

RELATIVE SIZE OF AVIAN BRAIN COMPONENTS OF THE MAGELLANIC
PENGUIN, THE GREATER RHEA AND THE TATAUPA TINAMOU

N. BEE DE SPERONI & P. PIRLOT

Received 27 October 1986, accepted 17 August 1987

ABSTRACT

Size relationships between brain and body as well as between brain parts and total brain or brain-stem are examined in representatives of three bird families. Two expressions are used: simple ratios (with functional emphasis) and cerebral indices (with phylogenetic emphasis). The Magellanic Penguin *Spheniscus magellanicus* exhibits an unexpectedly progressive development of some higher brain parts with parallel limitation of olfactory and lower components. The Tataupa Tinamou *Crypturellus tataupa* suggest an opposite trend. The Greater Rhea or Nandu *Rhea americana* stands apart or partly in between. The striatal components are a mixed group requiring separate analysis. Clearly, these results invite comparative investigations of the behavioural correlates of brain and brain component sizes in those birds from adaptive and evolutionary standpoints.

INTRODUCTION

Several descriptions of avian brains have been published in the past (Portmann & Stingelin 1961, Ariens-Kappers *et al.* 1965, Papez 1967, Karten 1969, Pearson 1972). They sometimes include quantitative data but usually consider external and gross features only.

In the 19th century, the relative development of the brain with respect to the body was estimated for many vertebrates and a well-known general equation relating both variates was often used under a form equivalent to the more recent allometric expression $y = bx^k$, where y = brain size and x = body size, with $k < 1,00$ in most cases and b representing a specific encephalization factor. Early in the 20th century, an exponent $k = 0,56$ was frequently considered to be valid for at least all homeotherms. However, the generality of the equation and exponent was soon questioned by many authors. Better expressions of the Br/Bo (brain/body) quantitative relation were proposed subsequently. A short but excellent historical note on this subject can be found in Pearson (1972).

Among all species of birds, some relative rare types, that is, some of the most restricted in geographical distribution, have seldom been mentioned in the past works on avian brains: for

example penguins (Sphenisciformes), ostriches (Struthioniformes) and tinamous (Tinamiformes). These inhabit regions of the southern hemisphere that have been studied less intensively than corresponding areas of the north, in spite of the historic presence of such famous naturalists as Charles Darwin. Thanks to the facilities enjoyed by the first author in Córdoba, Argentina, we were able to secure a few birds from those three little-studied orders, and we can now report some new basic information on the quantitative composition of their brains. This study will be followed by more detailed neuromorphological investigations on the brains of the same and other related species. But this will take time, and we therefore wish to publish the present note without delay, in order to identify some of the problems related to the interpretation of the avian encephalic organization in relation to the behaviour of these three specially adapted bird orders. Our approach falls into the general field of contemporary neuroethology as reviewed by Pirlot (1987).

MATERIALS, TECHNIQUES AND METHODS

The birds selected for this study all belong to the Argentinian avifauna; two (the Greater Rhea or *Nandu Rhea americana*, and the Magellanic Penguin *Spheniscus magellanicus*) are flightless species, one, (the Tataupa Tinamou *Crypturellus tataupa*) is a mediocre flier. The technique for estimating brain component volumes was based on common histological procedures. The methods for comparisons included ratios and indices.

We used one brain of each of the following birds. A male Rhea with a body mass of 25,00 kg and a brain mass of 19,9 g; a female Magellanic Penguin with a body mass of 3,3 kg and a brain mass of 17,3 g; a female Tinamou with 225 g and a brain mass of 1,64 g. All animals were obtained through contacts made by the first author.

In order to study the internal encephalic organization in the three species, we fixed their brains in 1/7 formalin/water, embedded them in paraffin and prepared serial sections from anterior to posterior end with the following thickness: 25 μm for the Rhea, 15 μm for the Magellanic Penguin and 10 μm for the Tinamou. All sections were Nissl-stained. The volumes of 11 brain components were estimated using the technique applied to mammals by various authors and explained by Stephan & Pirlot (1970). The area measurements involved in this technique were performed with an electronic image analyzer for the Rhea and the Magellanic Penguin (in the second author's laboratory) and by the cutting and weighting procedure for the Tinamou (in the first author's department). Results from these two techniques have been found in the past to be consistent with one another. Comparative data for the Domestic Pigeon *Columba livia* were obtained from material lent by Boire (1986).

