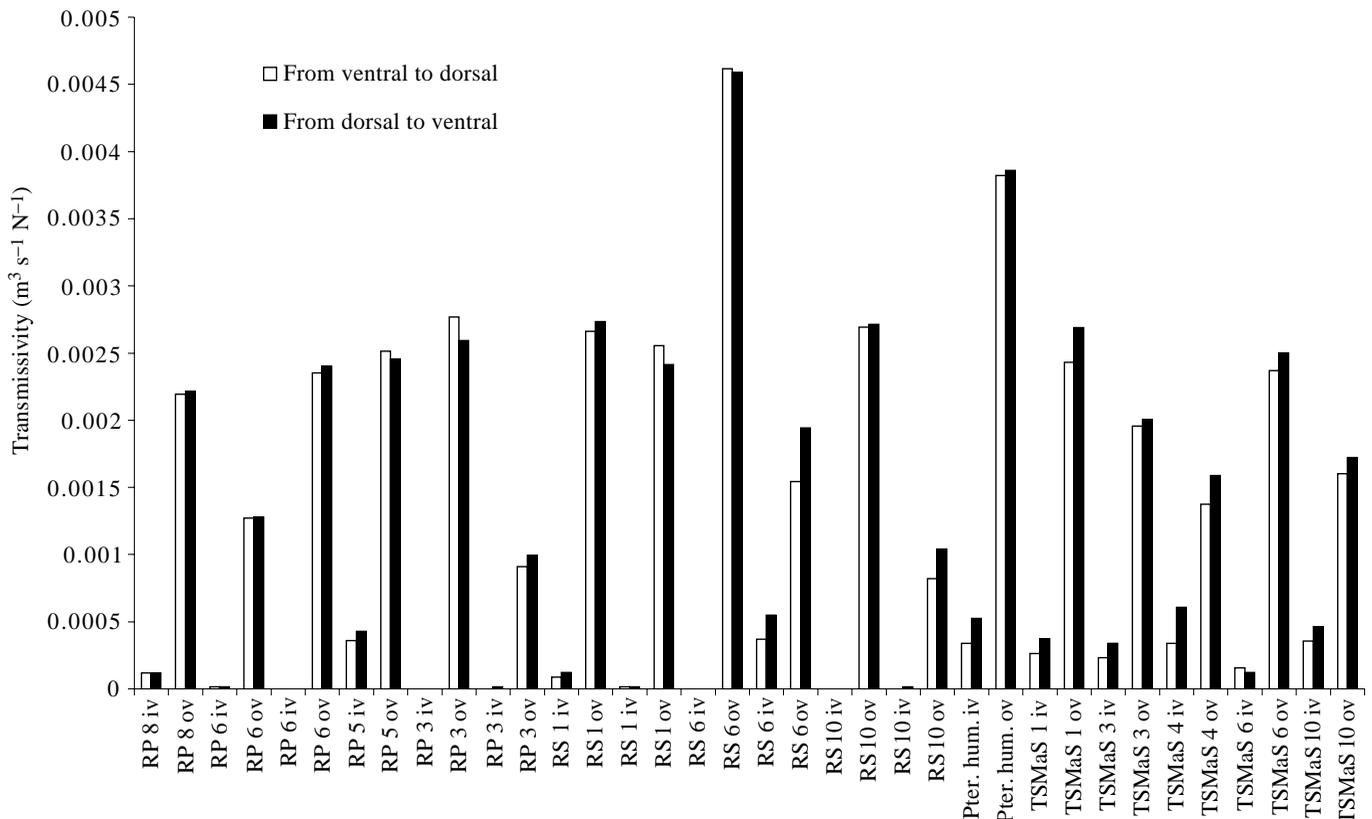


Fig. 4. Transmissivity of the feathers of a kestrel *Falco tinnunculus*. Transmissivity was measured using glued-on metal washers (method 1, see Fig. 2B). Air was drawn through the feathers from ventral to dorsal (open columns) and from dorsal to ventral (filled columns). For each measuring location on the inner vane of a feather, the corresponding location on the outer vane was also measured. Missing values are where transmissivity was too small to be measured with the method used ($<1.34\times 10^{-5} \text{m}^3 \text{s}^{-1} \text{N}^{-1}$). Abbreviations of names of feathers are given in Table 2. iv, inner vane; ov, outer vane.

