J Comp Physiol A (2006) 192:1313–1326
DOI 10.1007/s00359-006-0161-2

ORIGINAL PAPER

The evolution of stereopsis and the Wulst in caprimulgiform birds: a comparative analysis

Andrew N. Iwaniuk · Douglas R. W. Wylie

Received: 27 March 2006 / Revised: 3 August 2006 / Accepted: 6 August 2006 / Published online: 30 August 2006

Abstract Owls possess stereopsis (i.e., the ability to perceive depth from retinal disparity cues), but its distribution amongst other birds has remained largely unexplored. Here, we present data on species variation in brain and telencephalon size and features of the Wulst, the neuroanatomical substrate that subserves stereopsis, in a putative sister-group to owls, the order Caprimulgiformes. The caprimulgiforms we examined included nightjars (Caprimulgidae), owlet-nightjars (Aegothelidae), potoos (Nyctibiidae), frogmouths (Podargidae) and the Oilbird (Steatornithidae). The owlet-nightjars and frogmouths shared almost identical relative brain, telencephalic and Wulst volumes as well as overall brain morphology and Wulst morphology with owls. Specifically, the owls, frogmouths and owlet-nightjars possess relatively large brains and telencephalic and Wulst volumes, had a characteristic brain shape and displayed prominent laminae in the Wulst. In contrast, potoos and nightjars both had relatively small brains and telencephala, and Wulst volumes that are typical for similarly sized birds from other orders. The Oilbird had a large brain, telencephalon and Wulst, although these measures were not quite as large as those of the owls. This gradation of owl-like versus nightjar-like brains within caprimulgiforms has significant implications for understanding the evolution of stereopsis and the Wulst both within the order and birds in general.

Keywords Wulst · Caprimulgiformes · Evolution · Stereopsis · Strigiformes

Introduction

A series of neurophysiological, neuroanatomical and behavioral experiments has demonstrated that owls possess a visual system that is very similar to primates (van der Willigen et al. 1998) and cats insofar as it is designed to subserve stereopsis. At least two features of the owl visual system sets them apart from most other birds. First, owl eyes are positioned frontally, such that they have a large area of binocular visual field overlap [44 to >50° horizontally; Barn Owl (*Tyto alba*), Pettigrew and Konishi 1984; Tawny Owl (*Strix aluco*), Martin 1984; Northern Saw-whet Owl (*Aegolius acadicus*), Wylie et al. 1994]. Although all birds have some degree of binocular overlap (Martin and Katzir 1999), the magnitude pales in comparison to that of owls (Martin and Coetzee 2004). Second, compared to other species, owls have a grossly hypertrophied visual Wulst (Stingelin 1958; Karten et al. 1973; Pettigrew 1979; Iwaniuk and Hurd 2005), the putative homolog of mammalian primary visual cortex (V1) (e.g., Shimizu and Karten 1993; Medina and Reiner 2000; Reiner et al. 2005). Recordings from the owl Wulst reveal that it is functionally like V1; Wulst neurons are selective for orientation, movement direction, spatial frequency and binocular disparity (Pettigrew and Konishi 1976; Pettigrew 1979; Porciatti et al. 1990; Wagner and Frost 1993; Nieder and Wagner 2000, 2001). Critically, the

---

A. N. Iwaniuk (✉) · D. R. W. Wylie
Department of Psychology, University of Alberta,
Edmonton, AB, Canada T6G 2E9
e-mail: brainsize@yahoo.ca

D. R. W. Wylie
Centre for Neuroscience, University of Alberta,
Edmonton, AB, Canada T6G 2E9

vast majority (86%) of neurons are binocular and tuned to a particular disparity (Pettigrew 1979). Binocular neurons are present in the Wulst of other species, but they are not as numerous as they are in owls (e.g., Perisic et al. 1971; Pettigrew 1978; Wilson 1980; Denton 1981). Although the role of the Wulst in stereopsis has yet to be definitively proven, the available neural evidence from owls suggests that the Wulst mediates stereopsis.

While it is clear that the owls have evolved global stereopsis (i.e., depth perception throughout all or most of the visual field) independently from mammals (Pettigrew 1986), its evolution and phylogenetic distribution within birds has not been investigated. Owls are considered by some to be closely related to the order Caprimulgiformes (Sibley and Ahlquist 1990; Livezey and Zusi 2001), which is a diverse assemblage of nocturnal birds. Three families within the Caprimulgiformes possess frontal eye position comparable to owls: frogmouths (Podargidae; binocular overlap = 50° horizontally; Wallman and Pettigrew 1985), owlet-nightjars (Aegothelidae) and Oilbird (*Steatornis caripensis*, Steatornithidae; binocular overlap = 38–50°, Pettigrew and Konishi 1984; Martin et al. 2004a, b). Nightjars (Caprimulgidae), on the other hand, have a narrower binocular visual field (25°; Martin et al. 2004b). Lastly, nothing is known about the visual field or abilities of the fifth family: the potoos (Nyctibiidae).

Stereopsis is thought to be present in both owlet-nightjars and frogmouths (Pettigrew 1986) because of their frontal eye position and an area of binocular visual overlap comparable to that of owls (Wallman and Pettigrew 1985; Pettigrew 1986). However, there are no behavioral studies that demonstrate stereopsis and no reports of electrophysiological investigations of the Wulst for either family. With respect to the Oilbird, electrophysiological investigations failed to find any binocular neurons in the Wulst (Pettigrew and Konishi 1984), despite the presence of a broad area of binocular visual field overlap (Pettigrew and Konishi 1984; Martin et al. 2004a, b). Finally, Pettigrew (1986) reported that there was no evidence of binocular neurons in the Wulst of nightjars based on both electrophysiological and anatomical investigations, but details are lacking.

Given that both the owls and frogmouths possess a grossly enlarged Wulst (Pettigrew 1986; Iwaniuk and Hurd 2005) and owls, and possibly frogmouths, possess stereopsis (Pettigrew 1986), it is conceivable that Wulst enlargement underlies functional global stereopsis. Currently, little is known about how the relative size of the Wulst varies among birds and this is especially true of caprimulgiforms. Stingelin (1958) documented a large amount of variation in Wulst size and structure in birds, but did not provide any detailed volumetric data for the Wulst or its constituent regions and only included a single caprimulgiform (*Caprimulgus europaeus*). If claims of stereopsis in the owlet-nightjar and frogmouth are correct (Pettigrew 1986), then we would expect to see an enlargement of the Wulst in both families such that they are similar to owls. Similarly, the relative size of the Wulst could indicate whether potoos have stereoscopic vision or not. Enlargement of the Wulst can also result in an increase in overall brain and telencephalic volumes (Iwaniuk et al. 2005; Iwaniuk and Hurd 2005) and changes in Wulst morphology (Stingelin 1958). We therefore surveyed the five currently recognized caprimulgiform families and examined the following features: brain size and morphology, telencephalic size and Wulst size and morphology.

Methods

Specimens

Brain volumes were measured from fixed brains as well as endocranial volumes (Iwaniuk and Nelson 2002) of skeletal specimens (Table 1). These data included measurements from over 200 individuals representing 18 caprimulgiform and 40 owl (Strigiformes) species. Fixed brains of a Spotted Nightjar (*Eurostopodus argus*), Barn Owl (*Tyto alba*) Boobook Owls (*Ninox boobook*, $n = 2$) and Tawny Frogmouths (*Podargus strigoides*, $n = 3$) were extracted from carcasses obtained as roadkills and from Healesville Sanctuary (Healesville, VIC, Australia). Grey Potoo (*Nyctibius griseus*), Oilbird, Pauraque (*Nyctidromus albicollis*) and Feline Owlet-nightjar (*Aegotheles insignis*) specimens were loaned to us from the National Museum of Natural History (Washington, DC, USA) and the Bishop Museum (Honolulu, HI, USA) and a Northern Saw-whet Owl was donated by B.J. Frost (see Table 2). The brains of all of the museum specimens, which were all stored in 70% ethanol for up to 45 years, were extracted and placed into buffered 4% paraformaldehyde. They were subsequently placed into 30% sucrose in 0.1 M phosphate buffered saline until they sank. The brains were then embedded in gelatin and serially sectioned in the transverse plane on a freezing stage microtome at 40 μm. The sections were collected in 0.1 M phosphate buffered saline, mounted onto gelatinized slides, stained for Nissl substance with thionin and coverslipped with Permount.