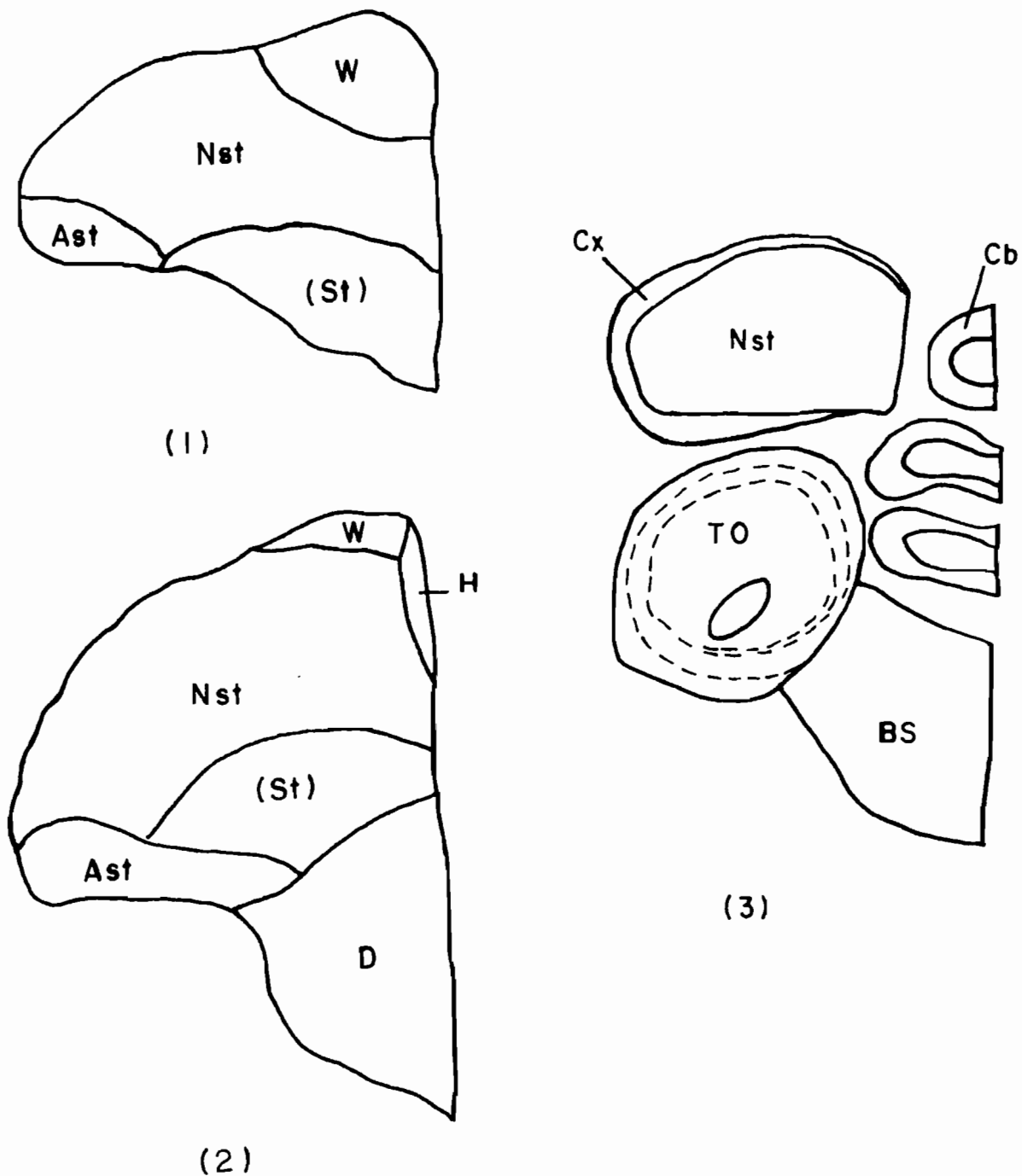


Figure 1

Sections through the brain (right half) of the Tinamou *Crypturellus tataupa*, to illustrate schematically the relative sizes of the components considered in this study (except B0).

F.1 Fore-brain; W = Wulst; Nst = neostriatum;
 Ast = archistriatum; (St) = striatum sensu stricto. F.2 Mid-brain. H = hippocampus; D = diencephalon. F.3 Hind-brain. Cx = cortex; TO = tectum opticum; Cb = cerebellum; BS = brain stem.

The comparisons presented here are based on the following relations: (1) relationship of brain size to body size; (2) relationships of brain components to total brain; (3) relationships of higher to lower brain components. Tentative remarks will be proposed on the possible ecological and ethological significance of some of these quantitative relations. Abbreviations will often be used in the text for brain components and their meaning is explained in Table 1. The terminology for components does not seem to be the same in all published works dealing with avian neuroanatomy. In the main, we have followed Karten & Hodos (1967) whose concordance with other authors can be appreciated in Baumel et al. (1979, Table 1). In this book, the International Committee on Avian Anatomical Nomenclature (ICAN) took a position which seems to harmonize the earlier nomenclature of Ariens-Kappers et al. (1965) with later usage. We are by and large in agreement with the ICAN terminology. One slight discordance consists in our using the German name "Wulst" for the sagittal eminence or crest (*Eminentia sagittalis*, that is, mainly the *Hyperstriatum accessorium*, as explained in Baumel et al. 1979, p. 447). Admittedly, the proper English name is "eminence" but a fair number of authors still use the term Wulst.

