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By Frederic Wood Jones, D.Sc., F.Z.S., F.R.S., Professor of Anatomy in the University of Adelaide.

[From "Transactions of the Royal Society of South Australia," vol. 1., 1926.]





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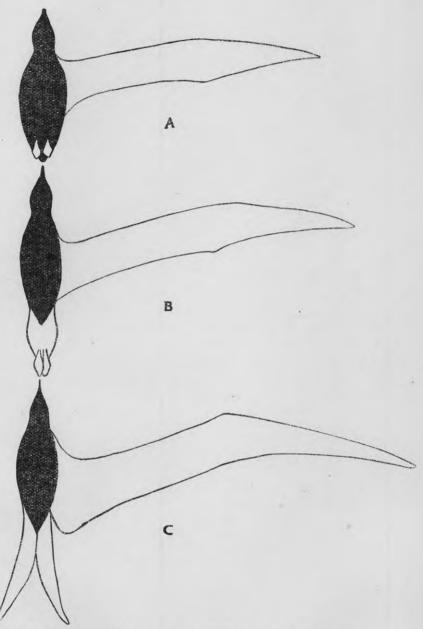
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[Read June 10, 1926.]

It has probably struck every observant ocean traveller that there is a wellmarked distribution of those more or less thorough-going pelagic birds that are encountered upon any protracted sea trip. This sharpness of the definition of distribution is far more pronounced when we travel from Pole to Pole than when the voyage is made more or less along one of the parallels of latitude. It must be a very remarkable experience for anyone to note the birds encountered on an ocean trip from, say, 40° S. latitude to 50° N. latitude. A repetition of the voyage only serves to make the wonder the greater, for there is thrust upon the observer two very obvious facts: (1) that there is a very definite zoning of distribution which is normally but little transgressed, and (2) that there is a repetition of general morphological type at latitudes roughly equidistant north and south of the Equator. If we make such a journey from south to north we first encounter, as the most conspicuous of the pelagic birds, the giant Albatross, and, by a succession of smaller species and the Mollyhawks or Mollymawks of sailors, the passage is made to the larger Gulls; these in their turn drop out and smaller Gulls are encountered until the Equator is passed. Having passed the Equator small Gulls are again encountered, then larger Gulls, and finally Razorbills, Guillemots, Puffins, and Awks. This is only a very rough summary of the types observed on an individual journey. The first question that must naturally arise is: Why do the Albatrosses desert a ship sailing northwards from southern latitudes? During my service on a cable ship, more than twenty years ago, I watched these birds for days on end. They would follow the ship when she steamed about, or sit on the water around her when she was on cable ground. They would glide all day regardless of the speed of the vessel, and, so far as I could learn, regardless of the direction of the wind; moreover, they would do this without altering their elevation or without, as far as one could see on close observation, moving any part of their wings. Save for the projection of their otherwise closely adpressed feet, when they wished to drop to the water to pick up food, their flight appeared to be merely an ability to slide ahead with no other power than their own weight and a presumably instantaneous ability to automatically readjust their planes and alter their cant and poise-largely by movements of the head.

As an Albatross is watched gliding ahead over the deck of a ship steaming fifteen knots, it seems as though the whole bird were rigid; save its head and eyes. It passes ahead and cants its whole body and wings, seemingly without any wing movement, but with a definite, and apparently purposeful, alteration of its head poise, and passes astern in a wide semi-circle high in the air. Almost gliding to sea level astern it comes round in another wide semi-circle—again without apparent wing movement—and overtakes the ship, gliding level above its decks, only to repeat the manoeuvre. In all this there is no flap of the wings—no visible wing movement. To one unskilled in aeronautics it seems as though the bird were a completely satisfactory and vitally adjusted plane, which dictated its planing activities largely by body poise, in which head and neck, rather than wing movements, played the greater part. But it is a thing anyone who has travelled northwards from the "roaring forties" must have noted that,



Diagrams to show the proportion of body to plane area of—A: a Southern Albatross (Diomedia exulans). B: a Northern Albatross (D. nigripes). C: a Mano'-War Bird (Fregetta aquilla). The body length of each diagram is reduced to the same scale.

though when in southern latitudes the Albatross seems to be so completely adapted and so entirely master of its element, it appears to lose its mastery as progress is made northward. One day on a northward journey there will be a dozen Albatrosses planing astern of the ship in perfect mastery of the air, the next there will be fewer, the next morning there will be, maybe, two, or a solitary individual making rather laboured flight. At about the latitude 34° S., before Fremantle is reached, the solitary individual is left flapping behind.

