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Morphometric Analysis of Telencephalic Structure in a Variety of Neognath and Paleognath Bird Species Reveals Regional Differences Associated with Specific Behavioral Traits

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Key Words

Comparative neuroanatomy · Kiwi · Mosaic evolution · Telencephalic evolution

Abstract

Birds exhibit a huge array of behavior, ecology and physiology, and occupy nearly every environment on earth, ranging from the desert outback of Australia to the tropical rain forests of Panama. Some birds have adopted a fully nocturnal lifestyle, such as the barn owl and kiwi, while others, such as the albatross, spend nearly their entire life flying over the ocean. Each species has evolved unique adaptations over millions of years to function in their respective niche. In order to increase processing power or network efficiency, many of these adaptations require enlargements and/or specializations of the brain as a whole or of specific brain regions. In this study, we examine the relative size and morphology of 9 telencephalic regions in a number of Paleognath and Neognath birds and relate the findings to differences in behavior and sensory ecology. We pay particular attention to those species that have undergone a relative enlargement of the telencephalon to determine whether this relative increase in telencephalic size is homogeneous across different brain regions or whether particular regions have become differen-

tially enlarged. The analysis indicates that changes in the relative size of telencephalic regions are not homogeneous, with every species showing hypertrophy or hypotrophy of at least one of them. The three-dimensional structure of these regions in different species was also variable, in particular that of the mesopallium in kiwi. The findings from this study provide further evidence that the changes in relative brain size in birds reflect a process of mosaic evolution.

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Introduction

Distinct sets of nuclei in the vertebrate brain are generally associated with different primary functions, so it is likely that behavioral changes associated with specific motor or sensory demands may lead to concomitant changes in the size of specific brain regions and/or in the organization of these regions. It is generally accepted that having a larger brain or brain region increases its information-processing power, thereby providing better integration and storage of information about the social and physical environment or the ability to modify or invent new behaviors [Jerison, 1973; Cluttonbrock and Harvey, 1980; Harvey et al., 1980; Lefebvre et al., 1997; Sol et al.,

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2005]. Brains are thought to become enlarged through two different mechanisms: either the brain and major brain regions are enlarged as a whole (referred to as concerted evolution, passive or 'easy' mode) or specific regions are differentially enlarged (referred to as mosaic evolution, active or 'difficult' mode) [Jerison, 1985; Finlay and Darlington, 1995; Aboitiz, 1996; Finlay et al., 2001]. Variation in the size or makeup of individual brain regions indicates that mosaic evolution characterizes at least some of the diversification of avian and mammalian brain composition [Portmann, 1946; Cobb, 1964; Bang and Cobb, 1968; Bennett and Harvey, 1985; Healy and Guilford, 1990; Devoogd et al., 1993; Barton, 1996; Healy and Krebs, 1996; Glendenning and Masterton, 1998; Barton and Harvey, 2000; Timmermans et al., 2000; Clack et al., 2001; de Winter and Oxnard, 2001; Lefebvre et al., 2002; Whiting and Barton, 2003; Kubke et al., 2004; Iwaniuk and Wylie, 2006; Iwaniuk et al., 2008].

Neognathan birds, particularly parrots (Psittaciformes) and songbirds (Passeriformes) – especially corvids – have the largest relative telencephalon size [Portmann, 1946; Rehkämper et al., 1991; Iwaniuk and Hurd, 2005]. This enlargement has been suggested to be associated with a higher level of cognition (e.g. problem solving and memory) that allows these birds to perform complex tasks such as tool use, mirror self-recognition and planning for the future [Hunt, 1996; Clayton and Dickinson, 1998; Weir et al., 2002; Emery and Clayton, 2004; Emery, 2006; Prior et al., 2008; Raby et al., 2007]. The New Zealand kea (*Nestor notabilis*), for instance, is a species of parrot capable of great behavioral flexibility, sensorimotor intelligence and observational learning [Huber and Gajdon, 2006]. Similar cognitive abilities are also present in corvids, such as Western scrub jays (*Aphelocoma californica*), which demonstrate episodic-like memory and have the ability to remember specific past events [Clayton and Dickinson, 1998]. Also, New Caledonian crows are able to manufacture and use tools in the wild [Hunt, 1996].

In addition to an overall enlargement of the telencephalon, the enlargement of more specific brain regions and/or the subdivisions of these regions are also correlated with specific behaviors in certain species [Cobb, 1964; Bang and Cobb, 1968; Bennett and Harvey, 1985; Healy and Guilford, 1990; Devoogd et al., 1993; Healy and Krebs, 1996; Timmermans et al., 2000; Lefebvre et al., 2002; Kubke et al., 2004; Iwaniuk and Wylie, 2006; Cnotka et al., 2008; Iwaniuk et al., 2008]. The ability for vocal learning, for instance, is well known to be restricted to only a few groups of birds (songbirds, hummingbirds and

parrots), and in these species different nuclei make up the 'song system' distributed within several of the major telencephalic regions, with size differences that mirror the sexual dimorphism in song production [Nottebohm, 1981; Nottebohm et al., 1986; Devoogd et al., 1993; Smith et al., 1997].

Apart from oscines and parrots, the only other known taxon that has undergone a similar gross enlargement of the telencephalon is the New Zealand kiwi (*Apteryx* spp.) [Corfield et al., 2008]. Kiwi have adopted a nocturnal, ground-dwelling niche, in which they face a number of sensory challenges. Kiwi are unlikely to rely heavily on vision [Martin et al., 2007] and there is evidence that other sensory modalities, namely olfaction, somatosensation and audition, are well developed [Cobb, 1960; Bang and Cobb, 1968; Wenzel, 1968; 1971; Cunningham et al., 2007; Martin et al., 2007; Cunningham et al., 2009; Corfield et al., 2011].

We set out to examine the relative size of 9 telencephalic regions in a number of Neognath and Palaeognath birds to determine whether these regions scale homogeneously, especially in those species that show a telencephalic enlargement. Because morphological changes have also been observed in the telencephalon of birds [Stingelin and Senn, 1969], we also examined the overall morphology of the individual telencephalic regions using three-dimensional reconstructions. Our analysis indicates that different regions of the telencephalon are modified in size to different degrees, suggesting that avian telencephalic enlargements occur through mosaic evolution.

Materials and Methods

Three-dimensional modeling and volumetric estimation of telencephalic regions were undertaken on the brains of 13 bird species (table 1). Data from Corfield [2009] were augmented in the present study by the examination of additional specimens to increase sample sizes, thereby strengthening statistical power. Some discrepancies between the two studies probably resulted from these increases, and because the plots shown in the study by Corfield [2009: chapter 3] did not include any data on the olfactory bulb, entopallium or nucleus basorostralis. All material was obtained following University of Auckland and Department of Conservation regulations (research permits: NO-16732-FAU, NO-18095-DOA and WA-24648-RES). All protected specimens were provided to us dead by conservation authorities or wildlife veterinarians. All other specimens were provided to us dead by local farmers or hunters, and thus no further ethics approvals were required.