As is usual in studies of relative brain development, we shall use some simple ratios in the comparisons just indicated; these ratios give a rough idea of the functional importance of each part within a brain, relative to other parts. We shall also employ indices which refer the relative size of a brain component to standard value, that is, to the size of a given structure in a theoretical type chosen as the most "generalized" available, possibly the closest to an hypothetical ancestor. This method, that may have some phylogenetic implication, was devised by Portmann (1946, 1947) and applied by his collaborators and other researchers for many years, not only to birds but also to mammals (e.g. Pirlot & Pottier 1977, Pirlot & Speroni in press). An important remark must be made here. We have had only three individual birds at our disposal and we are fully aware that such a small sample is not satisfactory for a conventional statistical approach. This situation has been experienced in many studies of relative brain size in vertebrates, especially in mammals, by a number of authors. It is due to the fact that the work, time and expenses involved in preparing complete serial sections of brains, as well as the scarcity of such materials, precludes using large samples. This problem in methodology is reviewed by Pirlot (1987). They are restricted to relatively high and widely separated taxonomic units and do not require exact testing of mean differences and variances. In fact, our approach is modest in scope: it is essentially introductory and basic at the same time; it has its limitations from a statistical standpoint but no more than the use of measurements taken on single but none the less informative fossil specimens.

RESULTS AND DISCUSSION

We will first consider total brain, then brain components.

Total brain

An equation relating total brain mass to body mass has been evaluated by Martin (1981) on the basis of data for 180 species of birds provided by Portmann (1946, 1947). It reads $Y = 0,576 X + 2,112$ where Y is log brain mass (BrM) and X is log body mass (BoM). From this equation, one would obtain for the Rhea specimen a brain mass of 21,6 g instead of the observed 19,9 g; for the Magellanic Penguin, a brain of 17,2 g instead of the observed 17,3 g; for the Tinamou, 1,21 g instead of 1,64 g. The agreement is quite close for the Magellanic Penguin; the discrepancy is small (8 % in excess) for the Rhea, but rather substantial (some 26 %) for the Tinamou. On a log Y/ log X graph (see Martin 1981, Fig. 2) the Magellanic Penguin and the Tinamou would be located well within the main cluster of dots, and the Rhea would be conspicuously visible in the right upper sector, close to the calculated regression line.

Although such ratios are not very useful in this study which deals with three individuals only, and because many students estimate them as a routine, we wish to mention here the simple brain/body ratios as percentages: 0,08 % for the Rhea, 0,51 % for the Magellanic Penguin and 0,73 % for the Tinamou, which is not surprising, the Tinamou being the smallest of the three birds in absolute size, and the Rhea the largest.

In conclusion, no "abnormality" is apparent, at least at first sight, in the brain-to-body relationship for the three species studied. Note that, for the Domestic Chicken *Gallus domesticus*, the brain percentage is 0,46 % (Portmann 1946, 1947) and for the Domestic Pigeon, it is reported to be 0,69 % (Boire 1986).

Brain components

The relative developments of several brain components will now be considered.

Brain parts versus total brain

In Table 1, we show the percentage ratios for all brain parts plus that for the telencephalon.

TABLE 1

PERCENTAGE COMPARISONS OF BRAIN PART VOLUMES

Species	Rhea	Magellanic Penguin	Tinamou	Domestic Pigeon
BO	0,45 (0,80)	0,29 (0,44)	1,13 (2,09)	0,61 (1,12)
St	6,63 (11,84)	8,29 (12,73)	6,46 (11,94)	7,15 (13,12)
Ast	1,65 (2,94)	1,69 (2,59)	2,79 (5,16)	2,38 (4,37)
Nst	30,35 (54,17)	38,21 (58,70)	35,87 (66,32)	33,32 (61,17)
W	13,12 (23,42)	13,78 (21,17)	4,18 (7,27)	5,82 (10,68)
Cx	2,13 (3,80)	2,15 (3,30)	1,20 (2,22)	2,99 (5,49)
H	1,70 (3,03)	0,70 (1,07)	2,46 (4,55)	2,21 (4,05)
Tel	56,03 (100 %)	65,09 (100 %)	54,09 (100 %)	54,48 (100 %)
TO	6,63	3,84	10,06	7,92
D	5,64	3,92	7,86	6,87
Cm	16,19	16,61	12,74	17,01
BS	15,51	10,54	15,25	13,79
	100 %	100 %	100 %	100 %

Abbreviations: BO = bulbus olfactorius; St = striatum sensu stricto (all parts except next two); Ast = archistriatum; Nst = neostriatum; W = Wulst; Cx = cortex; H = hippocampal component; Tel = telencephalon; TO = tectum opticum; D = diencephalon; Cm = cerebellum; BS = brain stem.