Now it must occur to anyone to ask: Why does the last Albatross desert in this latitude? Why does a straggler, or so, hold on and fly in a laboured fashion and then fall astern? In the first place, it is obviously not because its food supply is lacking. Even if the bird is only depending on the ship as a source of food, it is just as prolific north as it was south of that latitude. Nor can it be the loss of its habitual pelagic food, for, so far as one can see, it has as good a diet from ocean flotsam on the Equator as it has at 40° S. Again, it cannot be that it is getting unduly far from home. Already it is probably thousands of miles from what may be considered its home, and, within the limits of its southern latitude, distance seems to be no object. It seems as though it were merely the travel northwards that was prohibited: there appears to be some factor which forbids it to enter Equatorial regions.

There appears to be a perfect mastery of aerial conditions in the south, a lessening mastery further north, and a positive disability when the journey is made towards the Equator. The last solitary flapping representative seems to tell the story of an inability to adjust flying conditions to an Equatorial

The same facts hold true with regard to the northern representatives (Diomedia nigripes, D. albatrus, and Talassogeron culminatus) of the Albatross, for these birds will follow a ship sailing southwards in the Pacific in the same way that the southern Albatrosses follow from the south in the northward journey. But there is this difference, that the northern representatives range nearer to the Equator. These birds roam along the western coast of North America, and great colonies have their nesting sites on Laysan Island, in latitude 25.40° N. Some species, it is said, notably D. nigripes, even range as far south as the Tropic of Cancer, and one (D. irrorata) even resorts to the Galapagos Islands for its breeding grounds.

Just as the Pacific Gull of the south (Gabianus pacificus) affords a most remarkable parallel to the greater Black-backed Gull (Larus marinus) of the north; so does the northern Sooty Albatross (D. nigripes) show the most striking

general similarity to the southern Phoebetria fuliginosa.

Here, however, there is a remarkable distinction, for whereas in the southern Albatrosses the tail is almost absent, in the northern members (especially in D. nigripes) it is of considerable length, and, moreover, this bird carries its

feet projecting behind the tip of its tail.

In my observations upon the gliding birds that may be observed from the deck of a steamer, I have been unable to confirm a great many statements that have been made from time to time concerning the method and conditions of flight. In particular I have been quite unable to detect certain "wing adjustments" mentioned by Dr. Hankin (On observations of transiently visible movements, "Aeronaut. Journ.," July-Sept., 1915, vol. xix., No. 75, p. 104), and this inability, as I have previously stated, extends to the recognition of the "wing flapping" he has recorded in connection with what I have termed the planing of flying fish. Dr. Hankin has made an effective plea that this power of observing such movements is a matter of highly trained practice; and it is, therefore, easy to assume that other observers have not had sufficient practice or do not possess sufficiently acute vision. Be that as it may, it can hardly be due to any lack of



training or acuity of vision, that I have been quite unable to detect any evidence of the presence of the "soarable air," possessing some special physical quality, which Dr. Hankin has discerned as existing in the wake of a ship. Of this "soarable air" he says (On the Flight of Sea Gulls, "Aeronaut. Journ.," Supra, p. 84): "With rare exceptions, Gulls are only able to soar near sea level in a curiously restricted area on the leeward side of the stern of a steamer. The passage of the steamer has caused some change in the air in virtue of which air otherwise appearing as "unsoarable" now behaves as "soarable air."

I quite agree with Lilienthal ("Zeitschrifé fur Flugtechnik und Motorluftschiffahrt," June, 1914, p. 196) that observations made at sea do not tend to confirm the existence of any specially "soarable" area in the neighbourhood of the wake of a ship, and the fact that sea birds glide about in the wake is merely evidence that they are following a ship in search of food. Indeed, when Dr. Hankin cites as a demonstration of the existence of this "soarable area" the fact that a Gull gliding around the flagstaff of a moving ship, perched on the staff when the ship slowed down, and glided off again when she gathered way, he seems to me to draw an entirely unwarranted inference from his simple observation. In this behaviour of the Gull I see no more evidence of the existence of any specially "soarable area" in the wake of a ship than could be inferred for the existence of a "walkable" area behind a cart because the carter's dog sat down in the road when the vehicle stopped.