Table 1 A list of the caprimulgiform and owl species measured, sample sizes and means of brain volume (mm^3) and body mass (g)

Order	Family	Species		*n*	Brain volume (mm^3)	Body mass (g)
Caprimulgiformes	Aegothelidae	Australian owlet-nightjar	*Aegotheles cristatus*	8	1,420	41.0
	Caprimulgidae	Chuck-will's-widow	*Caprimulgus carolinensis*	9	1,360	109.5
		European nightjar	*Caprimulgus europaeus*	10	880	67.0
		Large-tailed nightjar	*Caprimulgus macrurus*	9	1,010	78.0
		Whip-poor-will	*Caprimulgus vociferus*	10	820	50.8
		Common nighthawk	*Chordeiles minor*	10	850	57.1
		Spotted nightjar	*Eurostopodus argus*	2	1,240	72.0
		Great eared-nightjar	*Eurostopodus macrotis*	5	1,460	168.8
		White-throated nightjar	*Eurostopodus mystacialis*	2	1,330	170.0
		Pennant-winged nightjar	*Macrodipteryx vexillarius*	6	870	66.1
		Pauraque	*Nyctidromus albicollis*	8	910	56.6
		Ocellated poorwill	*Nyctiphrynus ocellatus*	3	740	39.0
		Band-tailed nighthawk	*Nyctiprogne leucopyga*	4	510	23.0
		Common poorwill	*Phalaenoptilus nuttallii*	2	530	51.6
		Nacunda nighthawk	*Podager nacunda*	5	1,290	213.3
	Nyctibiidae	Grey potoo	*Nyctibius griseus*	5	1,980	257.4
	Podargidae	Tawny frogmouth	*Podargus strigoides*	15	4,860	387.3
	Steatornithidae	Oilbird	*Steatornis caripensis*	1	3,900	414.0
Strigiformes	Strigidae	Saw-whet owl	*Aegolius acadicus*	9	3,360	73.1
		Boreal owl	*Aegolius funereus*	6	4,020	91.2
		African marsh owl	*Asio capensis*	5	5,980	310.0
		Short-eared owl	*Asio flammeus*	26	5,300	309.8
		Long-eared owl	*Asio otus*	12	5,310	214.7
		Burrowing owl	*Athene cunicularia*	10	3,780	152.8
		Little owl	*Athene noctua*	5	3,700	164
		Spotted eagle owl	*Bubo africanus*	4	8,600	635.0
		Eurasian eagle owl	*Bubo bubo*	5	17,090	2,686.0
		Great horned owl	*Bubo virginianus*	40	14,730	1,415.8
		Ferruginous pygmy owl	*Glaucidium brasilianum*	5	2,510	68.3
		Mountain pygmy owl	*Glaucidium gnoma*	1	3,600	61.9
		Eurasian pygmy owl	*Glaucidium passerinum*	6	2,590	58.5
		Buffy fish-owl	*Ketupa ketupu*	1	12,750	770.0
		Elf owl	*Micrathene whitneyi*	1	1,400	35.0
		Barking owl	*Ninox connivens*	1	6,400	700.0
		Boobook owl	*Ninox booook*	13	5,530	231.4
		Bismark hawk owl	*Ninox solomonis*	3	4,380	130.0
		Moluccan hawk owl	*Ninox squamipila*	1	4,400	175.7
		Powerful owl	*Ninox strenua*	3	11,440	1,359.9
		Snowy owl	*Nyctea scandiaca*	8	15,870	1,894.0
		Eastern screech owl	*Otus asio*	9	4,910	180.5
		Indian scops owl	*Otus bakkamoena*	5	4,040	139.1
		Tropical screech owl	*Otus choliba*	3	3,410	121.5
		Moluccan scops owl	*Otus magicus*	3	3,760	165.0
		Puerto Rican screech owl	*Otus nudipes*	5	3,710	142.5
		Scops owl	*Otus scops*	10	2,490	77.1
		Spectacled owl	*Pulsatrix perspicillata*	1	10,600	873.0
		Tawny owl	*Strix aluco*	5	9,080	426.0
		Grey owl	*Strix nebulosa*	12	14,660	1,056.1
		Black and white owl	*Strix nigrolineata*	5	7,400	527.5
		Ural owl	*Strix uralensis*	5	11,210	784.5
		Barred owl	*Strix varia*	10	12,550	700.0
		Mottled owl	*Strix virgata*	4	6,100	229.5
		Northern hawk-owl	*Surnia ulula*	5	7,480	286.4
	Tytonidae	Barn owl	*Tyto alba*	11	6,510	354.7
		African grass owl	*Tyto capensis*	3	5,230	419.0
		Eastern grass owl	*Tyto longimembris*	1	5,250	478.0
		Australian masked owl	*Tyto novaehollandiae*	9	8,470	766.6
		Greater sooty owl	*Tyto tenebricosa*	3	12,700	671.5

Table 2 A list of the caprimulgiform and owl families surveyed for stereopsis and their body masses (g), brain volumes (mm^3), telencephalic volumes (mm^3) and Wulst volumes (mm^3)

Order	Family	Species	*n*	Body mass (g)	Brain volume (mm^3)	Telencephalon volume (mm^3)	Wulst volum (mm^3)	Wulst/ Brain volume	Wulst/ Telencephalon volume	Source
Caprimulgiformes	Aegothelidae	*Aegotheles insignis*	1	–	1,540	1,107.99	363.63	0.2361	0.3282	This study (BBM NG101365)
	Caprimulgidae	*Caprimulgus sp.*	1	53	734	342.75	51.62	0.0703	0.1506	Boire (1989)
		Eurostopodus argus	1	72.0	982	426.73	59.30	0.0604	0.1390	This study
		Nyctidromus albicollis	1	56.6	910	414.83	66.03	0.0726	0.1592	This study (USNM504211)
	Nyctibiidae	*Nyctibius griseus*	1	257.4	1,980	1,004.67	176.67	0.0892	0.1758	This study (USNM504184)
	Podargidae	*Podargus strigoides*	3	387.0	5,311	3,826.81	1,226.89	0.2310	0.3206	This study
	Steatornithidae	*Steatornis caripensis*	1	414.0	3,900	2,887.70	749.53	0.1922	0.2596	This study (USNM431365)
Strigiformes	Strigidae	*Aegolius acadicus*	1	86.0	2,857	2,009.90	743.75	0.2603	0.3700	This study (donated by B.J. Frost)
		Athene cunicularia	1	167.0	5,878	4,813.80	1,707.67	0.2905	0.3547	Alma and Bee de Speroni (1995)
		Ninox boobook	2	231.4	5,626	3,920.44	1,503.68	0.2673	0.3835	This study
	Tytonidae	*Tyto alba*	2	450.0	6,149	4,108.53	1,605.41	0.2611	0.3908	Alma and Bee de Speroni (1995) and This study

Note that for all species, with the exception of the Boobook Owl ($n = 2$) and Tawny Frogmouth ($n = 3$), only one specimen was measured

USNM National Museum of Natural History, Washington, DC, *BBM* Bernice Bishop Museum, Honolulu, HI

For measurements of the telencephalon and Wulst, data was collected from seven caprimulgiforms and three owls (Table 2). In addition, data for numerous other species was gleaned from the literature (Table 3). For the museum specimens, shrinkage was estimated by comparing the brain volumes of the specimens measured with known brain volumes of the species (see Table 1 and Iwaniuk and Nelson 2003). This enabled volumes to be reconstructed that could be compared with body masses. The only species that we could not calculate a shrinkage factor for was the Feline Owlet-nightjar. For this specimen, we related the size of the telencephalon and Wulst only to the brain volume of the specimen that we examined.