In parentheses: percentages of parts within the telencephalon. On line Tel: percentage of telencephalon within the total brain.

Higher over lower brain components

Table 1 suggests some of the quantitative relationships that exist between components. One of the most interesting is, of course, the ratio of total Tel to brain stem, that is the comparison between the "extreme" parts of the brain. It is 3,61 in the Rhea, 6,17 in the Magellanic Penguin and 3,55 in the Tinamou. The difference between the Rhea and the Tinamou is not great but the Magellanic Penguin presents a remarkably high figure. The TO corresponds by mass to 0,43 of the brain stem in the Rhea, 0,36 in the Magellanic Penguin and 0,66 in the Tinamou. The Wulst (W) which is believed to have special relations with the TO, exhibits with it a ratio of 1,98 in the Rhea, 3,59 in the Magellanic Penguin and 0,41 in the Tinamou, an extraordinary diversity; the same predominance of W in the Magellanic Penguin is visible in the W/BS ratios which are 0,84; 1,31; and 0,27 for the three birds respectively in the same order as above. The Nst has about the same size relations in all three species with respect to either total brain or Tel, but it is most developed in the Magellanic Penguin with respect to the BS (ratio Nst/BS = 3,62) where as it is smaller in the Rhea (Nst/BS = 1,95) and in the Tinamou (Nst/BS = 2,35). Both the BO and the II are lowest in the Magellanic Penguin and highest in the Tinamou.

Cerebral indices

We do not so far possess canonical equations expressing the relative progression of total brain or brain parts with reference to an assumed ancestral form (Boire 1986). Such a "progression index method" has been used extensively for the quantitative study of the mammalian brain by P. Pirlot and others (see, for example, Pirlot & Kamiya 1985 and references therein, Pirlot & Speroni in press). The approach is essentially phylogenetic and evolutionary; it is also relatively superficial in that it is as "purely descriptive" as can be. In fact, in spite of the limitation of their usefulness in comparative biometry, simple ratios such as those shown in Table 1 do suggest distinct activity levels within the brain, providing thus indications, however unspecified in themselves, as to the functional meaning of the structure (see Pirlot 1986, 1987, for a discussion).

While awaiting canonical curves applicable to avian brain evolution, we can turn to a procedure introduced (as far as we know) by Portmann (1946, 1947) and perhaps unduly neglected by brain biometricians since then. This is the "cerebral index method". It is based on the arbitrary but meaningful choice of one avian type as a standard comparison type. To estimate the relative development of a given brain component, its mass is compared to the mass of the brain-stem of a hypothetical chicken that would have the same body mass as the animal under study. We have had some problem applying this method because Portmann (1946, 1947) did not study our three species and he does not give the value of the constant to be applied in the allometric equation $y = bx^k$. Although he does not say

so explicitly, we have assumed that he used the Domestic Chicken individual included in his table (II, p.6., tableau annexe) for rewriting his basic equation. This animal's mass was 550 g and the value reported for its brain-stem is 0,437, whereas the allometry exponent for the brain-stem in the genus ("Galli") is given as 0,52 (I, p.13, tableau B). We reworked the brain/body equation on the above assumption and obtained a b value of 0,01642 for the brain-stem. Hence, the basal number ("chiffre basal") was calculated for each of our birds (Table 2). For more comments on this method, see Portmann (1946, 1947). From the three basal numbers, the cerebral indices were estimated, that is, the ratio of the actual mass of each brain part to the corresponding basal number. This was done for six components (Tel, BO, W, TO, D and Cm, Table 2). There is a slight possibility of some discrepancy between our results and those which would have been obtained with Portmann's techniques because we worked from serial sections whereas Portmann dissected the main parts of the brain and apparently weighed them fresh. Also, we had to assume that the hemispheres in Portmann's work are identical with the telencephalon in ours. These small differences in our respective techniques cannot affect our comparisons seriously.

Special comparative data

Since the three species which are the subject of this paper are rather unusual both in the geographic and systematic senses, we have thought that a limited reference to a more familiar bird could help the reader appreciate the potential peculiarities of our "special" types. For this, we chose the Domestic Pigeon, which has been studied by Boire (1986). The percentage composition of the brain of the Domestic Pigeon is given in the last column of Table 1.