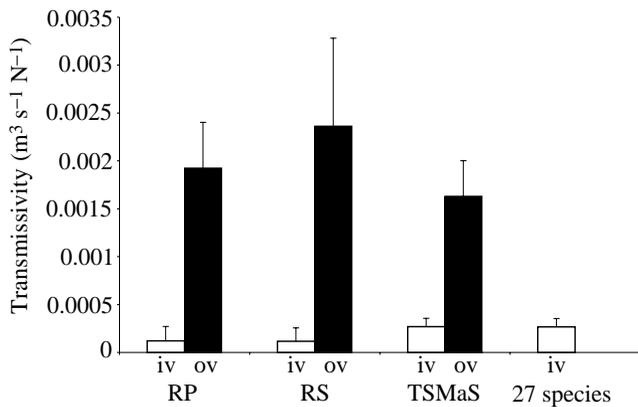


Fig. 5. Transmissivity of groups of feathers of a kestrel *Falco tinnunculus*. Data from Fig. 4 for the primaries (RP), the secondaries (RS) and the upper major secondary coverts (TSMaS) have been grouped. Values are means + s.d. ($N=5$). The mean value for all six feathers for all 27 species is also shown. Only measurements from ventral to dorsal are depicted. iv, inner vane; ov, outer vane.

responsible for the air-tightness of the feather vanes are the ventral margins of both the proximal and distal barbules, which are greatly extended and apposed to the base of the adjacent barbule, thus forming an almost complete, continuous surface (Fig. 6) (for excellent scanning electron micrographs see Dyck, 1985). These structures can be found in the primaries and secondaries and their coverts, in the alula and its coverts, in the feathers of the humeral tract and in the rectrices. The extent of the enlargement of the ventral margin of the barbules varies consistently with the transmissivity, being more pronounced in the inner than in the outer vanes.

Discussion

Our finding that there is only a 10% difference in transmissivity between ventral-to-dorsal and dorsal-to-ventral measurements is in disagreement with the tenfold difference attributed to V. Lougheed by Raspet (1960, p. 193). Because the source of this value could not be located, it can only be speculated that Lougheed used excessive pressure, resulting in the ventral margins of the barbules moving off the adjacent barbule when suction was applied from the ventral side (see Fig. 6). It is conceivable that the slight flexibility of these ventral margins causes them to act like a one-way valve and may account for the 10% difference in transmissivity with airflow direction measured in the present study.

That the coverts have the same transmissivity as the primaries and secondaries is at first somewhat surprising. Coverts are often omitted in discussions of flight feathers or they are treated as body contour feathers. Yet, when the embryonic origin of the coverts is taken into account, it is clear that they are basically small remiges. The feather primordia form during an early stage of ontogeny. The future leading and trailing edges of the wing are still rounded. The primordia of the alar tract start as a row along the future trailing edge. A new row of primordia then forms on each side of the first one

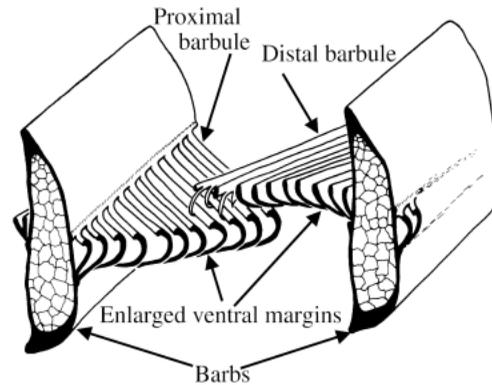


Fig. 6. Diagrammatic representation of two barbules of a feather, cut perpendicularly, to show enlarged ventral margins on both the proximal and distal barbules.

and so on. Subsequently, the wing flattens and those primordia that are located at the edge will become the remiges, while the others become coverts (Lucas and Stettenheim, 1972, pp. 83 and 347).

Only Hempel (1931, p. 684) has stated explicitly that the coverts also feature the enlarged ventral margins of the barbules that are the structural elements that make the feathers air-tight. The functional significance of upper coverts with little transmissivity could be explained as a mechanism of sealing off the area of the aerofoil where the bases of the remiges do not bear vanes. For the underwing coverts, or tectrices aversae, the same functional interpretation holds true. This would lead to a functional explanation for the existence of underwing coverts rather than the commonly used explanation of their embryonic origin.

The most striking result with the most far-reaching aerodynamic implications is the significant difference between the transmissivity of the outer and inner vanes of both the remiges and coverts. The functional significance of this is the requirement for a smooth, continuous wing surface. The outstretched wing of a gliding bird presents a surprisingly smooth surface (Fig. 7) considering that it is made up of separate feathers.

That the remiges are pressed against one another in flight is commonly explained as resulting from the asymmetry of the surface area of the vanes, which causes a tilting moment around the shaft, pushing the larger, inner vane upwards towards the smaller outer vane of the adjacent remex which, in turn, is pushed downwards (Fig. 8A).