From experience gained in a cable ship when lying on cable ground and watching Albatrosses gliding over the sea in all directions without special relation to the stationary vessel, I am forced to agree with Lilienthal in his objection to Hankin's conception of a special "soarable area" in the lee of a moving ship. I am far from denying that birds may take advantage of eddies caused by the wind striking any impediment, but I think that if Hankin's thesis were to be accepted, and the explanation of the gliding of pelagic birds were to be looked for in the presence of specialised air currents, ascending or descending, caused by the ship, the investigation of the question as a whole would be seriously hampered.

Indeed, it may be urged that even Barstow has dismissed the question of bird flight in rather summary fashion when he says, "The smaller birds fly with ease and with a very rapid flapping of the wings; larger birds spend long periods on the wing, but general information indicates that they are soaring birds taking advantage of up currents behind cliffs or a larger steamer" ("Applied Aerodynamics," 1920, p. 8). To this statement it might be objected that ease of flight rapid flapping of the wings, and that to presuppose the presence of a steamer or anything else in the open wastes of the ocean as necessary to the soaring of the Albatross is manifestly incorrect.

I shall therefore regard the soaring and gliding flight of pelagic birds, as I have observed it, as a phenomenon due rather to the morphological adaptation of the bird as an adjusted plane, than to any special and chance condition of "up currents" or "soarable air" caused by impediments to the passage of air across the open ocean.

Regarded in this way, the zoned north and south distribution of the different morphological types of sea birds and the failure of the Albatross to follow the ship into the tropics, must be investigated from the point of view of the mechanics of bird structure correlated to the environment to which it appears to be adapted.

The great Southern Albatross is an extremely heavy bird, weighing as much as 12.7 kilos. (Pettigrew), and it is a bird of rather peculiar form, having wings

which, though long, are very narrow (with a long span but a short chord); moreover, it has practically no tail. It is, in fact, a bird that has a large heavy body and a small plane surface. Indeed, were an Albatross to have the same proportion of plane surface to body weight as has a Swallow, it would need wings with a span of about 40 feet and a chord of 3 feet.

It has repeatedly struck me that the desertion of a ship nearing Equatorial latitudes was accompanied by, if not indeed directly due to, a lessening mastery of the air on the part of the Albatross. It, therefore, appears to be worth inquiring if an Albatross, as a morphological avian type, possesses a ratio of body weight and plane area which makes it adapted to planing flight in what may be termed, in the language of aerodynamics, a definite standard atmosphere. In this case the standard atmosphere would be constituted by a relatively very low temperature and a pressure at about sea level.

Under such conditions the atmosphere is of its maximum density, and therefore has the greatest sustaining power for any body planing in its medium. Is it possible that an Albatross as an adjusted plane is of necessity confined, as far as its planing activities are concerned, within the limits of distribution of its peculiar standard atmosphere, which is characterised by a maximum of density and, therefore, of sustaining power? For the present we may neglect the factor of absolute or aneroid height, for we are dealing only with those pelagic birds which plane at or about sea level, and the temperature of the air need, therefore, alone be considered. With rise of temperature there is a very rapid decrease of density, and therefore a very rapid decrease in the sustaining power of the atmosphere. For a simple statement of this principle I am indebted to Professor Kerr Grant: "The density per unit volume is equal to the weight per unit volume. This varies inversely as the absolute temperature. Thus, the weight at 38° C. (=100° F.): the weight at 0° C. (=32° F.)::273+0°:273+38°=273:311. Thus the buoyancy at 100° F. is diminished, as compared with that at the freezing point, by approximately 4 parts in 31, or 13 per cent. The effect of the higher percentage of water vapour in warm air over the ocean will be to produce an alteration of density in the same direction as that due to temperature. If the air be saturated at both the above temperatures, the loss in buoyancy at the higher temperature may be shown to be approximately 21 per cent." It is therefore obvious that at the Equator the buoyancy of the atmosphere may suffer a diminution of more than 15 per cent. when compared with the conditions prevailing in colder latitudes; and this diminution is, of course, a very considerable one.