All brains were submersion fixed in 4% paraformaldehyde in 0.01 M phosphate-buffered saline (PBS), sectioned mid-sagittally

Table 1. Volumes of the total brain, telencephalon, hindbrain and 9 telencephalic regions (mm³)

Order	Common name	Species	n	Brain	Tel.	HB	A	SPC	Hp	H	M	OB	Bas.	E	N
Anseriformes	paradise shelduck	<i>Tadorna variegata</i>	3	4,157	2,690	322	117	319	215	417	444	23	46	21	1,004
Charadriiformes	bar-tailed godwit	<i>Limosa lapponica</i>	2	2,417	1,563	158	76	248	124	101	303	3	30	13	620
	spur-winged plover	<i>Vanellus miles novaehollandiae</i>	3	2,067	1,186	138	68	164	103	104	192	8	10	22	477
Columbiformes	pigeon	<i>Columba livia</i>	3	1,706	893	124	45	114	88	87	149	7	5	22	349
Galliformes	peacock	<i>Pavo cristatus</i>	3	4,560	2,665	349	131	320	281	357	401	12	8	41	1,027
	turkey	<i>Meleagris gallopavo</i>	3	5,274	2,915	417	136	350	253	434	459	7	10	52	1,145
Passeriformes	Australian magpie	<i>Gymnorhina tibicen</i>	4	4,664	3,444	155	127	370	120	494	590	1	5	34	1,665
Psittaciformes	Eastern rosella	<i>Platycercus eximius</i>	4	2,686	2,032	105	79	340	101	219	367	2	9	11	852
Rallidae	pukeko	<i>Porphyrio porphyrio melanotus</i>	3	4,186	2,771	255	123	376	236	324	488	35	19	29	1,057
Struthioniformes	emu	<i>Dromaius novaehollandiae</i>	1	21,830	13,696	1,418	360	1,338	926	4,388	1,838	218	108	153	4,101
	North Island brown kiwi	<i>Apteryx mantelli</i>	2	5,299	4,268	237	124	668	294	224	937	81	41	4	1,778
Tinamiformes	Darwin's nothura	<i>Nothura darwinii</i>	1	1,482	809	126	38	140	86	80	114	3	5	19	304
	great tinamous	<i>Tinamus major</i>	1	2,242	1,222	184	66	169	134	94	201	14	7	30	472

Tel. = Telencephalon; HB = hindbrain; A = arcopallium; Hp = hippocampus; H = hyperpallium; M = mesopallium; OB = olfactory bulb; Bas. = nucleus basorostralis; E = entopallium; N = nidopallium.

into left and right hemispheres, and cryoprotected in 30% sucrose. Each hemisphere was placed in a solution of 15% gelatine with 30% sucrose at 40°C for 1 h. The brains were then placed into a custom-made mold so that fiducial points could be made in the gelatine for later alignment of tissue sections. The mold consisted of a plastic base with small holes drilled in a grid pattern. The base of the mold was covered with 15% gelatine containing 30% sucrose in PBS and the gelatine was allowed to set. The brains were then placed on the gelatine base, with the midline facing down. Five to seven small pins were inserted into the holes that had been drilled in the base of the mold so that they surrounded the brain and ran in a rostral-caudal direction. A 15% gelatine, 30% sucrose and PBS solution containing black fabric dye (to darken the gelatine solution) was then poured over the brain. Once set, the gelatine block, including the brain, was removed, trimmed and placed, along with the pins, into 4% paraformaldehyde overnight. The pins were then removed and the block was sectioned on a sliding freezing microtome at 50- μ m thickness in the sagittal plane. Sections were collected in PBS-sodium azide 0.01%. For each species, except for emu (*Dromaius novaehollandiae*), every second section was mounted serially onto gelatine chrome-alum-subbed slides, stained with cresyl violet, dehydrated and coverslipped with DePeX from xylene. For emu, every fourth section was processed because of the large size of the brain. Sections and fiducial points in the surrounding gelatine were imaged using a Leica stereomicroscope, and the images subsequently loaded into AMIRA (v 5.2; Visage Imaging, San Diego, Calif., USA) for alignment and modeling as described below.

3D Modeling in AMIRA

Individual images of the brain sections were loaded into AMIRA. An Alignslice module was attached to the data and each section was aligned according to the fiducial points. A LabelField module was attached to the newly aligned image series and new materials were created to correspond with each brain region that

was to be modeled. Each brain region was segmented out from each image using the brush tool and assigned its corresponding material. A small amount of label smoothing was undertaken to fine-tune the slice alignment. A SurfaceGen module was attached to the LabelField module and the 3D model was visualized by attaching a SurfaceView module.

Nine telencephalic regions were identified using boundary lines that could be recognized from the cresyl violet in the AMIRA stack. Boundaries were identified with the aid of sections stained for immunocytochemistry, namely the calcium-binding proteins calretinin, calbindin and parvalbumin (Swant, Bellinzona, Switzerland) and guided by several brain atlases [Karten and Hodos, 1967; Kuenzel and Masson, 1988; Puelles et al., 2007] and named according to the Consortium Nomenclature [Reiner et al., 2004]. Some examples of the telencephalic boundaries in 4 species of birds are shown in figure 1; the telencephalic boundary used is also shown in this study. The areas that were modeled were: olfactory bulb, the mesopallium (which included both dorsal and ventral subdivisions), nidopallium (excluding nucleus basorostralis or entopallium), arcopallium, entopallium, striatopallidal complex (SPC; mediale and laterale), nucleus basorostralis, hyperpallium (which included the Wulst components hyperpallium densocellulare, intercalatum and apicale, and the nucleus interstitialis hyperpallii apicalis) and hippocampus. Because the lateral boundary of the hippocampus was difficult to determine in sagittal sections, the caudodorsolateral pallium (CDL) was included in the hippocampus volume for all species. A volume was obtained for the hippocampus, but 3D models were not created. After the different brain regions were outlined in AMIRA, the stack of images was exported as a series of TIFF files. In these, a given region is filled in black against a white background. These TIFF stacks were then used for volumetric estimates of each region. All TIFF stacks were produced prior to the label smoothing that was applied to the 3-D models.