Digital photographs were taken throughout the brain for every second or fourth section, depending upon the size of the brain such that 60–80 sections were measured for each brain. It should be noted that varying the sampling interval in this fashion does not significantly affect volumetric measurements (Iwaniuk et al. 2006). The volumes of the telencephalon and Wulst were measured with the public domain NIH Image program (http://www.rsb.info.nih.gov/nih-image/). All hyperpallial structures were included in the Wulst measurements: the apical hyperpallium (HA), interstitial part of the hyperpallium (HI), intercalated part of the apical hyperpallium (IHA), and densocellular part of the hyperpallium (HD) (Shimizu and Karten 1993; Reiner et al. 2005). It was not possible to calculate the volumetric fractions of each of these Wulst subdivisions because they could not be reliably delineated throughout the extent of the Wulst for all specimens. Borders were delineated by: the vallecula laterally, the superior frontal lamina ventrally and the ventricle medially. We defined the caudal pole as the point at which the vallecula could no longer be recognized and the hippocampal formation was present. The border between the HA and the hippocampal formation was identified by a marked increase in cell density within the hippocampal formation, as shown in previous cytoarchitectonic studies (e.g., Sherry et al. 1989). Due to difficulties in identifying the transition between the parahippocampal area and HA, however, it is possible that some of the hippocampal formation was included as part of the Wulst and vice versa. Although this is potentially a source of error, the borders we drew were replicable and the differences between groups so large (see below), that it is unlikely that this error would significantly affect our conclusions.

Table 3 A list of the other species used to calculate the least-squares regression lines and 95% confidence intervals for the scatterplots shown in Fig. 3

Order	Species
Anseriformes	*Anas platyrhynchos*, *Anser anser*, *Dendrocygna eytoni*
Apodiformes	*Chaetura pelagica*
Charadriiformes	*Calidris minutilla*, *Charadrius vociferus*, *Limnodromus griseus*, *Sterna hirundo*, *Vanellus miles*
Ciconiiformes	*Ardea cinerea*, *Egretta thula*, *Nycticorax caledonicus*
Columbiformes	*Columba leucomela*, *Columba livia*, *Phaps elegans*, *Streptopelia risoria*
Coraciiformes	*Dacelo novaeguineae*, *Todiramphus sanctus*
Falconiformes	*Accipiter fasciatus*, *Falco cenchroides*, *Falco longipennis*
Galliformes	*Alectoris chukar*, *Chrysolophus pictus*, *Colinus virginianus*, *Gallus domesticus*, *Meleagris gallopavo*, *Numida meleagris*, *Ortalis canicollis*, *Pavo meleagris*, *Perdix perdix*, *Phasianus colchicus*
Gruiformes	*Fulica armillata*
Passeriformes	*Corvus corone*, *Entomyzon cyanotis*, *Garrulus glandarius*, *Passer domesticus*, *Strepera versicolor*, *Taeniopygia guttata*
Pelecaniformes	*Phalacrocorax auritus*
Podicipediformes	*Rollandia rolland*
Procellariiformes	*Puffinus tenuirostris*
Psittaciformes	*Agapornis personata*, *Agapornis roseicollis*, *Alisterus scapularis*, *Amazona aestiva*, *Aratinga acuticaudata*, *Cacatua roseicapilla*, *Calyptorhynchus funereus*, *Eclectus roratus*, *Glossopsitta concinna*, *Melopsittacus undulatus*, *Myiopsitta monachus*, *Neopsephotus bourkii*, *Nymphicus hollandicus*, *Pionus menstruus*, *Platycercus elegans*, *Platycercus eximius*, *Polytelis swainsonii*, *Psephotus haematonotus*, *Psittacula eupatria*, *Psittacula krameri*, *Psittacus erithacus*, *Pyrrhura molinae*, *Trichoglossus haematodus*
Sphenisciformes	*Spheniscus magellanicus*
Struthioniformes	*Rhea americana*
Tinamiformes	*Rhynchotus rufescens*
Trochiliformes	*Chlorostilbon mellisugus*

Data for these species was derived from Ebinger (1995), Ebinger and Röhrs (1995), Boire (1989), Carezzano and Bee de Speroni (1995), Ebinger and Löhmer (1984, 1987), Rehkamper et al. (1991), Fernandez et al. (1997) and Iwaniuk and Hurd (2005)

Furthermore, these borders are the same as those used in previous volumetric studies (Ebinger and Löhmer 1984, 1987; Boire 1989; Rehkämper et al. 1991; Ebinger 1995; Ebinger and Röhrs 1995) from which we gleaned Wulst volumes for several additional species (Table 3).

Statistical analysis

We performed multiple comparisons of both telencephalic and Wulst volumes (Deacon 1990; Deaner et al. 2000; Iwaniuk et al. 2005). Telencephalic volumes were scaled relative to body mass and the volume of the brain minus that of the telencephalon. Wulst volumes were scaled relative to body mass, volume of the brain minus the Wulst and volume of the telencephalon minus the Wulst. Using species as independent data points, we calculated least-squares regression lines and 95% confidence intervals. To account for possible phylogenetic effects, we also calculated regression lines and 95% confidence intervals using the independent contrasts approach as shown in Garland and Ives (2000). Phylogenetic relationships among the additional species used to calculate the 95% confidence intervals (Table 3) were taken primarily from Sibley and Ahlquist (1990), with additional resolution provided by Christidis et al. (1991), Sheldon et al. (2000), Dimcheff et al. (2002) and Wink et al. (2004). Given the uncertain relationships among the caprimulgiform families (see Sibley and Ahlquist 1990; Mayr 2002; Cracraft et al. 2004), we did test alternative topologies of the phylogenetic tree, but the results were qualitatively identical to those presented here. That is, there were no changes in the significance of the results among the different branching patterns. The tree was entered into the PDTREE module of the Phenotypic Diversity Analysis Programs (PDAP) software package (available from T. Garland). Because we relied upon multiple sources for the phylogenetic tree, we tested several arbitrary branch length models. Only equal branch lengths adequately standardized the data (Garland et al. 1992) and were therefore used in all phylogenetically based statistics. Independent contrasts were then calculated and the 95% confidence interval around a least-squares linear regression line (as calculated in PDTREE) was plotted onto the original plot of species as independent data points (Garland and Ives 2000). This provides a means of determining whether individual species fall outside of the 95% confidence interval of the data without the difficulties that can be associated with interpreting independent contrasts plots.

Results

Relative brain volume

Figure 1 is a plot of brain volume against body mass for caprimulgiforms and owls. The owls and nightjars cluster into two completely distinct groups: the owls possess relatively large brains, whereas the nightjars possess relatively small brains. In fact, there is a significant grade shift present between the nightjar and owl clusters as shown by a significant difference in intercepts ($F = 5.33$, $df = 1, 57$, $P = 0.02$), but not slopes ($F = 0.32$, $df = 1, 57$, $P = 0.58$) between the two groups. Most of the species from the other caprimulgiform families fall into one of these groups. For example, the potoo is clearly within the nightjar cluster whereas the frogmouth and owlet-nightjar are within the owl cluster. The relative brain volume of the Oilbird is more similar to the owls than the nightjars, but falls outside of the 95% confidence interval calculated for both groups. These differences among the caprimulgiforms remained once phylogeny was accounted for, except for the Oilbird, which was within the phylogeny-corrected 95% confidence interval calculated for the owls. Thus, there is a significant grade shift in relative brain size between