In order to carry the investigation a stage further, it is necessary to have some data concerning the body weight and the plane areas of different types of birds, and, fortunately, a very great deal of information upon this subject was gathered by Col. J. D. Fullerton in the First Report of the Aeronautical Society of Great Britain in 1911. Throughout this report wing area is alone given as plane area, and thereby the plane area of the tail is omitted from the calculations. This is an important point. Supposing a bird of a definite morphological type were to be more or less restricted to its zone of standard atmosphere by the relatively small plane area of its wings in proportion to its body weight, it would be possible to increase its plane area by increasing the size of its wings. But with increased size of wings there must be increased musculature for the movement of the wings, and increased musculature entails increased body weight. The flight muscles of a bird constitute a very considerable proportion of its body Weight of body

weight, averaging about 1/6 (Borelli): the formula

M

varying from 13.88 in the Black Kite (Milvus migrans) to 3.21 in a Ring Dove (Calumba palumba), according to Winter. The data for estimating the value of this formula in the Albatross are not available, but for the Common Gull (Larus

 $\frac{W}{M}$ =10.55, according to Legal and Reichel. It is, therefore, obvious that

birds cannot indefinitely enlarge their wing area and that the size of a flying bird must be limited. But though a bird cannot increase the plane area of its wings without increasing its body weight, it can add the very considerable, and adjustable, plane area of the tail, with the involvement of only a very small amount of musculature for its regulation. It would seem likely that this is one of the great purposes of the avian tail. We know that the tails of birds are adapted to many ends: they function—like the feet of the Albatross—as elevators or depressors of the flying bird; it is possible that they are used to a slight extent in lateral steering; like all parts of the plumage of a bird they may be modified as secondary sexual ornaments; but I think it might well be argued that the primary purpose for which they are developed is the provision of an extra plane which may be adjusted in its area and which does not require a great mass of musculature for its adjustment. The omission of the tail plane area in the data available is, therefore, a serious factor, and the results would be rendered far more striking were this factor included in the estimation of the plane area.

In order to arrive at some sort of formula to express the morphological form of a bird as a mechanical aeroplane, we may employ a method adopted by the

Bird Construction Committee and take $\frac{\text{Weight of bird in kilos}}{\text{Area of wing planes in sq. metres}} = \frac{W}{\text{W.A}}$ but it must be remembered that the full expression would be $\frac{W}{\text{Total plane area}} = \frac{W}{\text{P.A}}$ for the presentation of which we have as yet no data. In the case of the Albatross the value of $\frac{W}{W.A}$ is practically equivalent to $\frac{W}{P.A}$ since the plane area of the tail is almost negligible, but in the case of the Gulls, and especially so with

the smaller members, we must remember that the $ratio \frac{W}{W.A}$ is considerably larger W than -

P.A Taking those cases for which we have sufficient data, the formula $\frac{W}{W.A}$ in various pelagic birds is shown below.

TA	LE I.	
Species.	$\frac{W}{W.A}$	
Albatross (Diomedia exulans) Giant Petrel (Procellaria gigantea) Herring Gull (Larus argentatus) Common Gull (Larus canus) Black-headed Gull (Larus ridibundus	9.6, simp 4.81, avera 4.67, avera	age of 3 observations le observation age of 8 observations age of 5 observations age of 3 observations

It is therefore obvious that, even neglecting the tail plane area present in the Gulls included in the list, the plane area of the Black-headed Gull is vastly larger relative to the body weight, than is the plane area of the Albatross. I do not doubt that could the data for the whole series of pelagic birds encountered in a

direct line from Pole to Pole be collected, we should see a fall in the value of $\frac{W}{W.A}$

from South Pole to Equator and a rise from Equator to North Pole; the alteration being due in these birds that plane at sea level to the temperature and, therefore, the density of the air of the zones which they frequent.

It will be at once objected that there are many birds, which fly at or about sea level, that do not have a very remarkably restricted geographical range, even when that range is considered in the terms of temperature zones.

The answer to this criticism is that, although a bird may have, relatively to its weight, too small a plane area to sustain itself in gliding or soaring flight in a warm, and therefore less dense, atmosphere, a bird with a relatively large plane area will be able to use both warm and cold atmospheres at or near sea level. It is the small-planed, heavy bird that will show limitations of distribution. It must be remembered that the analogies between a bird in soaring or gliding flight and an aeroplane cannot be carried to extremes. In an aeroplane the ratio of body weight to plane area is fixed-it cannot increase its plane area when it encounters a less dense atmosphere, caused either by altitude or temperature; but it can increase its "lift," and so compensate for the loss of density, by increasing its speed by virtue of the added revolutions of its air screw. A bird cannot do this. If adjusted as a plane to a dense standard atmosphere it must cease to act as a plane and resort to laborious flapping in a rare atmosphere; or if it be a bird which possesses a sufficient tail it can increase its plane area by spreading its tail. For the practically tailless birds like the Albatross of the south or the Puffins, Razorbills, Guillemots, and Awks of the north, it is easy to see how their inadequate plane area and their relatively large heavy bodies have dictated a restricted range in southerly or northerly regions of cold air.

