THE SIZE OF THE OLFACTORY BULB IN 108 SPECIES OF BIRDS

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FOR at least 150 years anatomists (Meckel, 1816) and ornithologists (Audubon, 1831) have been interested in the olfactory sense of birds. Only within the last decade, however, have physiological experiments definitely shown that in some species of birds the chemoreceptors of the olfactory nerve respond to airborne odors (Michelsen, 1959; Tucker, 1965; Wenzel, 1965). In the intervening century or more, much rather fruitless discussion has ensued as to whether or not "birds have a sense of smell." The many field observations and maze experiments were not sufficiently controlled to give convincing evidence.

This communication brings together some of the morphological evidence for olfactory function in birds, first the comparative studies of the olfactory chambers in the nasal fossa (Bang, 1960–1966) and second, measurements of the comparative sizes of the olfactory bulbs in different species of birds (Cobb, 1960*a*, 1960*b*). The significance of such measurements rests on the general assumption that increase in size of a part of the brain indicates increase in function. As the different measurements and the comparative anatomy have been published in scattered papers, mostly in medical or morphological, not in ornithological journals, it seems worthwhile to bring these and a number of new observations together for ornithologists.

Turner (1891) wrote a long paper on the subject of the size of the olfactory bulbs in various birds. Unfortunately he did not describe his method clearly, so we cannot compare his measurements to ours. He pointed out that in a number of species of passerine birds, the two olfactory bulbs are fused into a small midline organ. He lists 26 species that had such single bulbs. These he found among what he calls the "higher groups," and adds that "the lobes are fused and almost completely imbedded in the prosencephalon." Our observations do not agree with this. Many species have paired bulbs that lie close together beneath the tips of the hemispheres, some even joined by an overlying connective tissue sheath, but microscopic examination of some of these has shown true fusion into a single bulb only in *Parus atricapillus*, *Passer domesticus*, and six fringillids. These are marked with an asterisk in Table 1.

Figure 1 shows that the anatomical relations of the olfactory bulbs differ widely from species to species. In some the bulbs are anterior to the frontal tips of the hemispheres and are quite separate, in others they are anterior but lie close to each other. In many species they lie beneath the anterior tips of the hemispheres, close together in some and quite separate

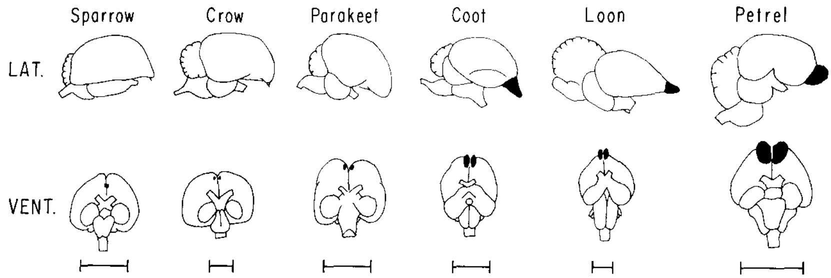

Figure 1. Anatomy of the olfactory bulb in six avian families.

in others. The most extreme condition is a true fusion of the two bulbs into a single midline bulb. In some very small birds where the bulbs are close together, it is difficult to say whether or not they have fused without sectioning and microscopic examination. Krabbe (1952) points out that where the two bulbs have fused, this takes place late in embryological development, so that variation in the final adult stage is to be expected.

In figuring the diameter of the fused bulb to compare with the diameter of the hemisphere, it was thought more significant to take *half* the diameter of the single bulb to use in computing the ratio, as this emphasizes the smallness of the olfactory bulb in these species.

Our method of estimating the comparative size of the bulb in different species is to measure with a millimeter ruler under a dissecting microscope when necessary the greatest diameter (no matter in what axis) of one olfactory bulb and the greatest diameter (no matter in what axis) of the corresponding cerebral hemisphere. The ratio of the former to the latter is expressed in per cent. For example, in the pigeon the bulb diameter averages 2 mm and the hemisphere diameter 11 mm. The fraction 2/11 equals 18/100 so the diameter of the bulb is 18% of that of the hemisphere.

