

There were some deviations which presumably are due to species, individual, age or other differences.

3. Evidence is presented which indicates that densities of the egg and of the shell are functions of egg volume.

4. Shell thickness decreases with a decrease in egg volume. The plot of $\log T_s$ against $\log V$ is represented fairly well by a straight line implying that

$$T_s = c V^b$$

where c and b are constants to be determined.

5. Percentage shell, percentage yolk, percentage albumen, and percentage shell membrane are similar functions of egg volume.

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FUNCTIONAL ASPECTS OF THE INNER VANE OF REMIGES

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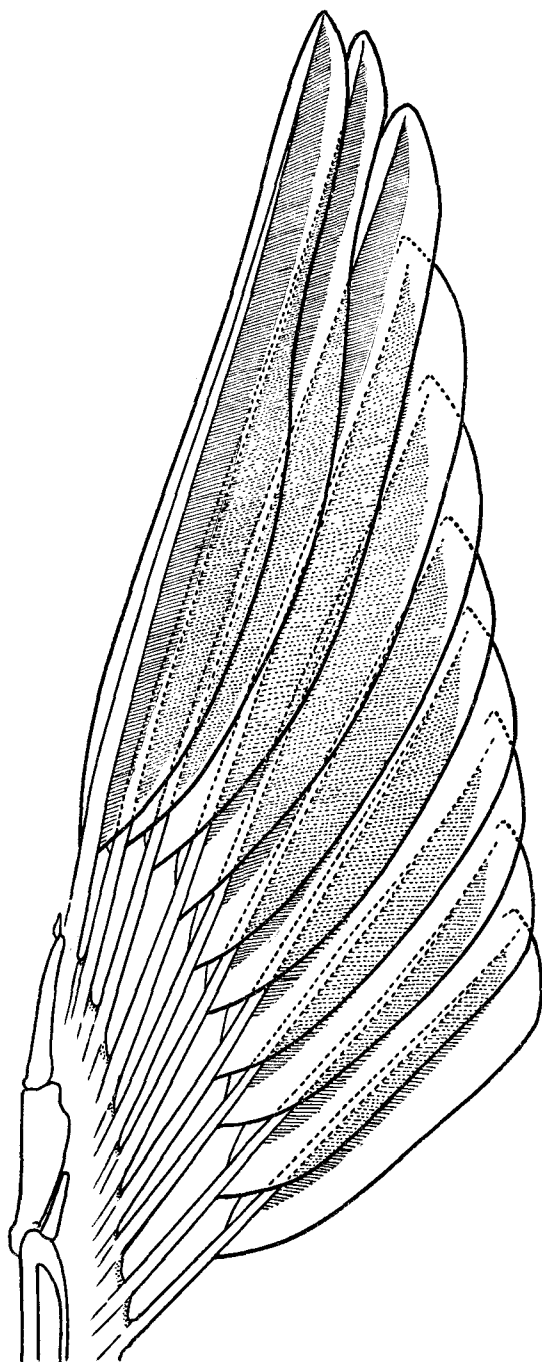
Plate 3, upper figure

THE perfection of bird flight has long been a subject of wonder, and the structure of the wings which make such flight possible has stimulated much research. Nevertheless, the detailed perfection of wing structure is not yet adequately understood. The purpose of this

paper is to discuss further a particular functional condition of the primary feathers of the wing. In certain birds, notably Anseriformes and some Galliformes, part of the inner vane of the primaries (and occasionally to some extent that of secondaries) is exceptionally stiffened. As Chandler (1916, p. 327) has written, there is a great development of the basal one-third to two-thirds of the ventral ridge of each ramus into a broad, thin, filmlike expansion. Each expansion extends over and presses against the ramus in front of it. This produces a conspicuous macroscopic effect on the ventral surface of the feather, giving that portion of the inner vane involved a shiny, glazed appearance (Plate 3, upper figure).