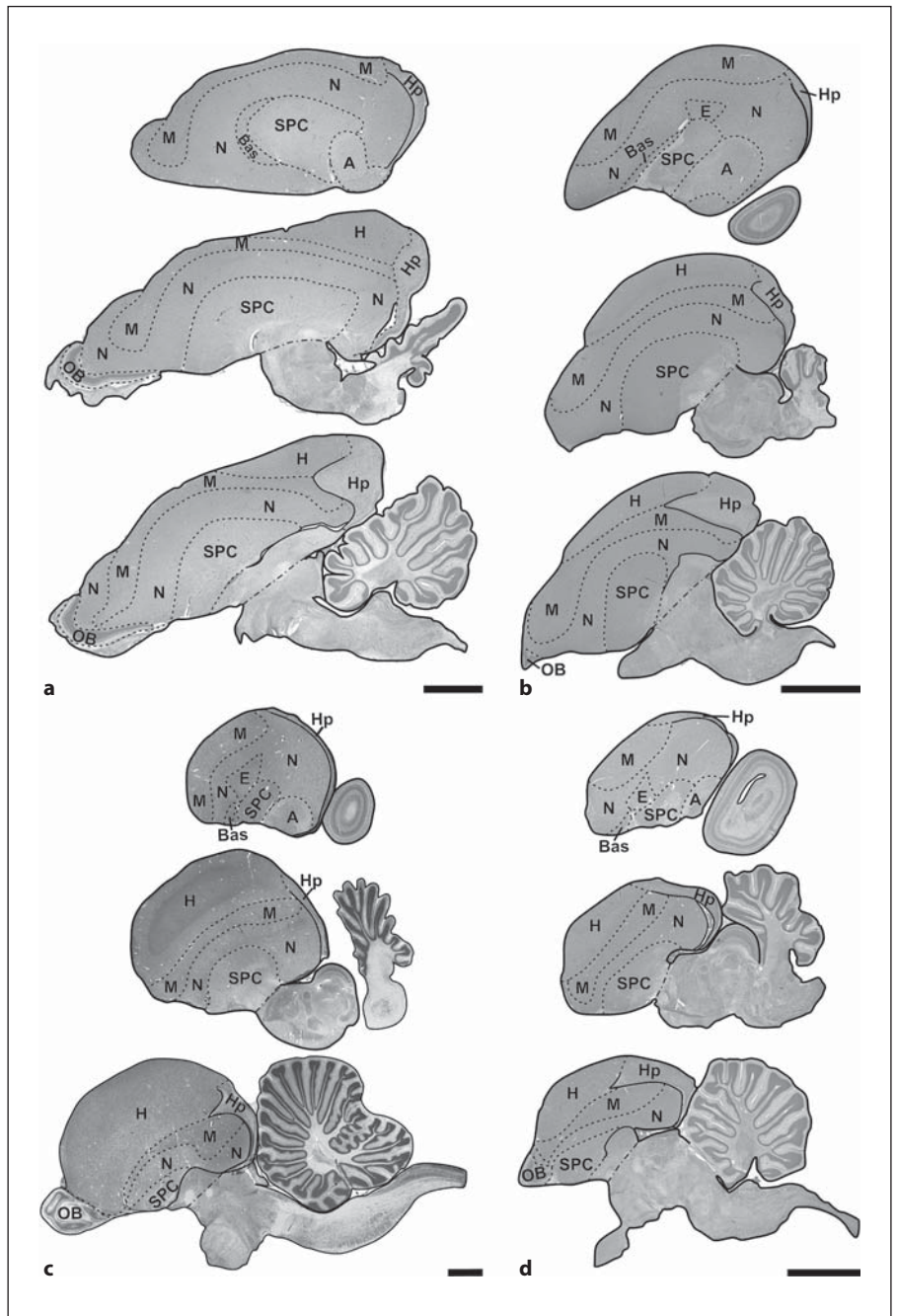


Fig. 1. Photomicrographs of sagittal sections stained with cresyl violet through the brain of 4 species of birds. Top sections are more lateral and bottom sections more medial. The broken black lines indicate the borders of telencephalic regions and the broken and dotted black lines the boundary of the telencephalon. **a** North Island brown kiwi (*Apteryx mantelli*). **b** Eastern rosella (*P. eximius*). **c** Emu (*D. novaehollandiae*). **d** Pigeon (*Columba livia*). A = Arcopallium; N = nidopallium; H = hyperpallium; Bas. = nucleus basorostralis; E = entopallium; OB = olfactory bulb; Hp = hippocampus; M = mesopallium. Scale bars = 5 mm.

Volumetric Estimates of Brain Regions

The TIFF stacks from each brain region for each species created with AMIRA were loaded into ImageJ (National Institutes of Health, Bethesda, Md., USA; <http://rsb.info.nih.gov/ij/>) and calibrated using a microscope calibration scale bar. The images were thresholded to select the brain or brain region outlines. Each image was then analyzed to obtain the cross-sectional area of the brain object. To obtain the volumes, the cross-sectional areas were summed for each brain region and then multiplied by the slice thickness and the number of

sections between stack slices, which for all species was 100 μm except for the emu, for which it was 200 μm .

A major axis model II non-linear regression was performed using SPSS (v. 15, SPSS, Chicago, Ill., USA) and $h = r^2 / (1 + b^2)$ as the loss function (where r is the residual and b is the slope). All regressions were performed on \log_{10} -transformed data. Each brain region was regressed against 'telencephalon rest' volume (total telencephalon volume – brain region volume) to avoid Deacon's whole-part fallacy [Deacon, 1990] and against the hindbrain

Table 2. Volumes of the telencephalon and 6 major telencephalic regions (mm³) in both the left and right hemispheres

	Paradise shelduck			Australian magpie		
	left	right	Δ%	left	right	Δ%
Tel.	1,566	1,507		1,361	1,473	
A	62 (3.94)	64 (4.22)	0.27	52 (3.82)	53 (3.59)	0.23
SPC	208 (13.28)	186 (12.33)	0.95	163 (11.96)	180 (12.22)	0.26
N	647 (41.33)	618 (41.00)	0.32	681 (50.05)	738 (50.14)	0.09
H	238 (15.19)	226 (15.02)	0.17	184 (13.54)	191 (12.99)	0.55
Hp	119 (7.60)	114 (7.56)	0.04	46 (3.40)	51 (3.44)	0.04
M	256 (16.34)	261 (17.34)	1.00	217 (15.93)	242 (16.42)	0.49

	Eastern rosella			Pukeko		
	left	right	Δ%	left	right	Δ%
Tel.	1,086	1,093		1,389	1,390	
A	39 (3.58)	33 (3.02)	0.56	70 (5.07)	64 (4.63)	0.44
SPC	184 (16.96)	194 (17.72)	0.76	194 (13.94)	186 (13.36)	0.58
N	471 (43.42)	477 (43.67)	0.26	566 (40.75)	574 (41.30)	0.55
H	117 (10.80)	119 (10.89)	0.09	166 (11.92)	166 (11.92)	0.00
Hp	49 (4.52)	48 (4.39)	0.12	116 (8.37)	119 (8.59)	0.22
M	197 (18.13)	195 (17.85)	0.27	239 (17.19)	254 (18.30)	1.11

Numbers in parentheses correspond to the percentage of each structure with respect to the size of the hemisphere from which the percentage differences (Δ%) were calculated. Data are from 1 specimen of each species. Tel. = Telencephalon; A = arcopallium; N = nidopallium; H = hyperpallium; Hp = hippocampus; M = mesopallium.

volume (defined as rostral border of the isthmus to the caudal border of pseudorhombomere 11, as described by Puelles [2007], less the cerebellum). Regression against the hindbrain shows how the absolute size of the region varies, while regression against telencephalon rest shows how the proportion of the region varies within the telencephalon.

A region was considered to be hypertrophied or hypotrophied if the individual value fell outside the 95% confidence interval calculated from the regression slope. The confidence intervals were computed from the best-fit values from the non-linear regression and the standard error (SE) of those best-fit values using the following equation: BestFit - t*SE and BestFit + t*SE, where t is the critical value from the t distribution.

Rather than to obtain volumes and create models for both hemispheres of the telencephalon, it was first determined whether there were any differences in the relative size of each region in the left versus right hemispheres in 4 species of birds. For all regions examined in all species, there was no more than a 1.1% difference between the left and right in the relative size of a specific region with respect to total size of the hemisphere (table 2). In the paradise shelduck (*Tadorna variegata*) and Australian magpie (*Gymnorhina tibicen*), the overall telencephalon size showed some variation between the left and right hemispheres (table 2). In the paradise shelduck, the left hemisphere was larger than the right (left: 1,566 mm³ vs. right: 1,507 mm³) and in the Australian magpie the right hemisphere was larger than the left (left: 1,361 mm³ vs. right: 1,473 mm³). Little variation occurred between the left

and right hemispheres in the Eastern rosella (*Platycercus eximius*; left: 1,086 mm³ vs. right: 1,093 mm³) and pukeko (*Porphyrio porphyrio melanotus*; left: 1,389 mm³ vs. right: 1,390 mm³; table 2). In summary, although there are some left/right asymmetries in the telencephalic hemispheres, the percentage that each region occupied within each hemisphere showed little or no difference in the 4 species examined. Therefore, apart from the paradise shelduck, Australian magpie, Eastern rosella and pukeko, volumes were only obtained from 1 hemisphere and then doubled.