In this explanation, it is assumed that the pressure distribution on a single feather is uniform. The forces acting on a single feather in an airflow can be analyzed using the thin wing theory (Azuma, 1992). It can be shown that the aerodynamic centre of the feather (i.e. the point at which the resultant force acts) usually lies close to a quarter-chord, which is the region where the shaft of an outer primary feather is located. However, these results are relevant only to single feathers in an airflow, especially to the winglets, i.e. the non-overlapping tips of the outermost primaries. In a fully



Fig. 7. A brown skua (*Catharacta skua*) in soaring flight illustrating the smooth wing surface (courtesy of Professor I. Rechenberg).

outstretched wing, the feathers overlap to a greater (in the secondaries) or lesser (in the primaries) extent. The area of a feather that is exposed to the air current in an outstretched wing is thus quite different from the case of a single feather. In Fig. 8B, it can be seen for the shaded feather that the area on which negative pressure can act on the upper side is approximately equal on either side of the shaft, so that no tilting moment would be created. Positive pressure can act on the ventral surface, but only in a region distant from the shaft. Because of the flexibility of the vane, this will contribute little to a tilting moment. Depending on the degree of overlap, a

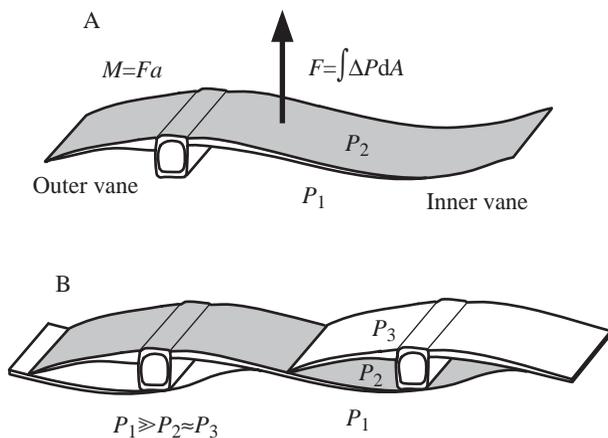


Fig. 8. Diagram illustrating the forces commonly thought to act on a single feather in an air current (A) and on an outstretched wing made up of many feather units (B) in an air current as explained by the pressure gradient that develops due to the different transmissivities of the inner and outer vanes. M is the moment created by the force F times the lever arm a . The force is the integral of the pressure difference ΔP times the area A . P_1 , P_2 and P_3 are pressures at different locations.

tilting moment in the opposite direction would be possible, lifting the outer vane off the underlying inner vane of the adjacent remex.

In this context, the functional significance of the different transmissivity of the outer and inner vanes can be explained as follows. The higher transmissivity of the outer vane allows the pressure on its dorsal side (P_3 in Fig. 8B) to be transmitted to its ventral side (P_2 in Fig. 8B). It has to be kept in mind that the volume of air underneath the outer vane is small, so that a small volume flow through the vane is sufficient to influence the pressure there. A pressure gradient will thus be set up that will result in the formation of a smooth surface on the ventral as well as on the dorsal surface of the wing. One might

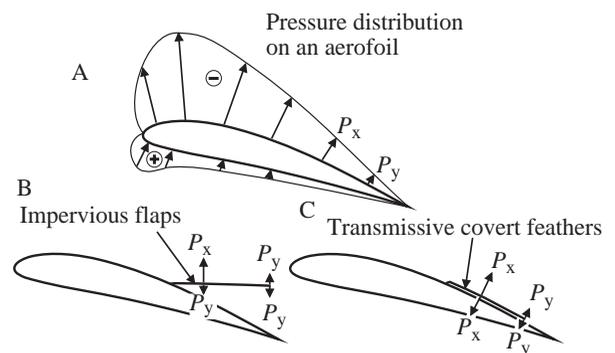


Fig. 9. Pressure distribution on an aerofoil without flaps (A), with impervious flaps (B) and with transmissive covert feathers (C). Minus and plus symbols refer to the pressure difference ΔP , with the size of the arrows indicating the magnitude of the pressure. P_x and P_y are the suction pressures at respective locations on the upper surface. Pressure underneath the impervious flaps will be P_y , whereas pressure underneath transmissive covert feathers will be the same as on the upper surface at each location.

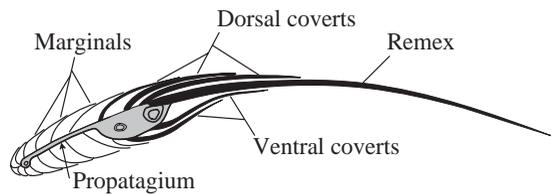


Fig. 10. Diagrammatic section through a bird's wing at the level of the lower arm. The shaded area indicates the impervious parts of the extremity.

visualize this best by thinking of a piece of paper which is pushed against either a grid or a second piece of paper by an air current. It would be difficult to hold the two sheets of paper together because of their identical transmissivity, whereas one sheet could be pushed or drawn firmly against a transmissive grid. In view of this explanation, the fact that the outer vane of a feather is more rigid in the dorsoventral direction than is the inner vane also attains a new significance. In a recent study, Ennos *et al.* (1995) performed mechanical tests on the vanes of the flight feathers of the pigeon *Columba livia*, but unfortunately only the inner vanes were used. It would be interesting to investigate the stiffness of the outer vanes with respect to their function as a holding grid for the adjacent inner vanes.