The condition just described has long been known. It is mentioned by Wray (1887, p. 421), but Ahlborn (1896, p. 20) appears to have been the first to publish an adequate description. Mascha (1905, pp. 1-30) further illustrates and compares the condition in various birds. Stubbs (1910, p. 329), though thinking the condition had not been described, gives clear illustrations and additional information. Chandler (1916, pp. 243-446) has further described such feather structure. All of these authors have contributed to the knowledge of the occurrence of the visibly stiffened vanes of primaries. Supplemented by my own investigations, the following birds may be listed as markedly exhibiting this condition: *Diomedea*, all Anseriformes (although nearly absent in *Erismatura*), eagles (*Aquila*), many Galliformes (*Dendragapus*, *Lagopus*, *Tympanuchus*, *Centrocercus*, *Perdix*, *Pucrasia*, *Phasianus*, *Chrysolophus*, and *Meleagris*) and certain owls (*Bubo maximus* and *Nyctea*). The modification is present in the Galliformes in all the Tetraonidae examined and certain of the Phasianinae. It is lacking in all the Odontophorinae examined (*Oreortyx*, *Callipepla*, *Lophortyx*, *Colinus*, and *Odontophorus*), in most of the Phasianinae (*Alectoris*, *Francolinus*, *Pternistes*, *Coturnix*, *Rollulus*, *Bambusicola*, *Tragopan*, *Crossoptilon*, *Gennaeus*, *Lophura*, *Gallus*, *Polyplectron*, and *Argusianus*), and in *Numida* and *Opisthocomus*. In the albatrosses, eagles, and owls the modification is marked near the base of the barbs but does not extend very far along them. Intermediate conditions are found in other birds too, as in *Grus*, but the ready visibility of the greater modification is unmistakable. A curious but not strictly comparable stiffening of the inner vane of a region of the primaries of adult males of *Cnipodectes*, a Central and South American tyrannid, has been described by Zimmer (1939, pp. 110-12).

The functional significance of the described modification is con-



TEXT-FIG. 1.—Ventral view of the left wing primaries of the Black Brant (*Branta bernicla nigricans*), times six-tenths. Traced and drawn from a dried specimen. The areas of stiffened rami on the primaries are shown by striations of solid lines when the stiffened area is visible, but striations of dotted lines when the area is covered by the inner vane of the preceding feather. It can be seen how the stiffened areas extend approximately from the shaft of one primary to that of the next, thus strengthening this feather region which must stand heavy air-pressure.

sidered by Mascha (1905, p. 11). He states that ". . . the secondary quills [barbs] are highest and as a consequence the feather vane the strongest and most capable of resistance where the greatest force is to be withstood." Apparently no author has stated that the overcurving of the ventral ridges of barbs must effectively close the gaps between the barbs especially when air is pushing against them. Furthermore, the relations between remiges, and the correlation of the modification with habits or types of flight, seem not to have been considered. The present paper is concerned chiefly with these latter problems. The effects of domestication, especially in view of the belief that domestication reduces specialization, is also discussed.

I gratefully acknowledge the use of the specimens of the Museum of Vertebrate Zoology of the University of California, directed by Dr. Alden H. Miller, in determining the phylogenetic occurrence of the modified wing feathers.

INTERRELATION OF PRIMARIES

Although many species have been studied with regard to modified primary barbs, it is convenient to choose one species as an example. The Black Brant (*Branta bernicla nigricans*) well serves as such an example because it, like the Anseriformes as a whole, has the modification highly developed (Text-fig. 1).

The barbs of the inner vanes of all the primaries are modified although modification is most marked on the outermost primaries and becomes least marked on the innermost ones. This is what might be expected from a functional point of view because the distal primaries (having a greater lever arm) necessarily strike the air with greater speed and meet with greater resistance.

The extent of the modification in the individual primaries seems most closely correlated with the overlapping of the primaries. As Text-fig. 1 shows, the shaft of each primary fits approximately above the outer margin of modified barbs of the preceding primary. This is true when the primaries are in the typical position for powerful flight, but less true when the primaries are more closed as in gliding or more open as in alighting. With the exception of the first primary, the modified area of the barbs of each remex is covered ventrally by the unstiffened margin of the inner vane of the preceding remex. The stiffening of the inner vane of the first primary, as might be expected from the fact that this area is directly exposed to air pressure, is definitely greater than that of the vanes of other primaries. The resistance of the latter is very effective, however, because air

pressure forces the overlapping margins of inner vanes close against and medial to the over-lying stiffened area. The outer vanes become stiffer and firmer in outer primaries, the elasticity of the barbs helping to keep them in order (Mascha, 1905, p. 10). The outer vane of the first primary, being the only outer vane completely exposed, is decidedly the most stiffened. Its resistance is augmented by extreme narrowness due to the barbs being set at a much smaller angle to the shaft (compare Text-fig. 1 and Plate 3).