One would like to interpret the relative differences in brain size or brain component sizes between the three birds in the light of ecological and behavioural features, that is with reference to the particular life habits of each species. Unfortunately, apart from the most obvious ones, little is known regarding those characteristics in natural environments. It remains therefore impossible for the time being to suggest more than a very few relationships between quantitative neuromorphological traits and qualitative ecoethological features which is the essence of the so-called cociation relationships (Pirlot 1986, 1987). We will point out such possible relationships in some favourable cases, but the data for more progress in this respect will have to come mainly from behavioural studies.

(a) *Bulbus olfactorius* (BO). In percentage, the Magellanic Penguin has the smallest BO and the Tinamou the largest. Such percentages, as already pointed out, rest on one individual only and therefore lack statistical value. When differences are great between such figures, however, they hint at distinct intensities in the use of a brain part. In this

TABLE 2

CEREBRAL INDICES

Species	Rhea	Magellanic Penguin	Tinamou
Basal numbers	3,1790	1,1205	0,2744
Tel	3,3784	9,7627	3,1049
BO	0,0273	0,0442	0,0651
W	0,7908	2,0652	0,2404
TO	0,3998	0,5585	0,5774
D	0,3397	0,5880	0,4499
Cm	0,9757	2,4908	0,7315

Abbreviations: See Table 1. Basal number explained in text. The indices are obtained by dividing the actual mass of each brain part (in mg) by the basal number (mass of the brain-stem in a theoretical *Gallus* of same mass, with Portmann's recalculated b and k constants).

case, if there is any significant olfaction in these birds, it is possibly more active in the terrestrial Tinamou than in the aquatic Magellanic Penguin. The difference between Tinamou and Rhea is great too, and one may intuitively admit that a struthioniform bird is not likely to take a "sniffing" approach to its environment very often. All this, however, is a preliminary suggestion and we still ignore what the exact importance of olfaction is in the three birds. The Magellanic Penguin feeds on cephalopods, small fish and krill (crustaceans) (Scolaro & Badano 1986) which do not seem to require a sensitive olfaction ability to capture. However, one may wonder if the bird cannot appreciate olfactory properties in other objects, such as the oil with which it lubricates itself, as well as some "social" odours at its rather smelly breeding and roosting sites. Note that, according to data supplied by Cobb (in Pearson 1972), the proportion of the bulb over the hemisphere (in volume) in the Adélie Penguin *Pygoscelis adeliae* would be around 0,58 %; in the Magellanic Penguin, it is in the vicinity of 0,45 % (the Adélie Penguin is a little bigger than the Magellanic Penguin). In the Rhea, the same ratio would be 0,80 % and in the Tinamou 2,13 %, whereas it would be 1,13 % in the Domestic Pigeon. Taken together, both the Magellanic Penguin and the Rhea seem to be much more poorly equipped for conventional olfactory function than do the Domestic Pigeon and the Tinamou - if any such function significantly exists in any of them.

It may also be noted that, with reference to a standardized brain-stem, the Magellanic Penguin, which is intermediate in overall size, also shows a bulb intermediate in size (Table 2).

(b) *Neostriatum*. (Nst). The relative size of the neostriatum is of the same order of magnitude in the three species studied, as well as in the Domestic Pigeon. However, the Magellanic Penguin stands highest of all (25 % greater than the Rhea which is the lowest). Now, it is known that the trigeminal nerve, especially in its ophthalmic and maxillary branches and in relation with the sensitivity of the beak (including the Corpuscles of Grandry), sends a large quantity of information to the forebrain, such information being relayed to the basal nucleus, that is, the ventro-lateral side of the Nst (Pearson 1972). It is therefore worth noting that the Nst is largest in the Magellanic Penguin, the only aquatic species studied) and it is well known that sensitivity in the water depends largely on the trigeminal system in several vertebrates (for mammals, see Pirlot & Kamiya 1985). The so-called quinto-frontal component of nerve V also brings inputs from the skin of the head to the front brain (Ariens-Kappers et al. 1967, Vol.I). The role of the caudal Nst in auditory perceptions, as explained by Karten (1969), could also be important in all three birds under study but we have no indication of a significant behavioural difference between them from this viewpoint. So far, the best relations (cociations, as explained before) that we can find are with aquatic life and trigeminal perception.

(c) *Archistriatum*. (Ast). The two flightless birds exhibit a more reduced Ast than do the Tinamou and the Domestic Pigeon. The idea that the Ast is "an area of extensive autonomic integration" (Pearson 1972, p.531) with an important role in response to fear, cannot be confirmed from our observations, except to the extent that we know from local information that the Tinamous have the particular habit of crouching and freezing with great effectiveness, waiting for the danger to disappear. A Domestic Pigeon probably would fly away under the same circumstances. Data are missing on the specific role of the Ast and the characteristics of bird behaviour in dangerous situations. The Rhea, of course, runs away as soon as it is alerted but this does not occur at a great distance unless the ground is clear of tall shrubs and the bird can use vision, being relatively little sensitive to noise, according to observations made in Patagonia by one of us (PP). In any case, the relation between these behaviours and the size of the Ast is unknown to us.