Results

The Eastern rosella, the Australian magpie and kiwi all had relatively large telencephala compared to the other species (fig. 2; table 1). A relatively smaller telencephalic size was found in species belonging to the Galliformes (peacock and turkey) and Tinamiformes (Darwin's nothura and great tinamou). Overall, these species differences corroborate previous findings [Portmann, 1946; Rehkämper et al., 1991; Iwaniuk and Hurd, 2005; Corfield et al., 2008].

Every brain region showed hypertrophy in at least 1 species when the data were regressed against the hind-

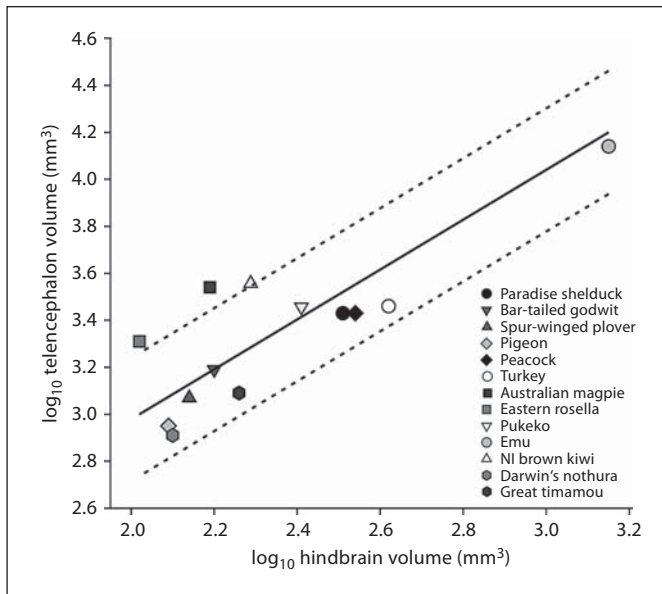


Fig. 2. Scatter plot of the volume of the telencephalon plotted as a function of hindbrain volume for all species examined. The solid line represents the regression line from the model II allometric analyses and the broken lines the 95% confidence intervals. NI = North Island.

brain volume. The arcopallium was hypertrophied in the Australian magpie and the Eastern rosella, and hypotrophied in Darwin's nothura (fig. 3a). The SPC was hypertrophied in the Australian magpie, Eastern rosella and kiwi, and hypotrophied in the pigeon, great tinamou, peacock and turkey (fig. 3b). The hippocampus/CDL was hypertrophied in the kiwi, but no hypertrophy or hypotrophy of this structure was seen in any of the other species (fig. 3c). The mesopallium was hypertrophied in the Australian magpie, the Eastern rosella and the kiwi, and hypotrophied in Darwin's nothura, great tinamou, emu, peacock and turkey (fig. 3d). The hyperpallium was hypertrophied in the Australian magpie and Eastern rosella, and hypotrophied only in the great tinamou (fig. 3e). The olfactory bulb was hypertrophied in the pigeon, spur-winged plover, pukeko, great tinamou and kiwi, and hypotrophied in the Australian magpie, peacock, turkey and emu (fig. 3f). The nidopallium was hypertrophied in the Australian magpie, Eastern rosella, and kiwi, and hypotrophied in Darwin's nothura and great tinamou (fig. 3g). The nucleus basorostralis was hypertrophied in Eastern rosella, paradise shelduck, bar-tailed godwit and kiwi, and hypotrophied in the emu, turkey and peacock (fig. 3h). The entopallium was hypertrophied in the pigeon and Australian magpie, but hypotrophied in kiwi,

emu and turkey (fig. 3i). Overall, when the data were regressed against the hindbrain, the SPC, olfactory bulb, nidopallium, nucleus basorostralis and entopallium showed the greatest degree of variation between species.

To determine the degree to which the volume of each region co-varied with the changes in overall telencephalic volumes, data for each region were regressed against the telencephalon – the telencephalic region (see Materials and Methods), and less extent of variation was seen (fig. 4). All volumes fell inside the 95% confidence interval in the SPC and the mesopallium (fig. 4b, d). In the arcopallium and hyperpallium, only the kiwi showed hypotrophy (fig. 4a, e). The hippocampus/CDL of the Australian magpie and Eastern rosella showed hypotrophy, while the values for all other species fell inside the 95% confidence interval (fig. 4c). The olfactory bulb was hypertrophied in Darwin's nothura, great tinamou, pigeon and spur-winged plover, and hypotrophied in the Australian magpie, Eastern rosella and emu (fig. 4f). The Australian magpie was the only species to show hypertrophy of the nidopallium (fig. 4g). The nucleus basorostralis was hypertrophied in the bar-tailed godwit, spur-winged plover and paradise shelduck, and hypotrophied in the peacock, turkey and Australian magpie (fig. 4h). Finally, the entopallium was hypertrophied in Darwin's nothura, great tinamou, pigeon and spur-winged plover, and hypotrophied in the emu, kiwi and Eastern rosella (fig. 4i). The greatest extent of relative size variation when data were regressed against telencephalic volume was seen in the olfactory bulb, entopallium and nucleus basorostralis. The proportion that each of the regions occupies in the telencephalon is shown in figure 5.

When regressed against either the hindbrain or telencephalon – the telencephalic region volume, the emu, peacock and turkey only showed hypotrophy of specific telencephalic regions, while the paradise shelduck, bar-tailed godwit, spur-winged plover and pukeko only showed hypertrophy of telencephalic regions. For all other species, both hypertrophy and hypotrophy were seen. The kiwi showed no hypertrophy of any brain region when the data were regressed against telencephalic size, suggesting that no specific region is enlarged beyond that expected from the overall enlargement of the telencephalon. The same is true for the Eastern rosella. In contrast, in the Australian magpie, the nidopallium is enlarged beyond that expected from the enlargement of the telencephalon as a whole. Other specific enlargements beyond those expected from the enlargement of the telencephalon as a whole include the olfactory bulb in the pigeon, the spur-winged plover, the great tinamou and Darwin's