The difficulty of measuring accurately the "longest diameter" of organs that are not spherical is obvious. Choosing the point where olfactory bulb merges into stalk and nerve is arbitrary in gross specimens. Some groups of birds (e.g., the Rallidae) have long, oval bulbs and their cerebral hemispheres are not elongated, so the diameter ratio gives an impression that the bulb is larger than it actually is. With these sources of error in mind, we grant that our ratio is a rough approximation, useful only in a general survey. Weighing the parts of the brain would certainly be better, but dissecting the parts out from formalin-fixed specimens is not an accurate procedure and spoils the whole brain for microscopic study. Estimates of the volumes of different parts of the brain can be made from serial sections, but large errors, difficult to estimate, come with fixation and embedding. The method we use is simple and we believe that it gives a significant ratio, but it cannot be said to represent accurately either volume or mass of the olfactory bulb or hemisphere.

The list follows:

TABLE 1

COMPARISON OF DIAMETERS OF OLFACTORY BULBS AND CEREBRAL HEMISPHERES[1]

ORDER and species	*Diam. bulb mm*	*Diam. hemi. mm*	*Ratio per cent*	*No. of specim.*
APTERYGIFORMES Ratio 34				
Kiwi *Apteryx australia*	12.0	35.0	34.0	1
PROCELLARIIFORMES Mean ratio 29				
Snow Petrel *Pagodroma nivea*	6.7	18.0	37.0	2
Wilson's petrel *Oceanites oceanicus*	3.6	10.8	33.0	4
Wedge-tailed Shearwater *Puffinus pacificus*	5.5	17.8	30.0	2
Greater Shearwater *Puffinus gravis*	6.0	20.0	30.0	1
Dove Prion *Pachyptila desolata*	4.1	14.0	29.5	1
Black-footed Albatross *Diomedea nigripes*	8.0	28.0	29.0	2
California Shearwater *Puffinus opisthomelas*	5.0	17.0	29.0	1
Cape Pigeon *Daption capensis*	5.5	20.0	27.5	1
Fulmar *Fulmarus glacialis*	5.7	21.0	27.0	2
Diving Petrel *Pelecanoides georgicus*	2.0	11.3	18.0	1
PODICIPEDIFORMES Mean ratio 24.5				
Horned Grebe *Podiceps auritus*	4.0	15.0	27.0	1
Little Grebe *Podiceps ruficollis*	3.0	13.5	22.0	2
CAPRIMULGIFORMES Mean ratio 23.8				
Whip-poor-will *Caprimulgus vociferus*	2.5	10.0	25.0	1
Oilbird *Steatornis caripensis*	3.7	15.0	23.0	1
Indian Nightjar *Caprimulgus asiaticus*	2.2	10.0	22.0	2
GRUIFORMES Mean ratio 22.2				
Tasmanian Water-hen *Tribonyx mortierii*	4.0	15.3	26.0	5
Virginia Rail *Rallus limicola*	3.2	12.5	25.6	1
Indian Coot *Fulica atra*	4.3	17.3	25.0	2
Black-tailed Water-hen *Tribonyx ventralis*	4.3	18.0	24.0	4
Weka *Gallirallus australis*	4.6	19.0	24.0	1
American Coot *Fulica americana*	4.0	17.0	24.0	2
Ruddy Crake *Porzana fusca*	2.5	10.8	23.0	2
Pukeko *Porphyrio poliocephalus*	4.6	19.7	23.0	4
White-breasted Water-hen *Amaurornis phoenicurus*	3.5	15.5	23.0	5
Purple Moorhen *Porphyrio porphyrio*	4.0	19.0	21.0	2
Gallinule *Gallinula chloropus*	3.0	15.0	20.0	1
Clapper Rail *Rallus longirostris*	3.0	15.0	20.0	1
King Rail *Rallus elegans*	3.2	16.0	20.0	1
Button Quail *Turnix suscitator*	1.0	8.0	12.5	1
CICONIIFORMES Mean ratio 20.7				
Pigmy Flamingo *Phoeniconaias minor*	5.0	23.0	21.7	2
Night Heron *Nycticorax nycticorax*	4.3	21.3	20.0	2

[1] The ratio of the bulb to the hemisphere is expressed as a per cent. The number of specimens measured is noted in the last column; when more than one specimen of a species was measured, the averaged measurements are given. Orders and species within orders are arranged from the larger to the smaller ratios, except for the Hoatzin. Species with fused bulbs are marked with an asterisk.