(d) *Wulst*. (W). This is the *Eminentia Sagittalis* or sagittal eminence. The Wulst is relatively much larger in the Rhea and the Magellanic Penguin than in the other two species, although, from the viewpoint of size evolution (referring to the standard type), this component is not very developed in the Rhea. It is surprising to find that the Magellanic Penguin has a larger W than the others, and especially one three times as big as that of the Tinamou. The Wulst is traditionally believed to be related with the ability to solve rather complex and unexpected problems, involving shape and perhaps colour discriminations (Pearson 1972, Mazzi & Fassolo 1977). In which ways (opposite ways, perhaps) would a struthioniform bird and a Domestic Pigeon solve complex problems? This is an interesting question that has been raised elsewhere (Pirlot 1980) concerning homeotherms with little physical ability to defend themselves but nevertheless quite successful in using strategies such as hiding. More behavioural data in relation to this question would be welcome in view of the successful millennial survival of struthioniform and sphenisciform birds in spite of their inability to fly and consequent vulnerability, running fast and diving deep being obviously partial compensations for this.

(e) *Cortex*. (Cx). We will abstain from commenting extensively on the cortex, the development of which is relatively limited in the Tinamou, because we lack data on its behavioural significance. Salzen & Parker (1975) also note that data are lacking for this brain component. Perhaps, on the basis of general observations on avian brains, one could expect the Cx to be less developed in relatively unprogressive species, with relatively more developed BO. This suggestion would require a review of many species to be substantiated.

(f) *Hippocampus*. (H). The proportion of hippocampus is smallest in the Magellanic Penguin. In fact, it is remarkable that BO and H seem to vary in parallel fashion in the four species considered here. Phylogenetically, this parallelism may seem to be logical or expected if it is true

that there has been some ancestral correlation between the two components, a functional link of which this could be a trace. Salzen & Parker (1975) declare that the avian hippocampus is, in their view, mainly associated with "the inhibition of reorientation" (p. 235). We do not know of sufficient experimental evidence about this function of H in birds.

(g) *Tectum opticum*. (TO). There is here a contrast between the cerebral indices and the percentages. The former indicates that the Magellanic Penguin has developed a "reasonably" large tectum, just as the Tinamou has, with reference to an assumed primitive condition. The Rhea lags behind the others in this respect. However, this does not reveal much about the functions of the TO. The simple proportions (Table 1) suggest that the tectum is relatively large in the Tinamou and relatively small in the Magellanic Penguin, with the Rhea and the Domestic Pigeon occupying intermediate positions. We must again regret our shortage of data on the visual physiology of these four species. It looks as if the Tinamou would have more developed tecto-fugal pathways whereas the Magellanic Penguin would rely more on thalamo-fugal routes (Karten 1969). This again is an interesting problem that could be approached in a promising way through investigations of the terminations of the visual impulses either in the ectostriatum (tecto-fugal pathways) or in the Wulst (thalamo-fugal pathways).

(h) *Striatum sensu stricto and diencephalon*. (St and D). The grouping together of these two components may seem to be artificial, but is justified by the fact that, in this mainly quantitative study, the within-brain proportions of these two adjoining parts do not vary much between birds. The diencephalon is a crossroad of all functions, many of them autonomic, and it is often very closely correlated with the higher encephalic centers in mammals (Pirlot & Jolicoeur 1982). Taken together, St and D do not exhibit much variation in the four species studied (Table 1) although St is clearly larger in the Magellanic Penguin than in the other three species. However, the relative volume of D is smaller in the Magellanic Penguin (3,92 % against the others ranging from 5,64 to 7,86 %). Referred to the standardized size of the BS, nevertheless, the D appears highest in the Magellanic Penguin (Table 2; 0,588). This is a particular situation that agrees with the relative greater development of some telencephalic parts in the Magellanic Penguin, especially Nst and W, but is not easy to interpret physiologically or behaviourally.

The relative volume of St (all striatal components not included in Ast or Nst) is once again highest in the Magellanic Penguin. This is also curious if it is true (Mazzi & Fassolo 1977) that St is especially associated with the diencephalon in general (infundibulum, ventral thalamus).