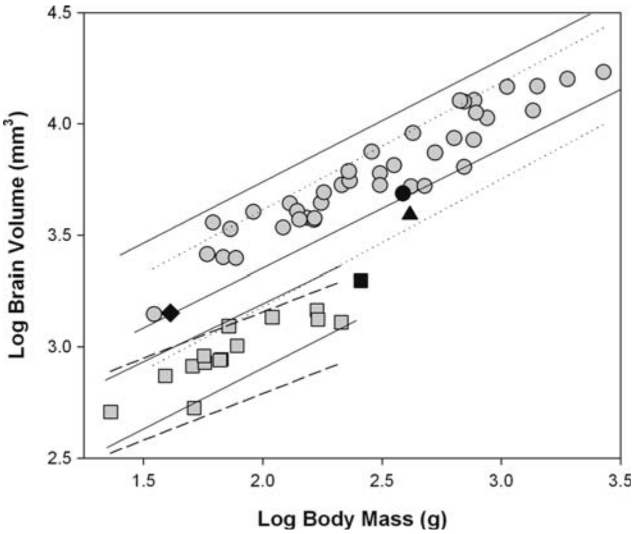


Fig. 1 A scatterplot of log-transformed brain volumes (mm^3) against log-transformed body masses (g) for all caprimulgiform and owl species measured (see Table 1). The symbols refer to the following: *black diamond* Aegothelidae (Australian Owlet-nightjar, *Aegotheles cristatus*); *grey squares* Caprimulgidae (nightjars); *black square* Nyctibiidae (Grey Potoo, *Nyctibius griseus*); *black circle* Podargidae (Tawny Frogmouth, *Podargus strigoides*); *black triangle* Steatornithidae (Oilbird, *Steatornis caripensis*); and *grey circles* Strigiformes (owls). The *solid lines* indicate the 95% confidence intervals for the nightjars and owls. The two other sets of lines refer to the phylogeny-corrected 95% confidence intervals for the nightjars (*dashed lines*) and owls (*dotted lines*)

owls and nightjars and the remaining caprimulgiforms are found within the owls (owlet-nightjar, frogmouth and possibly the Oilbird) or the nightjars (potoo).

Macromorphology

Figure 2 shows photos taken from dorsal, lateral and ventral aspects of owl and caprimulgiform brains. Although only one nightjar brain (*Eurostopodus argus*) is shown, the nightjars and the Grey Potoo are all characterized by a prominent cerebellum and optic lobes in both dorsal and lateral aspects, pronounced olfactory bulbs and a narrow, long and medially oriented Wulst (Fig. 2). This is similar to the photographs of the European Nightjar (*Caprimulgus europaeus*) in Stingelin (1958). The remaining caprimulgiforms, however, vary considerably in overall brain shape. The Oilbird has large olfactory bulbs and large cerebral hemispheres with a prominent and wide Wulst clearly visible on the dorsal surface (Fig. 2). Both the frogmouth and owlet-nightjar possess cerebral hemispheres that are rounded at their rostral pole (Fig. 2). In fact, the curvature of the anterior hemispheres is so rounded that the olfactory bulbs can only be viewed on the ventral surface. The vallecula is prominent on the dorsal surface of the hemispheres and outlines a relatively large Wulst and a greater proportion of the cerebellum is obscured by the cerebral hemispheres than in the nightjar. These morphological features are shared with the Barn Owl (Fig. 2, Stingelin 1958). The Boobook Owl, on the other hand, also possesses a brain that is dominated by the cerebral hemispheres and has a prominent vallecula (Fig. 2). The anterior hemispheres are not, however, as rounded as the Tawny Frogmouth, Feline Owlet-nightjar or Barn Owl. Instead, they come to an acute angle and the olfactory bulbs are located at the rostral tip of the hemispheres, in a similar fashion to the Northern Saw-whet Owl that we examined and photographs of other strigid owl brains in Stingelin (1958). The Wulst also appears to extend more laterally, relative to the length of the brain than in the Barn Owl and Tawny Frogmouth. All of these features underlie significant differences in telencephalon and Wulst volume that are outlined below.

Relative telencephalon volume

Figure 3 shows scatterplots of telencephalic volume against body mass (Fig. 3a) and overall brain volume (Fig. 3b). In both instances, the owls, Oilbird, owlet-nightjar and frogmouth all had relatively large telencephala compared to the nightjars and potoo. The 95% confidence intervals (both conventional and phylogeny-corrected) were all relatively broad, however, such that none of the owls or caprimulgiforms were actually outside of them. Thus, any expansion of the Wulst that may be present does not manifest itself as a significant increase in relative telencephalic volume.

Wulst size and morphology

As a proportion of the entire volume of the brain and telencephalon, the owls possess much larger Wulst volumes than any other species (Table 2). This is also reflected in scatter plots of Wulst volume against body mass, brain volume minus Wulst volume and telencephalic volume minus Wulst volume (Fig. 4). Regardless of what scaling measure is used or whether phylogenetic information is included in the calculation of the interval or not, the owls are all above the 95% confidence interval. Two of the caprimulgiforms, the frogmouth and the owlet-nightjar, also possess large Wulsts that are above the upper limits of the 95% confidence intervals (Fig. 4b, c), but they are slightly smaller than that of the owls. The nightjars and potoo, on the other hand, possess relatively smaller Wulst volumes and are more similar to the other birds included in our analysis (see Table 3). Interestingly, the Oilbird has an enlarged Wulst relative to both brain volume (Fig. 4b) and telencephalic volume (Fig. 4c). In relation to the other species, the Oilbird is generally situated between the owls, frogmouth and owlet-nightjar on one hand and the nightjar and potoo on the other hand.

The morphology of the Wulst also varies between the nightjars and owls. The lamination of the Wulst layers in the owls is distinct and each layer can be readily identified cytoarchitectonically, as shown in the Boobook Owl (Fig. 5a). The HA is quite thick, the IHA appears as a dark band with both the dorsal and ventral subregions clearly visible. The HI is discernible in between IHA and HD and the HD can be readily distinguished from the underlying mesopallium (M) by a thick superior frontal lamina. This is almost identical to the Wulst architecture described by Karten et al. (1973) and Stingelin (1958) for other strigid owls. The morphology of the nightjar Wulst, however, is quite different (Fig. 5b). Unlike the owls, HI and IHA are difficult to define cytoarchitectonically and the lamina separating HD from M is not as noticeable. Furthermore, we had difficulty in finding any discernible division of the internal and external parts of the IHA. In the case of the Oilbird, which was a museum specimen stored in ethanol for an