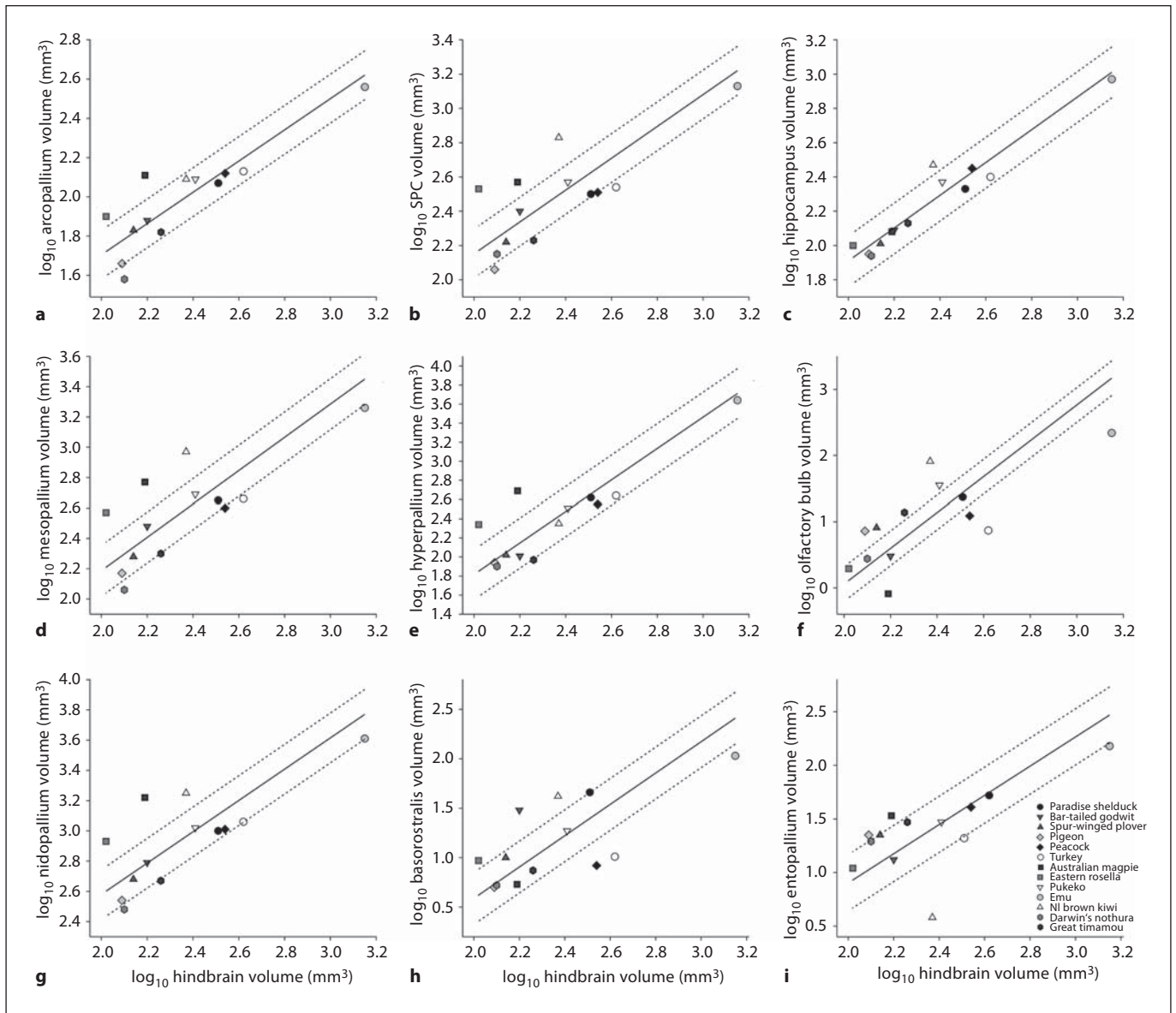


Fig. 3. Scatter plot of the volume of 9 telencephalic regions plotted as a function of hindbrain volume for all species examined. **a** Arcopallium. **b** SPC. **c** Hippocampus. **d** Mesopallium. **e** Hyperpallium. **f** Olfactory bulb. **g** Nidopallium. **h** Nucleus basorostralis.

i Entopallium. The solid line represents the regression line from the model II allometric analyses and the broken lines the 95% confidence intervals. NI = North Island.

nothura, the nucleus basorostralis in the paradise shelduck and bar-tailed godwit, and the entopallium in the pigeon, spur-winged plover, great tinamous and Darwin's nothura. Regions that were smaller than expected from telencephalic size included the arcopallium, entopallium and hyperpallium in the kiwi, the hippocampus/CDL in the Australian magpie and Eastern rosella, the olfactory bulb in the emu, Australian magpie and Eastern rosella,

nucleus basorostralis in the Australian magpie, peacock and turkey, and the entopallium in the emu and Eastern rosella. It seems, therefore, that the relative variation in size of specific structures is not specific to particular phylogenetic lineages, and that hypertrophy and hypotrophy can be found in both Palaeognath and Neognath birds.

Given the inhomogeneous variation of different telencephalic nuclei, we examined the proportion of volume

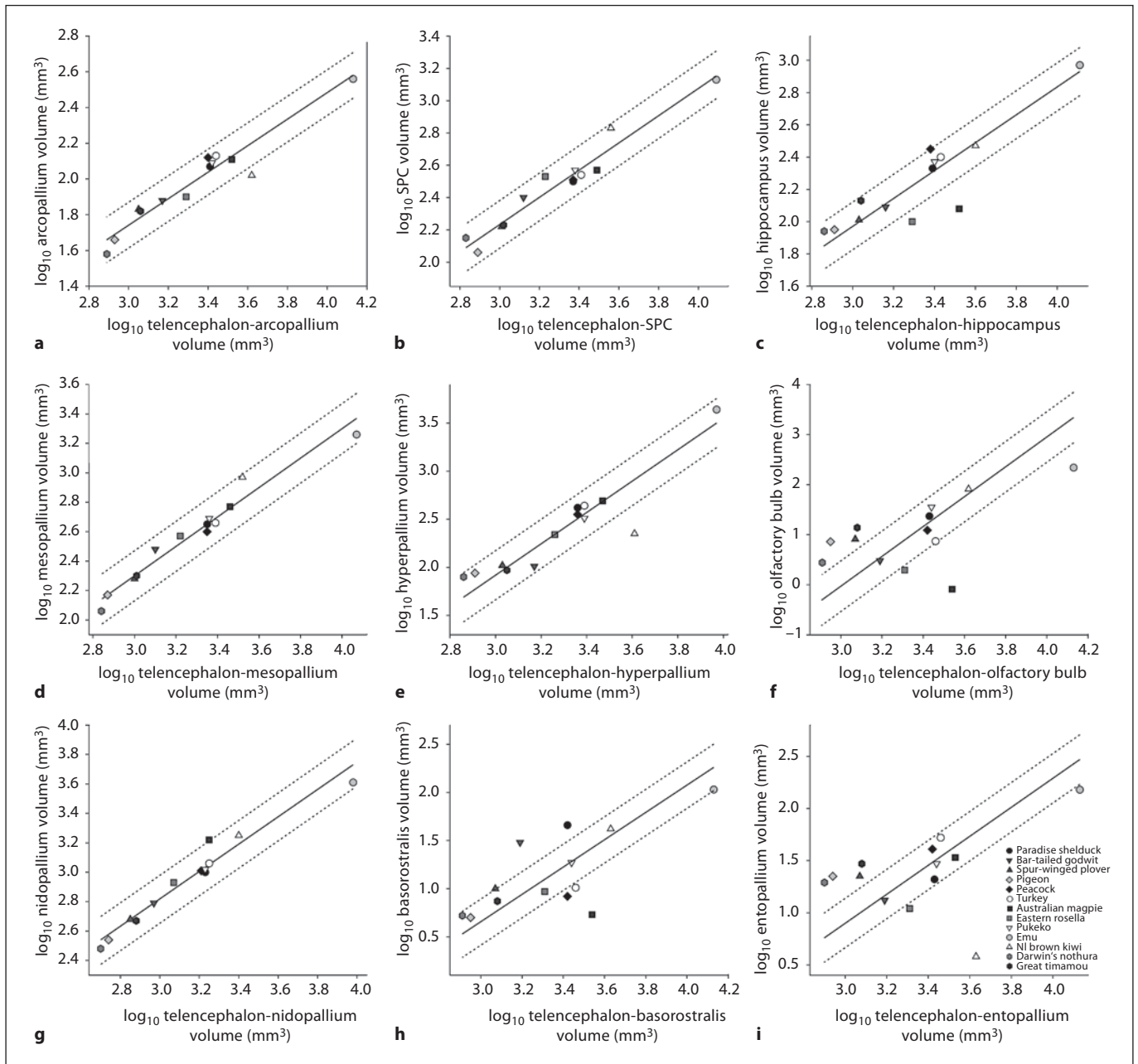


Fig. 4. Scatter plot of the volume of 9 telencephalic regions plotted as a function of the volume of the telencephalon minus the region of interest for all species examined. **a** Arcopallium. **b** SPC. **c** Hippocampus. **d** Mesopallium. **e** Hyperpallium. **f** Olfactory bulb.

g Nidopallium. **h** Nucleus basorostralis. **i** Entopallium. The solid line represents the regression line from the model II allometric analyses and the broken lines the 95% confidence intervals. NI = North Island.