(i) *Cerebellum*. (Cm). Regarding the size of the cerebellum, we wish to make one remark only. This component is as developed in the two non-flying birds as it is in the two

flyers. In fact the Tinamou, the only flyer (however bad) among the three South American species, has the smallest cerebellum. This recalls an intriguing observation made by Stephan & Pirlot (1970) and Pirlot & Pottier (1977) on the cerebellum of bats (Chiroptera). Among bats, this brain part is not best developed in the good flyers (insect hunters) but in species that have to perform complex movements in obtaining their food (Pirlot 1987). Amongst our three birds, the Magellanic Penguin has the most developed cerebellum in percentage (almost equal with the Domestic Pigeon) and the Rhea found almost at the same level from the same viewpoint. Concerning the standardized development (Indices; Table 2), on the other hand, the Magellanic Penguin stands out far above both the Rhea and the Tinamou. We have no interpretation to offer for those facts at the present time but we suspect that the Magellanic Penguin and the Rhea need a well developed cerebellum for certain specific movements that may be more demanding than flight on the higher control centers. It would be interesting to study closely the swimming performances of penguins (including their porpoising behaviour) as well as the mechanics of their walk when they hurry on land with little help from their flippers. The Rhea seems to have complex balance problems too when running with only limited assistance from its wings for balancing itself, or when turning abruptly around bushes on its stilt-like legs, or simply when collecting its food "from high" above ground. In fact, the whole question of which movements require most cerebellar control is still to be dealt with on the basis of behavioural observations in nature for most vertebrates. This is a neuroethological problem that deserves to be reworked comparatively for swimming, walking, climbing and flying species within the subphylum (see in this regard Portmann & Stingelin 1961, Eccles et al. 1967).

CONCLUSIONS

Although our data on the brains of the Magellanic Penguin, the Rhea and the Tinamou do not enable us to assess individual variation, our quantitative observations on a dozen of encephalic components (Tables 1 & 2) can be used for introductory comparisons that are not without value. The greater development of telencephalon, striatum, Wulst and cerebellum in the Magellanic Penguin in comparison with the other species under consideration here is both unexpected and intriguing. One may suspect that it is related to a more sophisticated behaviour in the penguin than is usually believed, and one including adaptations to aquatic life. Such behaviour may have been the key factor of the extraordinary survival of penguins against all odds. One should beware of considering too hastily that group as "primitive". A partly similar reasoning applies to the Rhea that, however, probably enjoys a much better development of visual functions together with an unusual ability to race at high speed. The Tinamou, in spite of the narrow margin of "superiority" which it may derive from its limited flying capability, might well be relatively primitive among the three

birds here studied: the respective developments of its Wulst, bulbus olfactorius, archistriatum, hippocampus point in that direction although its visual components may be relatively progressive. Altogether, our three "special" birds possess encephalic sensory-motor centres the evolution of which will not be understood unless through the collecting of many more behavioural data. They jointly provide most attractive material for quantitative investigations (including detailed histology) in functional brain morphology, from a general neuroethological perspective.

Finally, we fully agree with A.S. King (*in litt.*) that the chances of erratic variations in such morphometric studies are great. We hope to be able to follow his suggestion and repeat our observations on more individual specimens from more species of southern birds and are currently preparing a joint paper on three other species of penguins. Of course, this kind of material is rare, cannot be obtained without special permission and is expensive to prepare. But the little available certainly is better than nothing: one does not discard *Archaeopteryx* into the litter-bin because a "statistical" sample of fifty is not available.

ACKNOWLEDGEMENTS

We are indebted to the authorities of the Universidad Nacional de Córdoba, Argentina, for leave of absence to the first author; to the Natural Sciences and Engineering Research Council (NSERC) of Canada, International Exchange Service, for a travel grant that enabled her to spend a research period in the second author's laboratory; to the Director and staff of the Centro Patagónico, Puerto Madryn, Argentina, as well as to the Jardín Zoológico de Santiago del Estero, Argentina, for their help in collecting the material; to Engineer H. Speroni who assisted in the preparation of the brains; to the Department of Biology, Université de Montréal, for technical facilities; to Professor P. Jolicoeur, for checking the final text; and Professor A.S. King, The University of Liverpool, for his valued comments on a draft of this paper. The project as a whole was carried out within a regular programme (grant A 0778 to P. Pirlot) of the NSERC of Canada.

REFERENCES

- ARIENS-KAPPERS, C.U., HUBER, G.C. & CROSBY, E.C. 1967. The comparative anatomy of the nervous system of vertebrates including man. Vols. I & II. New York: Hafner.
- BAUMEL, J.J., KING, A.S., LUCAS, A.M., BREAZILE, J.E. & EVANS, H.E. 1979. *Nomina anatomica avium*. London: Academic Press.
- BOIRE, D. 1986. *Composition quantitative du cerveau de quelques groupes d'oiseaux*. Ph.D. thesis, Université de Montréal.
- ECCLES, J.C., ITO, M. & SZENTAGOTHAI, J. 1967. *The cerebellum as a neuro machine*. Heidelberg: Springer.