TABLE 1 (CONTINUED)

ORDER and species	*Diam. bulb mm*	*Diam. hemi. mm*	*Ratio per cent*	*No. of specim.*
GAVIIFORMES Ratio 20				
Loon *Gavia immer*	5.0	25.0	20.0	1
COLUMBIFORMES Mean ratio 20				
Wild Blue Rock Pigeon *Columba livia*	2.9	13.7	22.0	3
Domestic Rock Pigeon *Columba livia*	2.0	11.0	18.0	1
CUCULIFORMES Mean ratio 19.5				
Yellow-billed Cuckoo *Coccyzus americanus*	1.9	9.0	21.0	1
Brainfever Bird *Cuculus varius*	3.0	14.5	20.0	1
Koel *Eudynamis scolopacea*	3.1	16.0	19.0	4
Coucal *Centropus sinensis*	3.0	16.4	18.0	3
ANSERIFORMES Mean ratio 19.4				
Eider *Polysticta stelleri*	4.5	19.0	23.7	1
Green-winged Teal *Anas carolinensis*	3.0	15.0	20.0	1
Mallard *Anas platyrhynchos*	4.0	21.0	19.0	1
Red-breasted Merganser *Mergus serrator*	3.0	20.0	15.0	1
APODIFORMES Mean ratio 18.8				
Chimney Swift *Chaetura pelagica*	1.5	8.0	19.0	1
Common Swift *Apus affinis*	1.4	7.5	18.7	2
Palm Swift *Cypsiurus parvus*	1.4	7.5	18.7	1
STRIGIFORMES Mean ratio 18.5				
Short-eared Owl *Asio flammeus*	3.5	18.0	19.0	1
Great Horned Owl *Bubo virginianus*	4.5	25.0	18.0	1
FALCONIFORMES Mean ratio 18.0				
Turkey Vulture *Cathartes aura*	6.0	24.0	28.7	1
Black Vulture *Coragyps atratus*	4.0	24.0	17.0	1
Pariah Kite *Milvus migrans*	3.0	20.0	15.0	1
Osprey *Pandion haliaetus*	3.0	21.0	14.0	1
Brahminy Kite *Haliastur indus*	2.5	20.0	12.5	1
SPHENISCIFORMES Ratio 17				
Adélie Penguin *Pygoscelis adeliae*	5.0	30.0	17.0	1
CHARADRIIFORMES Mean ratio 16.4				
Redwattled Lapwing *Vanellus indicus*	3.1	14.1	22.0	2
Pheasant-tailed Jacana *Hydrophasianus chirurgus*	2.6	13.0	20.0	6
Woodcock *Philohela minor*	2.5	15.0	17.0	2
Herring Gull *Larus argentatus*	3.0	19.0	16.0	3
Semipalmated Plover *Charadrius semipalmatus*	1.5	10.0	15.0	1
Dowitcher *Limnodromus griseus*	2.0	13.0	15.0	1
Thick-billed Murre *Uria lomvia*	2.7	18.0	15.0	1
Wilson's Snipe *Capella gallinago*	2.0	14.0	14.0	5
Puffin *Fratercula arctica*	2.5	18.0	13.9	1
CORACIIFORMES Mean ratio 14.5				
Bee Eater *Merops orientalis*	1.5	8.0	18.7	2
Belted Kingfisher *Megaceryle alcyon*	2.3	13.5	17.0	2
Hoopoe *Upupa epops*	2.0	13.6	14.6	1
Roller *Coracias benghalensis*	2.0	14.0	14.0	1
Hornbill *Bicanistes subcylidricus*	2.0	26.0	8.0	1

TABLE 1 (CONTINUED)