that each nucleus occupied in the telencephalon (fig. 5; table 3). In kiwi, the proportions of the mesopallium (22.0%) and olfactory bulb (1.9%) are the greatest of any of the birds examined, whereas the hyperpallium (5.3%) is the least. The proportions of telencephalic regions in the emu are considerably different from those of all other

birds, with an overrepresentation of the hyperpallium (32.0%; fig. 5; table 3). In the emu, the proportion of SPC, mesopallium and especially the nidopallium are reduced, likely reflecting the massive expansion of the hyperpallium. Within the species that show an enlarged telencephalon, the Australian magpie has the largest propor-

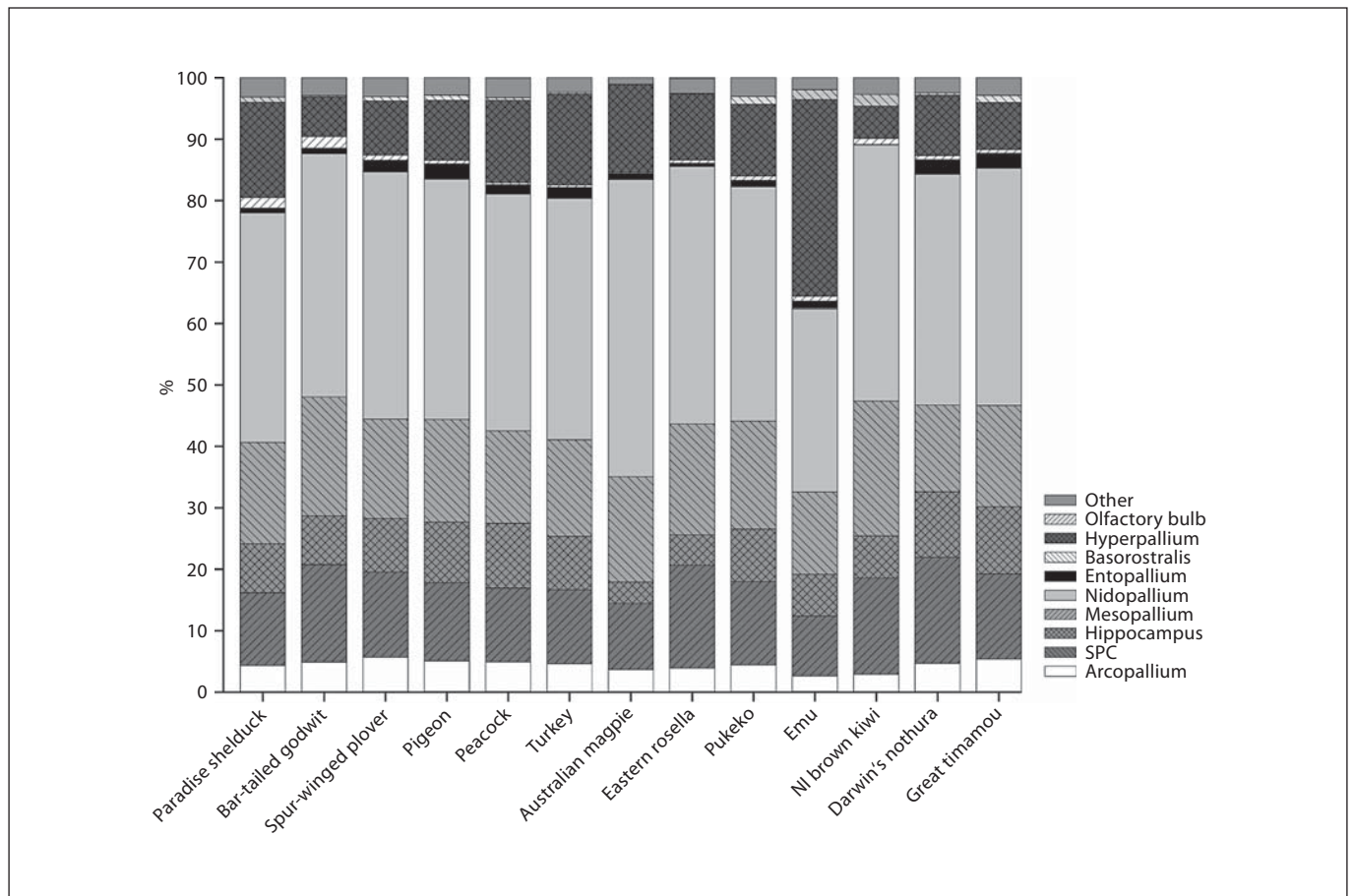
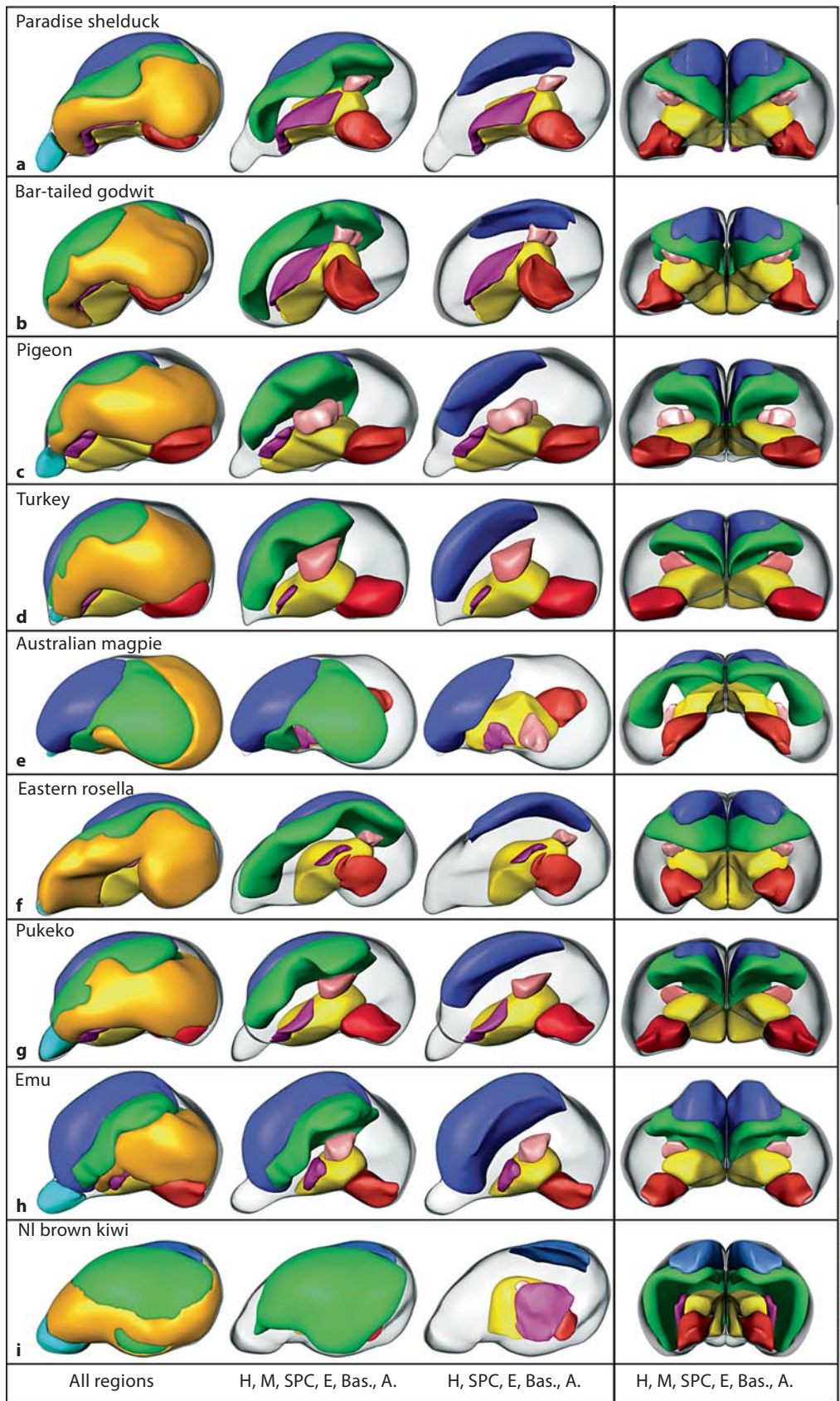


Fig. 5. The volume of arcopallium, SPC, hippocampus, mesopallium, nidopallium, entopallium, hyperpallium, nucleus basorostralis and the rest of the telencephalon plotted as a percentage of the telencephalon. NI = North Island.