- KARTEN, H.J. 1969. The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon. *Ann. N. York Acad. Sci.* 167: 164-179.
- KARTEN, H.J. & HODOS, W. 1967. A stereotaxic atlas of the brain of the pigeon. Baltimore: John Hopkins Press.
- MARTIN, R.D. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293: 57-60.
- MAZZI, V. & FASSOLO, A. 1977. Introduzione alla neurologia comparata dei vertebrati. Torino: Boringhieri.
- PAPEZ, J.W. 1967. Comparative neurology. New York: Hafner.
- PEARSON, R. 1972. The avian brain. New York: Academic Press.
- PIRLOT, P. 1980. Quantitative brain composition and histological features of the brain in two South American edentates. *J. Hirnf.* 221: 1-9.
- PIRLOT, P. 1986. Understanding taxa by comparing brains. *Persp. Biol. Med.* 29: 499-509.
- PIRLOT, P. 1987. Comparative brain morphology in ecological and ethological perspectives. *J. Hirnf.* 28: 145-211.
- PIRLOT, P. & DE SPERONI, N. Bee. In press. Encephalization and brain composition in South American rodents. *Mammalia*.
- PIRLOT, P. & JOLICOEUR, P. 1982. Correlations between major brain regions in Chiroptera. *Brain Behav. Evol.* 20: 172-181.
- PIRLOT, P. & KAMIYA, T. 1985. Qualitative and quantitative brain morphology in the sirenian *Dugong dugong* Erxl. *Z.f. zool. Syst. u. Evol. Forsch.* 23: 147-155.
- PIRLOT, P. & POTTIER, J. 1977. Encephalization and quantitative brain composition in bats in relation to their life-habits. *Rev. Can. Biol.* 36: 321-336.
- PORTMANN, A. 1946. Etudes sur la cérébralisation chez les oiseaux, I. *Alauda* 14: 2-20.
- PORTMANN, A. 1947. Etudes sur la cérébralisation chez les oiseaux, II. *Alauda* 15: 161-171.
- PORTMAN, A. & STINGELIN, W. 1961. The cerebral nervous system. In: Marshall, A.J. (Ed.). The biology and comparative physiology of birds. Vol. 2. New York: Academic Press: pp. 1-36.
- SALZEN, E. & PARKER, D.M. 1975. Arousal and orientation functions of the avian telencephalon. In: Wright, P., Caryl, P.G. & Vowles, D.M. (Eds.). Neural and endocrine aspects of behaviour in birds. Amsterdam: Elsevier. pp. 205-241.
- SCOLARO, J. & BADANO, L.A. 1986. Diet of the Magellanic Penguin *Spheniscus magellanicus* during the chick-rearing period. *Cormorant* 13: 91-97.
- STEPHAN, H., BAUCHOT, R. & ANDY, O. 1970. Data on size of the brain and of various brain parts in insectivores and primates. In: Noback, C. & Montagna, W. (Eds.). The primate brain. New York: Appleton-Century-Crofts. pp. 289-298.
- STEPHAN, H. & PIRLOT, P. 1970. Volumetric comparisons of brain structures in bats. *Z. F. zool. Syst. u. Evol. Forsch.* 8: 200-236.

*N. Bee de Speroni, Universidad Nacional de Córdoba.
Departamento de Zoología, Vélez Sarsfield 299, Córdoba 5000,
Argentina.*

*P. Pirlot, Department of Biology, Université de Montréal, C.P.
6128, Montreal H3C 357 Canada.*

GROUPEMENT D'INTERET SCIENTIFIQUE OISEAUX MARINS

The 'G.I.S. Oiseaux Marins' was created in September 1986 as an official structure aiming to develop contacts and exchanges between both amateur and professional seabird enthusiasts, and to promote and conduct fundamental or applied studies on seabirds and their environment.

Its geographical area of interest is France and its overseas territories, including the French Austral and Antarctic Territories. It could be extended to other countries in the case of cooperative activities. The 'G.I.S. Oiseaux Marins' acts as a research and advisory body. It is not directly involved in actions of protection and conservation, which remain the competence of specialized bodies and associations.

A specialized bulletin is not planned for the near future, but each member will receive an annual report of G.I.S. activities, abstracts of communications presented during the annual meeting and miscellaneous information including a regularly updated bibliography of the seabirds of France. For further information, please write to the Chairman.

*G. Hémery, Chairman, G.I.S. Oiseaux Marins, c/o Muséum National
d' Histoire Naturelle, 55 rue Buffon, 75005 Paris, France.*