Another functionally important point arises from the fact that, like the flight feathers, the covert feathers are not completely air-tight. This can also be explained by the requirement for a smooth wing surface. The pressure distribution on an aerofoil is such that on the upper surface the largest suction pressure occurs close to the leading edge and it decreases towards the trailing edge (Fig. 9A).

When an impervious flap is attached at its leading edge to the surface of an aerofoil using impervious tape, the pressure underneath the flap will be the same as that at the trailing edge of the flap (P_y in Fig. 9B), because the space underneath the flap communicates with the surrounding flow at that location. Since the suction pressure on the outer surface of the flap (P_x in Fig. 9B) is higher than that underneath the flap, the pressure difference results in a lifting force that acts to pull the flap off the wing surface. Obviously, this would be detrimental to the aerodynamic qualities of the aerofoil. When a transmissive flap such as a covert feather is attached to the wing (Fig. 9C), the pressure on the outer surface of the flap can be transmitted to the inner side. Note that only a small volume flow is necessary to influence the pressure underneath the flap since there is only a small volume of trapped air. The transmissivity of the covert feathers, although small, therefore allows equalization of the pressure on both sides of the feathers, preventing a pressure difference and the resulting lifting forces.

The transmissivities of the flight feathers and their coverts differ greatly from those of the remaining contour feathers that cover and 'make up' a wing (Fig. 10). The marginals that cover the front part of the wing were not investigated explicitly in our study; preliminary experiments indicated that their transmissivity was too high to be measured using our

experimental apparatus. What consequences does this have for the flow around a wing, especially for the boundary layer? If the marginals are so transmissive, air will constantly seep through these feathers and influence the boundary layer. Indeed, it has been suggested (Horstmann and Quast, 1981) that birds might make use of their porous marginal feathers in making the boundary layer intentionally turbulent in order to avoid detachment of laminar flow. Since birds fly at relatively low Reynolds numbers, at which detachment of laminar flow is almost inevitable and, hence, a serious problem, the advantage of making the boundary layer turbulent is obvious.

The transmissivities of the inner vanes of feathers from 27 species, including two specimens of the kestrel, are similar to those obtained (using the more detailed first method) for the inner vanes of the kestrel (Fig. 5). Therefore, it seems reasonable to use the results of these measurements as a preliminary comparison among the different species. Differences in the transmissivities among the species, if there are any, would be small since the values fall into the same order of magnitude. In order to decide whether there are differences that could be correlated to wing load, flight mode or phylogenetic relationships, further data have to be gathered, preferably using the first method (which is currently being done).

We recorded the wear of the individual feathers studied. The three specimens with excessive wear (peregrine falcon, European buzzard and a great spotted woodpecker) did not have unusually high transmissivity. Because the structural parts that are exposed to wear are not the ones that serve to seal the aerofoil, this lack of correlation between wear and transmissivity was not surprising.

Our transmissivity results agreed with our qualitative morphological observations. Under the dissecting microscope, one could 'guess', within certain limits, the transmissivity of a location. When the coherence of the barbules was somewhat disturbed, it was easy to predict that the transmissivity would be greatly increased. This illustrates nicely that the structural gaps in a perfect intact feather, which are responsible for its transmissivity, must be very small. The earliest observer (Hooke, 1665) and many after him believed that the meshwork of barbules was tight enough to form an impervious surface; however, he underestimated the significance of the low viscosity of air. The distance between barbules in flight feathers shows little variation among birds, ranging from 20 to 40 μm (e.g. Mascha, 1905). Enlargement of the ventral margins of the barbules and their apposition to the bases of adjacent barbules reduces the size of these gaps enough to allow the vanes to function as a relatively impervious surface. The transmissivity of feathers, as measured in the present study, also depends on the density and viscosity of air. Cheer and Koehl (1987) demonstrated convincingly that a given meshwork can act as a paddle or as a rake. Vogel (1983) showed that the viscosity of air had an appreciable effect on the transmissivity of the antenna of a silkworm *Actias luna* although, unfortunately, he did not give the size of the meshwork of the antenna.

From the discussion above, it becomes apparent that our present understanding of both the transmissivity of feathers and its aerodynamic effects is still very limited. Future studies are needed to broaden the data in terms of the transmissivities of different areas of feathers and of intra-individual, intraspecific and interspecific differences. At the same time, aerodynamic investigations on transmissive surfaces should be conducted with emphasis on conditions that are representative for birds, i.e. relatively low Reynolds numbers. By combining these approaches, one can expect to obtain a better understanding of aerodynamics in general and of bird flight in particular.

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