Table 3. Volumes of the arcopallium (A), SPC, hippocampus (Hp), hyperpallium (H), mesopallium (M), olfactory bulb (OB), nucleus basorostralis (Bas), entopallium (E), nidopallium (N) and the rest of the telencephalon (other) as a percentage of the telencephalon

Order	Common name	Species	A	SPC	Hp	H	M	OB	Bas.	E	N	Other
Anseriformes	paradise shelduck	<i>Tadorna variegata</i>	4.3	11.9	8.0	15.5	16.5	0.9	1.7	0.8	37.3	3.1
Charadriiformes	bar-tailed godwit	<i>Limosa lapponica</i>	4.9	15.9	7.9	6.5	19.4	0.2	1.9	0.8	39.6	2.9
	spur-winged plover	<i>Vanellus miles novaehollandiae</i>	5.7	13.9	8.7	8.8	16.2	0.7	0.8	1.9	40.2	3.1
Columbiformes	pigeon	<i>Columba livia</i>	5.1	12.7	9.9	9.7	16.7	0.8	0.6	2.5	39.1	2.9
Galliformes	peacock	<i>Pavo cristatus</i>	4.9	12.0	10.6	13.4	15.0	0.5	0.3	1.5	38.5	3.2
	turkey	<i>Meleagris gallopavo</i>	4.7	12.0	8.7	14.9	15.7	0.3	0.3	1.8	39.3	2.3
Passeriformes	Australian magpie	<i>Gymnorhina tibicen</i>	3.7	10.7	3.5	14.4	17.1	0.0	0.2	1.0	48.4	1.1
Psittaciformes	Eastern rosella	<i>Platycercus eximius</i>	3.9	16.7	5.0	10.8	18.1	0.1	0.5	0.5	41.9	2.5
Rallidae	pukeko	<i>Porphyrio porphyrio melanotus</i>	4.5	13.6	8.5	11.7	17.6	1.3	0.7	1.1	38.1	3.0
Struthioniformes	emu	<i>Dromaius novaehollandiae</i>	2.6	9.8	6.8	32.0	13.4	1.6	0.8	1.1	29.9	1.9
	North Island brown kiwi	<i>Apteryx mantelli</i>	2.9	15.7	6.9	5.3	22.0	1.9	1.0	0.1	41.7	2.7
Tinamiformes	Darwin's nothura	<i>Nothura darwinii</i>	4.7	17.3	10.7	9.9	14.1	0.3	0.7	2.4	37.6	2.5
	great tinamous	<i>Tinamus major</i>	5.4	13.9	10.9	7.7	16.5	1.1	0.6	2.4	38.6	2.9



- Mesopallium
- N. basorostralis
- Striatopallidal complex
- Entopallium
- Hyperpallium
- Arcopallium
- Nidopallium
- Olfactory bulb

tion of nidopallium (48.4%) and the Eastern rosella a relatively high SPC (16.7%) and mesopallium (18.1%, fig. 5; table 3) proportion.

Morphology

Kiwi showed a rostral expansion of the telencephalon, due to an expansion of either the nidopallium or mesopallium (fig. 6; online suppl. fig. 3; for all suppl. material, see www.karger.com/doi/10.1159/000339828). This is also the case in the bar-tailed godwit, paradise shelduck and Eastern rosella (fig. 6; online suppl. fig. 1, 2). The mesopallium in kiwi extends throughout the rostrocaudal extent of the telencephalon and nearly to its ventral border, especially at the caudal pole (fig. 6; online suppl. fig. 3). It forms a relatively thin sheet that for the most part surrounds the entire nidopallium, and shows expansions at both the rostrocaudal and dorsoventral ends. In the magpie, the mesopallium shows a similar ventral expansion, although it does not extend to the caudal extremes as it does in the kiwi (fig. 6; online suppl. fig. 2). In the other birds examined, the mesopallium only occupies a dorsomedial strip ventral to the hyperpallium. The hyperpallium in kiwi is restricted to a caudal location, and this is also true to a lesser extent in the godwit and Eastern rosella (fig. 6; online suppl. fig. 1–3). In these birds, the hyperpallium does not show the rostral extension found in the other birds examined. In contrast, the emu (the closest relative of the kiwi) shows a massive rostral expansion of the hyperpallium (fig. 6; online suppl. fig. 3). Similarly, but not as extreme, the magpie also shows a rostral expansion of the hyperpallium, but it also extends further laterally (fig. 6; online suppl. fig. 2). The 3D structure of SPC and arcopallium was quite variable between species (fig. 6; online suppl. fig. 1–3).

Fig. 6. Lateral and caudal views of 3D reconstructions of the telencephalon and 8 telencephalic regions in 9 species of birds. The telencephalon is displayed as a transparent object while the telencephalic regions are colored as shown in the legend. The three lateral views for each species are first displayed with all regions and then without the nidopallium and olfactory bulb, and then with the mesopallium removed. This allows all regions to be visualized. Caudal views are also shown for each species. Species for which models are shown: **a** Paradise shelduck (*Tadorna variegata*). **b** Bar-tailed godwit (*Limosa lapponica*). **c** Rock pigeon (*C. livia*). **d** Turkey (*Meleagris gallopavo*). **e** Australian magpie (*G. tibicen*). **f** Eastern rosella (*P. eximius*). **g** Pukeko (*P. porphyrio melanotus*). **h** Emu (*D. novaehollandiae*). **i** North Island brown kiwi (*A. mantelli*). A = Arcopallium; H = hyperpallium; Bas. = nucleus basorostralis; E = entopallium; M = mesopallium.

Discussion

Our results suggest that in the bird species studied, changes in the relative size of telencephalic regions are not homogeneous. All species showed hypertrophy or hypotrophy of at least one telencephalic region. In addition, some species in this study showed morphological variations of the telencephalic regions examined, either in their rostrocaudal and mediolateral extent or in the relative position they occupy.

Of the 9 telencephalic regions examined, the mesopallium, nidopallium and SPC make up the majority of the telencephalon. Although we are only beginning to understand some of the functions of these regions, they have been associated with a wide range of behaviors. Enlargements of these regions are characteristic of some parrots (Psittaciformes) and songbirds (Passeriformes), including corvids, in which they are thought to reflect a high level of cognition, allowing them to perform complex tasks, such as vocal learning and tool manufacture [Hunt, 1996; Clayton and Dickinson, 1998; Weir et al., 2002; Emery and Clayton, 2004; Emery, 2006; Huber and Gajdon, 2006; Raby et al., 2007; Prior et al., 2008; Seed et al., 2008, 2009]. In addition, the mesopallium has been associated with innovative feeding behaviors [Timmermans et al., 2000] and vocal perception/production [Gentner et al., 2000; Plummer and Striedter, 2002]. SPC is thought to be involved in the control of stereotyped, species-specific behavioral responses [Reiner et al., 1984; Dubbeldam, 1998] and has also been implicated in learning [Parent, 1986; Scharff and Nottebohm, 1991; Stewart et al., 1996; Csillag, 1999; Mezey et al., 1999; Watanabe, 2001].