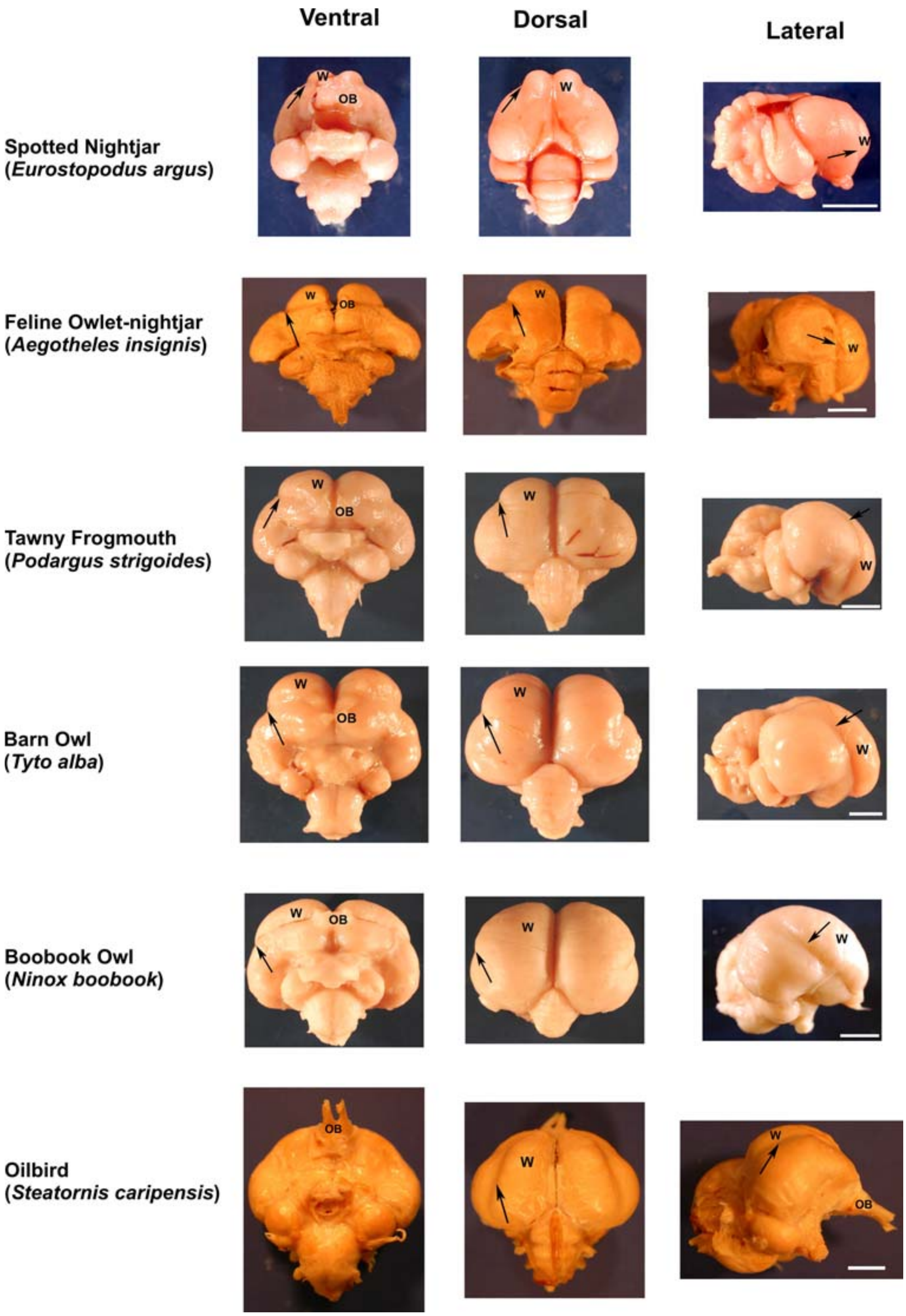


Fig. 2 Photographs taken from ventral, dorsal and lateral views are shown for (from top to bottom): Spotted Nightjar (*Eurostopodus argus*); Feline Owlet-nightjar (*Aegothelis insignis*) (BBM-NG101365); Tawny Frogmouth (*Podargus strigoides*); Barn Owl (*Tyto alba*); Boobook Owl (*Ninox boobook*); and Oilbird (*Steatornis caripensis*) (USNM431365). Shown on each view are vallecula (*arrow*); olfactory bulbs (*OB*); and Wulst (*W*) (scale bar = 5 mm). Note that the discoloration of the owlet-nightjar and oilbird are the result of long-term storage in 70% ethanol

extended period of time (45 years), the quality of staining throughout the telencephalon was relatively poor. As such, although we were able to obtain the volume of the Wulst, we were unable to accurately define the borders of structures within the Wulst of the Oilbird.

As with the volumetric comparisons already discussed, the other caprimulgiforms vary as to whether they are owl-like or nightjar-like. The frogmouth Wulst is strikingly similar to the owl (Fig. 5c). Again, each of the layers can be readily distinguished from one another and the morphology of each layer is consistent with that of the owl. That is, the IHA is darkly stained relative to HA and the dorsal and ventral parts can be distinguished from one another, HI is distinct and HD is separated from M by a discrete superior frontal lamina. The same is also true of the owlet-nightjar (Fig. 5d). The owlet-nightjar Wulst also

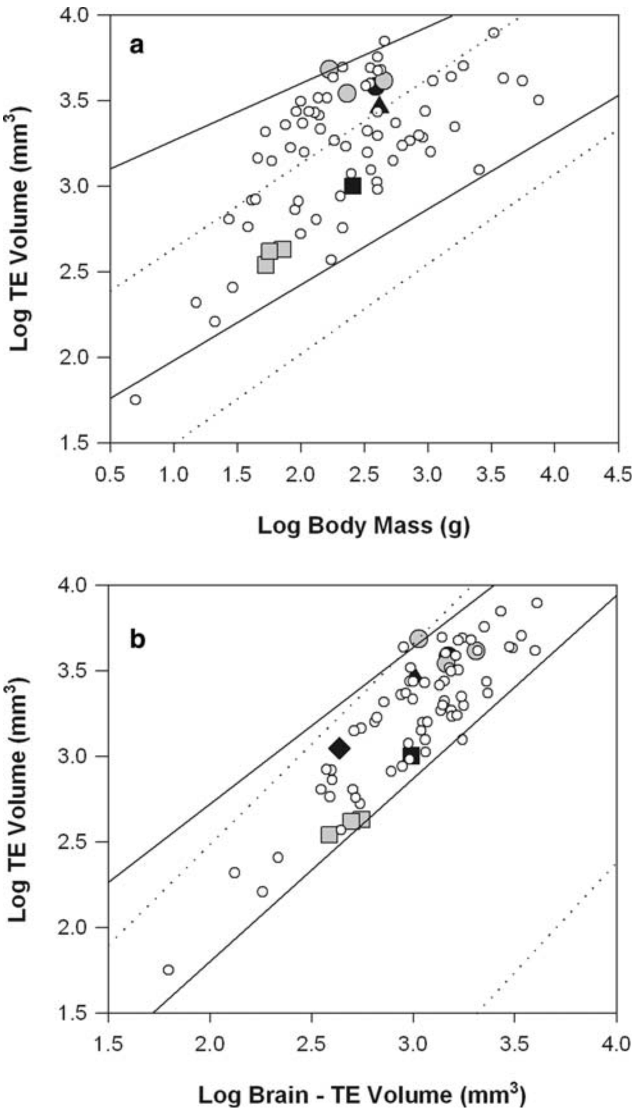


Fig. 3 A scatterplot of log-transformed telencephalic volumes (mm^3) against: **a** log-transformed body masses (g); and **b** log transformed brain volume minus Wulst volume (mm^3; see Table 2). The symbols refer to the following: *black diamond* Aegothelidae (Feline Owlet-nightjar, *Aegotheles insignis*); *grey squares* Caprimulgidae (nightjars); *black square* Nyctibiidae (Grey Potoo, *Nyctibius griseus*); *black circle* Podargidae (Tawny Frogmouth, *Podargus strigoides*); *black triangle* Steatornithidae (Oilbird, *Steatornis caripensis*); *grey circles* Strigiformes (owls); and *open circles* all other birds. Two sets of 95% confidence intervals are shown based upon least-squares linear regression lines calculated for all other species of birds (see Table 3): conventional statistics (*solid lines*) and statistics that include phylogenetic information (*dotted lines*). Note that the Feline Owlet-nightjar is not included in the comparison of Wulst volume and body mass because body mass was not available for the specimen examined nor could an average body mass for this species be found in the literature