ORDER and species	*Diam. bulb mm*	*Diam. hemi. mm*	*Ratio per cent*	*No. of specim.*
GALLIFORMES Mean ratio 14.2				
Domestic Fowl *Gallus gallus*	2.0	13.0	15.0	1
Ruffed Grouse *Bonasa umbellus*	2.0	14.0	14.0	1
Turkey *Meleagris gallapavo*	2.5	18.5	13.5	1
Hoatzin *Opisthocomus hoazin* Ratio 24.2	4.0	16.5	24.2	1
PELECANIFORMES Mean ratio 12.1				
Little Black Cormorant *Phalacrocorax niger*	3.0	19.0	15.8	2
Great Cormorant *Phalacrocorax carbo*	2.9	20.0	14.5	1
Double-crested Cormorant *Phalacrocorax auritus*	3.0	29.0	10.0	1
Pelagic Cormorant *Phalacrocorax pelagicus*			8.0	1
PICIFORMES Mean ratio 10.0				
Blue-throated Barbet *Megalaima asiatica*	2.0	13.0	15.4	1
Rufous Woodpecker *Micropternus brachyurus*	2.0	14.0	14.3	1
Downy Woodpecker *Dendrocopos pubescens*	1.5	15.0	10.0	1
Coppersmith *Megalaima haemocephala*	0.9	9.7	9.3	1
Flicker *Colaptes auratus*	1.5	18.0	8.0	1
PASSERIFORMES Mean ratio 9.7				
Pitta *Pitta brachyurus*	2.2	12.1	18.0	1
Woodshrike *Tephrodornis pondicerianus*	2.2	12.3	17.8	2
Drongo *Dicrurus adsimilis*	2.2	13.3	16.2	2
Rufous-backed Shrike *Lanius schach*	2.3	14.4	16.0	3
Large-pied Wagtail *Motacilla maderas patensis*	2.1	12.6	16.0	3
Swallow *Hirundo rustica*	1.5	10.0	15.0	2
Yellow Wagtail *Motacilla flava*	1.5	11.0	13.6	1
Black-headed Oriole *Oriolus xanthornus*	2.0	15.0	13.0	1
Grey-headed Myna *Sturnus malabaricus*	1.8	14.2	13.0	2
Sunbird *Nectarinia zeylonica*	1.2	9.3	12.9	3
Starling *Sturnus vulgaris*	1.4	14.5	9.7	1
Common Grackle *Quiscalus quiscula*	1.5	16.0	9.0	1
Hill Myna *Gracula religiosa*	1.0	13.0	8.0	1
Robin *Turdus migratorius*	1.2	14.0	8.0	1
Tree Pie *Dendrocitta vagabunda*	1.3	18.0	7.0	1
Cowbird *Molothrus ater*	1.0	14.0	7.0	1
Babbler *Turdoides caudatus*	1.0	17.0	6.0	1
Blue Jay *Cyanocitta cristata*	1.0	16.0	6.0	1
*Canary *Serinus canaris*	1.5	12.5	6.0*	1
*Fox Sparrow *Passarella iliaca*	1.5	13.0	5.5*	1
*White-throated Sparrow *Zonotrichia albicollis*	1.3	14.0	4.5*	1
*Evening Grosbeak *Hesperiphona vespertina*	1.2	15.0	4.0*	1
*House Sparrow *Passer domesticus*	1.0	13.0	4.0*	1
*Purple Finch *Carpodacus purpureus*	1.1	13.0	4.0*	1
*Black-capped Chickadee *Parus atricapillus*	0.8	12.5	3.0*	1
PSITTACIFORMES Mean ratio 8.0				
Parakeet *Melopsittacus undulata*	0.8	13.0	6.0	1
Rose-ringed Parakeet *Psittacula krameri*	2.1	21.0	10.0	1

Looking over this list leads to speculation as to why certain orders and families of birds tend to have larger olfactory bulbs (as compared to cerebral hemispheres) than others. Before we can answer this question, much more work must be done on the physiology and ethology of these birds.

This list allows us to generalize somewhat more safely than Bumm who, in 1883, said that the olfactory bulbs are largest in swimming birds, medium-sized in marsh birds, and small in all others. Our survey suggests that in kiwis, in the tube-nosed marine birds, and in at least one vulture, olfaction is of primary importance, and that most water birds, marsh dwellers, and waders, and possibly echo-locating species, have a useful olfactory sense. In other species it may be relatively unimportant.

Some bulb measurements differ so greatly among members within the same order that they need special study, for example, the Turkey Vulture and especially the Hoatzin, a controversial bird now placed among the Galliformes, but whose olfactory bulbs are so much larger that we put it in a separate box in the table and did not average it with the other Galliformes. The position of some orders is surprising: the swifts and nightjars are high and the cormorants are low.

The long overdue job of putting olfaction in context in avian ethology is now under way; these crude olfactory ratios may serve as a guide to its relative importance in the listed species. Stager (1964) has shown in the field, and Wenzel (1965) and Tucker (1965) in electrophysiological studies, that birds respond positively to certain odorants. Birds have also been trained by operant olfactory conditioning (Michelsen, 1959; Sieck and Wenzel, 1966) and suppression (Henton *et al.*, 1966). Obviously the sense of smell is an attribute that has evolved differentially in the various lineages of birds.

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