These studies have undoubtedly provided insights into the functions of these regions, but because brains are not functionally organized on a one-function/one-region basis, but as dynamic, functionally interactive systems to which particular subregions contribute in specific ways in different contexts [Feenders et al., 2008], conclusions about the implications for behavior of a specific enlargement or reduction of a central structure must be drawn with extreme caution. In the present study, we were constrained to draw on knowledge of behavior, ecology and physiology for the species examined to make tentative suggestions as to the reason or reasons for an enlargement or reduction in size of a region.

As an example, consider the behavior of the kiwi, a nocturnal, flightless species that is adapted to occupying a ground-dwelling niche. Correspondingly, the organization of its telencephalon differed in many respects from

that of the other species examined in this study. Contributing to its enlarged telencephalon was an enlarged SPC, mesopallium, nucleus basorostralis, hippocampus/CDL, olfactory bulb and nidopallium, but not arcopallium, hyperpallium or entopallium. Why this particular suite of structural enlargements is present in kiwi is not altogether clear, but it can be noted that the bird seems to rely heavily on olfaction for locating food items [Wenzel, 1968, 1971]. Although comparatively little is known about the functional organization of the avian 'olfactory brain' in pigeons, projections from the olfactory bulb have been found throughout extensive regions of the telencephalon, including piriform cortex, mesopallium, medial striatum, globus pallidus, septum, nucleus taeniae of the amygdala and the dorsomedial hippocampus [Rieke and Wenzel, 1978; Reiner and Karten, 1985; Teuchert et al., 1986]. Several of these structures in kiwi are likely involved in processing olfactory information from the massive olfactory bulb, perhaps thereby accounting for their relative enlargement.

Among the species examined in the present study were those that likely rely heavily on tactile information from the beak and tongue. These species consist of the kiwi, bar-tailed godwit, Eastern rosella and paradise shelduck, and all have been shown to have a specialized arrangement of mechanoreceptors within pits at the bill tip and/or in the tongue [Cunningham et al., 2007; Martin et al., 2007]. Both kiwi and bar-tailed godwit, like many shorebirds, rely on this tactile sense for detecting and selecting food beneath the ground, ducks for detection, recognition, and transportation of food in the mouth, and parrots for complex manipulations of food items. In all these species, and likely accompanying these specialization of the beak and tongue, is the relatively enlarged nucleus basorostralis, which processes information from these peripheral structures via the principal sensory trigeminal nucleus [Witkovsky et al., 1973; Berkhoudt et al., 1981; Dubbeldam et al., 1981; Wild, 1985; Dubbeldam, 1990; Wild and Farabaugh, 1996; Wild et al., 2001]. The bar-tailed godwit and kiwi also share a caudal displacement of the hyperpallium, but the significance of this remains speculative. Since the hyperpallium is largely visual in nature, its caudal displacement could indicate a reduction in the importance of vision, as in kiwi [Martin et al., 2007]. But in most other avian species the hyperpallium extends to the rostral pole of the brain caudal to the olfactory bulbs, and its most rostral, minor part – the so-called rostral Wulst – is somatosensory in nature, receiving projections via the thalamus from parts of the body other than the beak [Wild, 1987; Funke, 1989; Wild, 1997; Wild

et al., 2008]. In kiwi, bar-tailed godwit, Eastern rosella and paradise shelduck, there is a massive rostral expansion of the frontal part of the telencephalon, but whether this region processes information from the beak and tongue and/or from other parts of the body is unknown [Stingelin and Senn, 1969; Pettigrew and Frost, 1985].

It is interesting to note that within the species that showed enlarged telencephalon, some regions did not enlarge with the rest of the telencephalon and some even appear to be smaller than expected. This is particularly true for the kiwi, in which the arcopallium and hyperpallium did not accompany the enlargement of the telencephalon, and the entopallium appeared to have reduced in size. The small size of the hyperpallium (visual and perhaps somatosensory Wulst) in kiwi is in contrast to that reported for other nocturnal species and is unlike that of its closest relative, the emu. Nocturnal owls, such as the boobook owl (*Ninox boobook*), Northern saw-whet owl (*Aegolius acadicus*) and barn owl (*Tyto alba*), show enlargement of the visual Wulst [Iwaniuk and Hurd, 2005; Iwaniuk et al., 2008], the primary telencephalic representation of the thalamofugal system [Güntürkün et al., 1993; Shimizu and Karten, 1993]. The most extreme hypotrophy in kiwi was seen in the entopallium, the end station of the tectofugal visual pathway. The small relative size of the hyperpallium and entopallium in kiwi is likely commensurate with the suggested reduction in the reliance on vision. Kiwi have small eyes, a small optic nerve and optic tectum and small visual fields, including a reduced frontal binocular field [Martin et al., 2007]. Similar to the hyperpallium, the arcopallium in kiwi has not increased in size relative to the hindbrain, and thus did not contribute to the enlargement of the telencephalon. Since visual output from the entopallium, in particular, reaches the arcopallium, the reduction in size of the latter in kiwi could also reflect a reduction in the functional importance of vision.

Also noteworthy is that the only region that did not accompany the telencephalic enlargement in the Eastern rosella and Australian magpie was the hippocampus. The hippocampus has been the focus of many studies and has been shown to be essential to learning and memory, with variations in size correlating with tasks involving an extra demand for spatial learning and memory [Krebs et al., 1989; Sherry et al., 1989; Healy and Krebs, 1992; Basil et al., 1996; Healy and Krebs, 1996; Clayton, 1998; Biegler et al., 2001]. The hippocampus is also interesting because hippocampal neurons are continually produced in birds through adult neurogenesis [Barnea and Nottebohm, 1994]. Why the hippocampus did not enlarge with the

rest of the telencephalon in the Eastern rosella and Australian magpie, as it did in the kiwi, is unknown, but these differences may reflect an enhanced reliance on learning and memory in the kiwi, or possibly differences in adult neurogenesis between the species. Unfortunately, it was not possible to include species in this data set that have been shown to have enhanced spatial learning and memory abilities to further examine variations in hippocampus size in birds.

The most interesting morphological feature of a region in the telencephalon was the rostrocaudal and dorsoventral expansion of the mesopallium in the kiwi. The mesopallium contributed to the enlargement of the telencephalon, but not beyond that expected from scaling to the telencephalon. It is not clear whether the changes in overall architecture of the mesopallium may represent differential growth of particular nuclei within the region, and if so, whether these are associated with particular behaviors. Alternatively, the changes in 3D shape could simply be the result of a reorganization of the different brain regions to adjust to the hypotrophy of the arcopallium, hyperpallium and entopallium.

Overall, this study has shown that the relative size and morphology of telencephalic areas is not homogeneous across birds, and large differences can be seen between

closely related species such as the kiwi and emu. Many of the enlargements and reductions of telencephalic regions seen in this study likely reflect the animal's behavior, ecology or physiology. This is especially true for regions, such as the entopallium, that are known to play a major role in vision, but is less clear for regions such as the mesopallium, due to the multiple sensory representations of the latter and its apparent role in a variety of different behaviors. Nevertheless, the results provide further evidence of mosaic evolution and highlight the importance of the environment in shaping the brain organization of birds.

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