The question of size in birds, when it is thus considered merely as a part of a necessary relation between body weight and plane area, becomes a very interesting one. A rapacious bird must necessarily be a bird of some size in order to overcome the smaller kinds, and it is fortunate that among the class of pelagic gliders there has been developed a group of rapacious birds of very considerable size and of very wide tropical range. In the Frigate or Man-o'-War Birds (Fregetta) we have birds large enough to overcome the smaller pelagic birds that live in the presumably rarer air of the Equatorial zone, and which, moreover, need to soar at considerable altitudes. Unfortunately, I have been unable to obtain any data concerning the weight and plane areas of the Frigate Birds; but I have been compensated in this by the opportunity of seeing the very instructive exhibition of flying birds in the Bird Hall of the New York Museum of Natural History. In this hall there are exhibited, suspended from the lofty ceiling, various birds with their wings extended in the natural position of flight. No more instructive exhibit could be made to demonstrate the small, light body and vast wing and tail plane areas of the Frigate Birds of the warm tropical airs and the large heavy body and restricted wing, and absent tail plane areas of the Albatross of the cold southern seas.

Again, other things being equal, a bird that habitually conducts its planing operations at great altitudes will need a larger plane area than one that is fitted to plane at sea level, and the contrast of a Condor with an Albatross is instructive

in this respect. A Condor (Sarcorhampus grypus) of the same weight as an Albatross has, according to the data given by Loughreed, a wing area twice as large, and an additional tail plane area into the bargain.

So far, only those birds that carry out most of the evolutions of flight by planing, soaring, or gliding have been considered, and it is not proposed to carry the inquiry into the more complicated questions of the adjustment of those birds which progress by varied forms of wing flapping.

Nevertheless, there is sufficient data to indicate that what might be termed

a general utility bird, which progressed by some method of flapping, has the $\frac{W}{W.A}$

ratio in the region of 4, and the additional benefit of an adjustable tail: such a combination is seen in the common Sparrow. Again, several very interesting problems arise in connection with members of avian families which inhabit

extremely different temperature zones. In the Northern Whooper Swan the $\frac{W}{W.A}$

ratio is as high as 21.3, and here it is very evident that an instructive comparison could be made with the Black Swan of Australia; but, unfortunately, no data are available for this bird. In the northern Ducks, again, the ratio is high, averaging about 12, and it is possible that in the Ducks of the warmer parts of the world some diminution of this ratio might be found.

These and other problems of avian structure must, however, await future investigation, since at the present time there are no data upon which conclusions could be justly based.

There is, however, one very remarkable phenomenon that cannot be dismissed in this way. We have seen that in passing from the Equator towards either Pole very much the same series of avian types is encountered as successive zones of temperature are traversed. One of the most astonishing features of this north and south parallelism is the extraordinary similarity of certain Gulls of comparable northern and southern latitudes, and of the most striking pairs of parallels I would instance the Great Black-backed Gull (Larus marinus) of Northern Europe and the southern Great Black-backed Gull or Pacific Gull (Gabianus pacificus) of the Australian coasts. There is surely food for reflection in the development of these two similar species, representatives of different genera in similar habitats. Both Larus marinus and Gabianus pacificus are on the road to what may be termed the heavy-bodied polar birds, but both have ample wing plane area. Towards the Poles, in the dense colder air, the wing plane area relative to the body weight diminishes, the birds still being efficient gliders in their standard atmospheres with considerably reduced planes. The large-bodied birds have relatively smaller wings, and the curious fact is that this tendency for wing area to decrease relatively to body weight culminates at both Poles in the production of flightless birds—the southern Penguins and their extraordinary parallels, the northern Awks.

At the present time it does not seem possible to go beyond mere speculation in this matter; but it would appear, at first sight, to be a remarkable train of events that could lead to a reduction of plane area owing to the increasing density of the supporting medium, and finally to such a degree of reduction as to render flight impossible. We seem to be face to face with a definite trend of morphological adaptation—the diminution of plane area relative to body weight, which