CORRELATION OF OCCURRENCE AND FLIGHT

The markedly different, although intergrading, types of flight in birds have been correlated with lengths of wing bones by Böker (1927). He has given the useful name *Flutterflug* to the rapid-whirring type of flight characteristic of the generally short-winged Anseriformes and Galliformes. The study of Poole (1938) comparing wing areas to weights of birds shows the wing areas of Anseriformes and certain Galliformes to be relatively much smaller than in birds lacking *Flutterflug* flight. Stiffened inner vanes of the primaries thus appear to be correlated both with the type of flight and with short length or small area of wings. The adaptive value of such stiffening, already discussed in regard to the individual wing and primaries, is again indicated in that *Flutterflug* flight causes more air pressure against the wings. Adequate resistance to this pressure must be necessary for efficient flight.

Some species, particularly grebes and some Galliformes (such as quail), have rapid-whirring flight and small wing area (Poole, 1938), but lack a stiffening of the vanes of primaries. Possibly their wings are adapted toward the same end by less noticeable modifications, or they may be less efficient as in having less power of sustained flight. Certain other birds, lacking *Flutterflug* flight, show a marked stiffening of vanes. Moreover, these birds, as well as certain owls (including *Nyctea nyctea* and *Bubo maximus*) and Falconiformes (including *Aquila*), have relatively large wing areas. In some such cases, as with *Aquila* and *Diomedea*, particular habits may reflect a need for stiffened wing vanes. The diving of the eagle with the accompanying great stress on wing feathers when checking speed, and the vigorous flapping necessitated by the albatross in taking off from the water, seem to be such habits. Lastly, in these species, and others such as *Grus*, having stiffened inner vanes but not whirring flight there is a tendency for the birds to be large and heavy. Wing areas listed by Poole (1938) show a probably correlated tendency

for large birds to have smaller relative wing areas. Small birds, as quail, even having whirring flight probably have less strain on their wings just because of this size factor.

The Ruddy Duck (*Erismatura*) appears to be the only one of the Anseriformes lacking marked stiffening of the inner vanes of the primaries. This is of special interest because *Erismatura* is considered to belong to a group, the Erismaturinae, which is primitive in certain respects. This may confirm a functional explanation of the stiffened vane area, suggesting that the condition is an adaptation which developed as the Anseriformes became increasingly specialized.

On the basis of the rather uniform occurrence of the modified primary vanes in the two not closely related orders, Anseriformes and Galliformes, we may consider this condition as an example of parallel adaptation meeting similar needs. The very similar form of the modification (i. e., the expansion of the ventral ridges of the rami) in these birds is of special interest because parallel adaptation is typically accomplished by slightly different modifications toward the same function. The several types of modification of the barbs of rectrices of tree-trunk foraging birds which use the tail for support, serve as an example (Richardson, 1942). It is to be pointed out, too, that the present adaptive condition and its need are generally associated with birds having relatively small wing areas. Apparently, then, similar types of flight and relative wing areas have resulted in parallel adaptation in the feather structure.

EFFECT OF DOMESTICATION

Stiffened inner vanes of primaries were found to be present in domestic ducks, geese, and turkeys. In the several hundred turkey primaries examined, for example, the modification seemed to be just as marked and microscopically the same as in wild birds. We may accordingly consider this condition of the primaries as an adaptation which is retained in domestic birds but probably has neither a beneficial nor a detrimental effect. In contrast to this, other adaptations, such as the length of the wing of ducks or the length of the hind leg of rabbits, show, according to Darwin (1876, vol. 1, pp. 135 and 300) and Holliger (1916, p. 489), marked reduction under domestication. Selective breeding would not encourage such reduction nor could natural selection operate to reduce adaptations now possibly disadvantageous. A Lamarckian theory of disuse or lack of exercise as proposed by Darwin (1876) seems to afford the best explanation but a mechanism for such a theory is not known. For a

further understanding of the whole problem we should study how much modification of different types of adaptations can take place during the development of an individual animal under conditions in which the adaptations are not used.

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