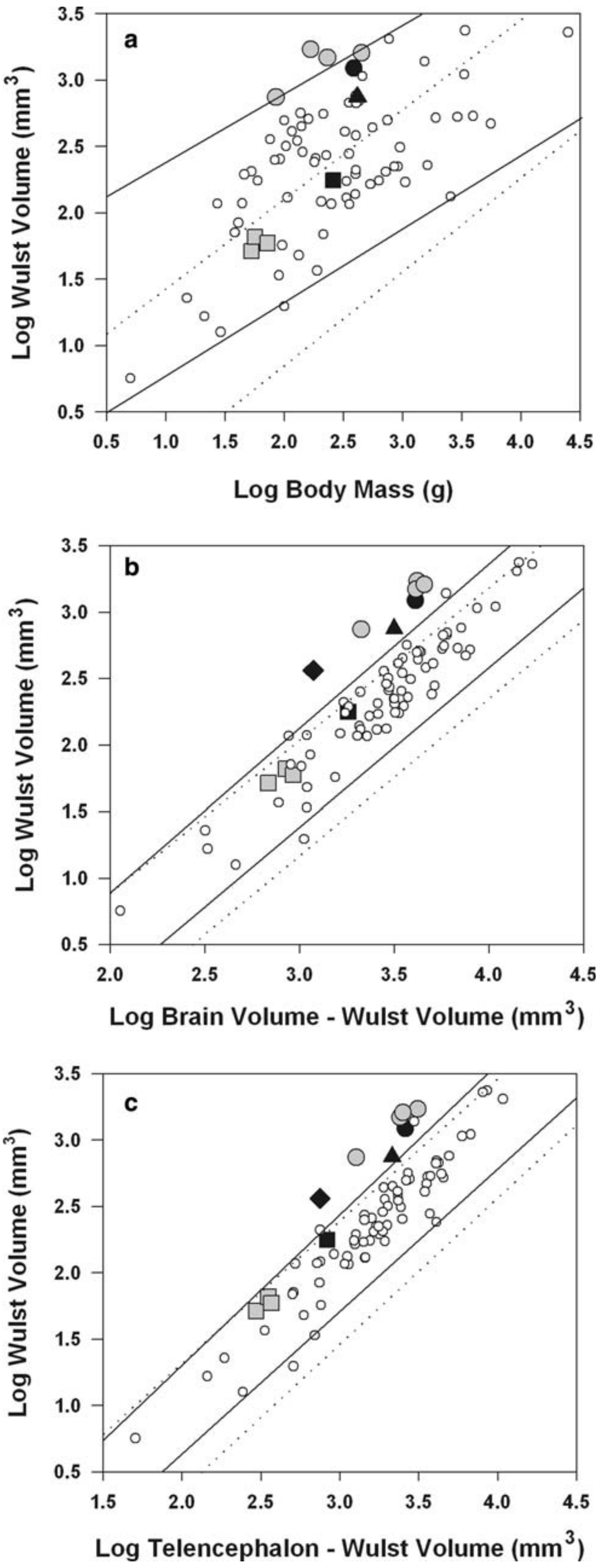
possesses a darkly stained IHA with both dorsal and ventral divisions visible, HI is reasonably distinct and the superior frontal lamina is clearly visible. The shape of the owlet-nightjar Wulst does, however, differ from the frogmouth and owls in that it extends far less laterally. This is also evident in the pictures of overall brain shape for the owlet-nightjar (Fig. 2). Lastly, although not shown, the potoo is almost identical to the nightjars. The layers of the Wulst are visible, but are difficult to discern from one another in Nissl stained sections.

Discussion

Nightjars and owls clearly possess markedly different brains. They differ not only in relative size and macromorphology, but also in the relative size of the telencephalon and Wulst and in Wulst morphology. Two of the other caprimulgiform families surveyed, the frogmouths and owlet-nightjars, shared similar relative brain size, macromorphology, telencephalon and Wulst size and Wulst morphology with the owls. The potoo, however, was almost identical to the nightjars in all these features. Lastly, the Oilbird was intermediate between the owls and nightjars, although it did have a moderately expanded telencephalon and Wulst.

Caveats

Although the comparisons presented herein relied upon relatively few species within each family, the differences between owls and nightjars is so large that the effects of sampling only a single species within each family are limited because there is little behavioral and/or ecological variability in three of the families surveyed. For example, the behavior and life history of owlet-nightjars, nightjars and potoos are highly conserved within their respective families (Cleere 1998; del Hoyo et al. 1999). The Podargidae is the only exception. Within this family, the genus *Batrachostomus* feeds almost exclusively on arthropods that are caught by pouncing from a perch or gleaning from branches and other surfaces (Cleere 1998; del Hoyo et al. 1999). However, *Podargus* species, such as the Tawny Frogmouth, feed on small vertebrates in addition to arthropods, all of which are caught by swooping down onto prey from a perch in a similar fashion to owls (Cleere 1998; del Hoyo et al. 1999; Higgins 1999). In addition to these behavioral differences between frogmouth genera, there are marked molecular and morphological differences that have led some authors to suggest that they should be placed in separate families (Sibley and Ahlquist 1990; Mariaux and Braun 1996). Because *Batrachostomus* specimens are extremely rare in



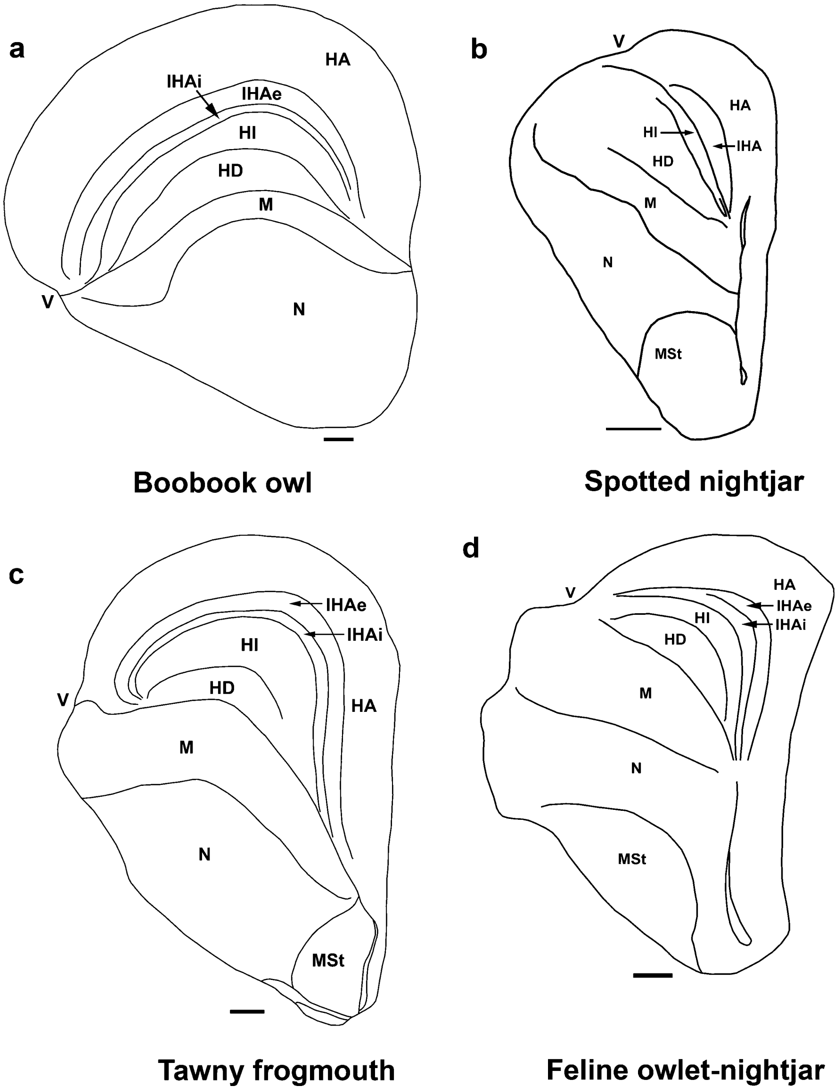
◄ **Fig. 4** A scatterplot of log-transformed Wulst volumes (mm^3) against **a** log-transformed body masses (g); **b** log-transformed brain volume minus Wulst volume (mm^3); and **c** log-transformed telencephalic volume minus Wulst volume (mm^3) for all caprimulgiform and owl species measured (Table 2). The symbols refer to the following: *black diamond* Aegothelidae (Feline Owlet-nightjar, *Aegotheles insignis*); *grey squares* Caprimulgidae (nightjars); *black square* Nyctibiidae (Grey Potoo, *Nyctibius griseus*); *black circle* Podargidae (Tawny Frogmouth, *Podargus strigoides*); *black triangle* Steatornithidae (Oilbird, *Steatornis caripensis*); *grey circles* Strigiformes (owls); and *open circles* all other birds. Two sets of 95% confidence intervals are shown based upon least-squares linear regression lines calculated for all other species of birds (see Table 3): conventional statistics (*solid lines*) and statistics that include phylogenetic information (*dotted lines*). As with Fig. 3, the Feline Owlet-nightjar is not included in the comparison of Wulst volume and body mass because body mass was not available for the specimen examined nor could an average body mass for this species be found in the literature

museum collections, we were unable to examine one, so this study only reflects the condition present in *Podargus* frogmouths.

Another potential source of error is the sampling of only a single individual of each species. It should be noted, however, that variation within species is generally far lower than that between species (Stephan and Pirlot 1970; Pirlot and Bee de Speroni 1987; A. N. Iwaniuk, unpublished data). Furthermore, the volumetric differences reported herein between the owl-like and nightjar-like birds are substantial and it is unlikely that even with the inclusion of additional specimens that our conclusions would be significantly altered.

Stereopsis and Wulst size

The combination of an enlarged Wulst and global stereopsis in owls suggests that Wulst size and stereopsis are correlated. This is supported by the presence of a similarly enlarged Wulst in owlet-nightjars and frogmouths, which are thought to have stereoscopic vision (Pettigrew 1986). Wulst expansion can, however, occur independently of stereopsis and vice versa. Diurnal raptors, for example, have stereoscopic vision (Fox et al. 1977) and large numbers of binocular neurons in the visual Wulst (Pettigrew 1978), but do not have an enlarged Wulst (Iwaniuk and Hurd 2005, this study). Perhaps part of the reason for this seemingly inconsistent relationship between stereopsis and Wulst size is that the Wulst is not an exclusively visual structure (Funke 1989; Wild 1997; Medina and Reiner 2000; Manger et al. 2002). Indeed, the rostral Wulst receives somatosensory projections (Wild 1997; Manger et al. 2002), has cells that are responsive to tactile stimulation of the body, limbs, head and neck (Funke 1989) and in species that forage using tactile information from the beak, the rostral Wulst is greatly expanded (Pettigrew and Frost 1985). Given that a large Wulst is not essential to stereopsis per se, why is the owl's Wulst enlarged?



Boobook owl

Spotted nightjar

Tawny frogmouth

Feline owlet-nightjar

Fig. 5 Shown here are schematic drawings of the Wulst architecture of: **a** Boobook Owl (*Ninox boobook*); **b** Spotted Nightjar (*Eurostopodus argus*); **c** Tawny Frogmouth (*Podargus strigoides*); and **d** Feline Owlet-nightjar (*Aegotheles insignis*) (scale bar = 1 mm). Each layer of the Wulst is indicated as follows: apical hyperpallium (*HA*), internal (*IHAi*) and external (*IHAe*) layers of the intercalated part of the apical hyperpallium, interstitial part of the hyperpallium (*HI*); densocellular part of the hyperpallium (*HD*) (following nomenclature in Reiner et al. 2004). Additional structures indicated on the drawings include: vallecula (*V*); medial striatum (*MSt*); mesopallium (*M*) and nidopallium (*N*)

One feature of the visual system that does set owls apart from other birds is the amount of binocular overlap in their visual field. As mentioned previously owls have a much larger area of horizontal field binocular overlap (44–50°; Martin 1984; Pettigrew and Konishi 1984; Wylie et al. 1994) than other birds (horizontal mean = 20°; data from Martin and Katzir 1999). The visual field of owls is so unique that in their categorization of avian visual fields, Martin and Coetzee (2004) placed owls in a category all their own because of the broad frontal binocular field and extensive blind areas above and behind the head. Other birds have binocular visual fields (Martin and Katzir 1999; Martin and Coetzee 2004) and are capable of stereopsis within this field (e.g., McFadden and Wild 1986), but this occupies only a small part of the entire visual field. For example, raptors have some degree of binocular overlap in their visual field, but the area of binocular overlap is much smaller than in owls (20–24° horizontally and 80° vertically) and as such, it is localized to only a portion of the entire visual field (Wallman and Pettigrew 1985; Martin and Katzir 1999). Despite the width of this field and the size of the Wulst, binocular neurons appear to far outnumber monocular neurons in the American Kestrel's (*Falco sparverius*) visual Wulst (Pettigrew 1978) and they too are capable of stereopsis (Fox et al. 1977). Perhaps the Wulst enlargement of owls reflects their wider stereoscopic field compared to diurnal raptors and other birds. Frogmouths do have a large binocular field similar to that of owls and convergent eye movements (Wallman and Pettigrew 1985), which suggests the presence of global stereopsis (Pettigrew 1986). Based upon Wulst size and morphology, it follows that owlet-nightjars might possess stereopsis as well, but this has yet to be demonstrated behaviorally or physiologically.

Curiously, the Oilbird has a moderately large degree of binocular overlap (38–50°; Pettigrew and Konishi 1984; Martin et al. 2004a, b) and a moderately enlarged Wulst (Table 2; Fig. 4), but an electrophysiological study failed to find binocular neurons in the Oilbird Wulst (Pettigrew and Konishi 1984). Given that the development of the owl visual Wulst is sensitive to visual input (Pettigrew and Konishi 1976), it is possible that binocular vision has been lost in the Oilbird as a consequence of roosting deep within caves. The moderately enlarged Wulst could therefore be a "carry-over" from a stereoscopic ancestor, like a frogmouth, that has since been co-opted for another purpose, such as somatosensory input to the rostral Wulst from the rictal bristles (see above).

Wulst lamination

In addition to variation in Wulst size, there was also significant variation in the degree of lamination observed in the Wulst. Although, the gradation in Wulst lamination could be an artifact of an enlarged Wulst, it is equally probable that it reflects functional differences related to stereoscopic vision. The construction of neuronal sheets (or lamina) appears to permit the construction of complex topographical maps that are functionally segregated in a variety of neural structures (Striedter 2005). In mammals, the lamination pattern of the neocortex varies significantly among mammalian taxa, such that some species possess more lamina than others (Preuss 2001) and this variation is at least partially related to species differences in connectivity (LaChica et al. 1993). The relatively poorly laminated Wulst in some birds (e.g., nightjar, potoo) compared to the relatively well-laminated Wulst of other birds (e.g., owls, frogmouth, owlet-nightjar) might also reflect functional differences. The darker staining of IHA and the prominence of the internal and external layers in the frogmouth, owlet-nightjar and owls compared to the nightjars and potoo probably reflects a higher density and/or number of cells and therefore a heavier input into the HA. While the IHA projects to telencephalic regions outside of the Wulst (e.g. frontolateral nidopallium), the bulk of the IHA afferents project dorsally to the HA (Shimizu et al. 1995). Because most of the binocular, disparity sensitive neurons are found within the HA (Pettigrew 1979; Nieder and Wagner 2000, 2001) an increase in the amount of input to the HA, such as that provided by a larger or more densely packed IHA, could reflect an increase in the number of binocular neurons. This, however, remains to be verified.

Acknowledgments We wish to thank Carla Kishinami (Bishop Museum, Honolulu, HI, USA) and the staff of the National Museum of Natural History (Washington, DC, USA) for loaning specimens to us, Peter Holz and David Middleton of Healesville Sanctuary for collecting frogmouths, owls and other species on our behalf, Barrie Frost for donating a saw-whet owl brain, the curatorial staff of the Queensland Museum, Provincial Museum of Alberta, National Museum of Natural History, South Australian Museum, Australian National Wildlife Collection and Museum of Victoria for access to their collections, Karen Dean, Sue Swann, Angela Nguyen, Kim Krueger and Erin Kelcher for technical assistance, Ted Garland for the PDAP software, Jack Pettigrew for helpful discussions on Wulst physiology and two anonymous reviewers for their comments. Funding for this study was provided by the Natural Sciences and Engineering Research Council of Canada, Alberta Ingenuity Fund and Canada Research Chairs Program to ANI and DRWW. All of the research reported herein was performed in accordance with the "Principles of animal care", publication No. 86–23, revised 1985 of the National Institute of Health and with the Canadian Council for Animal Care regulations.

References

Alma S, Bee de Speroni N (1992) Indices cerebrales y composicion cuantitativa encefalica en *Athene cunicularia* y *Tyto alba* (Strigiformes: Strigidae y Tytonidae). Facena 9:19–37

Boire D (1989) Comparaison quantitative de l'encephale de ses grades subdivisions et de relais visuals, trijumaux et acoustiques chez 28 especes. PhD Thesis, Universite de Montreal

Carezzano FJ, Bee de Speroni N (1995) Composicion volumetrica encefalica e indices cerebrales en tres aves de ambiente acuatico (Ardeidae, Podicipedidae, Rallidae). Facena 11:75–83

Christidis L, Schodde R, Shaw DD, Maynes SF (1991) Relationships among the Australo-Papuan parrots, lorikeets and cockatoos (Aves: Psittaciformes). Condor 93:302–317

Cleere N (1998) Nightjars: a guide to the nightjars, nighthawks, and their relatives. Yale University Press, New Haven

Cracraft J, Barker FK, Braun M, Harshman J, Dyke GJ, Feinstein J, Stanley S, Cibois A, Schikler P, Beresford P, Garcia-Moreno J, Sorenson MD, Yuri T, Mindell DP (2004) Phylogenetic relationships among modern birds (Neornithes). In: Cracraft J, Donoghue MJ (eds) Assembling the tree of life. Oxford University Press, New York pp 468–489

Deacon TW (1990) Fallacies of progression in theories of brain-size evolution. Int J Primatol 11:193–236

Deaner RO, Nunn CL, van Schaik CP (2000) Comparative tests of primate cognition: different scaling methods produce different results. Brain Behav Evol 55:44–52

del Hoyo J, Elliott A, Sargatal J (1999) Handbook of the birds of the world, vol 5. Barn owls to hummingbirds. Lynx Edicions, Barcelona

Denton CJ (1981) Topography of the hyperstriatal visual projection area in the young domestic chicken. Exp Neurol 74:482–498

Dimcheff DE. Drovetski SV, Mindell DP (2002) Phylogeny of Tetraoninae and other galliform birds using mitochondrial 12S and ND2 genes. Mol Phylogenet Evol 24:203–215

Ebinger P (1995) Domestication and plasticity of brain organization in mallards (*Anas platyrhynchos*). Brain Behav Evol 45:286–300

Ebinger P, Löhmer R (1984) Comparative quantitative investigations on brains of rock doves, domestic and urban pigeons (*Columba* L. *livia*). Z Zool Syst Evol Forsch 22:136–145

Ebinger P, Löhmer R (1987) A volumetric comparison of brains between greylag geese (*Anser anser* L.) and domestic geese. J Hirnforsch 3:291–299

Ebinger P, Röhrs M (1995) Volumetric analysis of brain structures, especially of the visual system in wild and domestic turkeys (*Meleagris gallopavo*). J Brain Res 36:219–228

Fernandez P, Carezzano F, Bee de Speroni N (1997) Análisis cuantitativo encefálico e índices cerebrales en *Aratinga acuticaudata* y *Myiopsitta monachus* de Argentina (Aves: Psittacidae). Rev Chil Hist Nat 70:269–275

Fox R, Lehmkuhle SW, Bush RC (1977) Stereopsis in the falcon. Science 197:79–81

Funke K (1989) Somatosensory areas in the telencephalon of the pigeon. I. Response characteristics. Exp Brain Res 76:603–619

Garland T Jr, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst Biol 41:18–32

Garland T Jr, Ives AR (2000) Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. Am Nat 155:346–364

Higgins PJ (1999) Handbook of Australian, New Zealand and Antarctic birds, vol 4: parrots to dollarbird. Oxford University Press, Melbourne

Iwaniuk AN, Dean KM, Nelson JE (2005) Interspecific allometry and the brain and brain regions in parrots (Psittaciformes): comparisons with other birds and primates. Brain Behav Evol 65:40–59

Iwaniuk AN, Hurd PL (2005) The evolution of cerebrotypes in birds. Brain Behav Evol 65:215–230

Iwaniuk AN, Hurd PL, Wylie DRW (2006) Comparative morphology of the avian cerebellum: I. Degree of foliation. Brain Behav Evol 68:45–62

Iwaniuk AN, Nelson JE (2003) Developmental differences are correlated with relative brain size in birds: a comparative analysis. Can J Zool 81:1913–1928

Iwaniuk AN, Nelson JE (2002) Can endocranial volume be used as an estimate of brain size in birds? Can J Zool 80:16–23

Karten HJ, Hodos W, Nauta WJH, Revzin AM (1973) Neural connections of the ‘visual Wulst’ of the avian telencephalon: Experimental studies in the pigeon (*Columba livia*) and owl (*Speotyto cunicularia*). J Comp Neurol 150:253–278

LaChica EA, Beck PD, Casagrande VA (1993) Intrinsic connections of layer III of striate cortex in squirrel monkey and bush baby: correlations with patterns of cytochrome oxidase. J Comp Neurol 329:163–187

Livezey BC, Zusi RL (2001) Higher-order phylogenetics of modern Aves based on comparative anatomy. Neth J Zool 51:179–205

Manger PR, Elston GN, Pettigrew JD (2002) Multiple maps and activity-dependent representational plasticity in the anterior Wulst of the adult barn owl (*Tyto alba*). Eur J Neurosci 16:743–750

Mariaux J, Braun MJ (1996) A molecular phylogenetic survey of the nightjars and allies (Caprimulgiformes) with special emphasis on the potoos (Nyctibiidae). Mol Phylogenet Evol 6:228–244

Martin GR (1984) The visual fields of the tawny owl, *Strix aluco* L. Vision Res 24:1739–1751

Martin GR, Coetzee HC (2004) Visual fields in hornbills: precision-grasping and sunshades. Ibis 146:18–26

Martin GR, Katzir G (1999) Visual fields in short-toed eagles, *Circaetus gallicus* (Accipitridae), and the function of binocularity in birds. Brain Behav Evol 53:55–66

Martin G, Rojas LM, Figueroa YMR, McNeil R (2004a) Binocular vision and nocturnal activity in oilbirds (*Steatornis caripensis*) and pauraques (*Nyctidromus albicollis*): Caprimulgiformes. Orn Neo 15:233–242

Martin G, Rojas LM, Ramirez Y, McNeil R (2004b) The eyes of oilbirds (*Steatornis caripensis*): pushing at the limits of sensitivity. Naturwiss 91:26–29

Mayr G (2002) Osteological evidence for paraphyly of the avian order Caprimulgiformes (nightjars and allies). J Ornithol 143:82–97

McFadden SA, Wild JM (1986) Binocular depth perception in the pigeon. J Exp Anal Behav 45:149–160

Medina L, Reiner A (2000) Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? Trends Neurosci 23:1–12

Nieder A, Wagner H (2001) Encoding of both vertical and horizontal disparity in random-dot stereograms by Wulst neurons of awake barn owls. Vis Neurosci 18:541–547

Nieder A, Wagner H (2000) Horizontal-disparity tuning of neurons in the visual forebrain of the behaving barn owl. J Neurophysiol 83:2967–2979

Perisic M, Mihailovic J, Cuenod M (1971) Electrophysiology of contralateral and ipsilateral visual projections to the Wulst in pigeon (*Columba livia*). Int J Neurosci 2:7–14

Pettigrew JD (1978) Comparison of the retinotopic organization of the visual wulst in nocturnal and diurnal raptors, with a note on the evolution of frontal vision. In: Cool SJ, Smith EL (eds) Frontiers in visual science. Springer, Berlin Heidelberg New York, pp 328–335

Pettigrew JD (1979) Binocular visual processing in the owl’s telencephalon. Proc R Soc Lond B 204:435–454

Pettigrew JD (1986) The evolution of binocular vision. In: Pettigrew JD, Sanderson KJ, Levick WR (eds) Visual neuroscience. Cambridge University Press, Cambridge, pp 208–222

Pettigrew JD, Frost BJ (1985) A tactile fovea in the Scolopacidae? Brain Behav Evol 26:95–105

Pettigrew JD, Konishi M (1976) Neurons selective for orientation and binocular disparity in the visual Wulst of the barn owl (*Tyto alba*). Science 193:675–678

Pettigrew JD, Konishi M (1984) Some observations on the visual system of the oilbird, *Steatornis caripensis*. Nat Geo Soc Res Rep 16:439–450

Pirlot P, Bee de Speroni N (1987) Encephalization and brain composition in South American rodents (Caviidae, Cricetidae, Dasyproctidae). Mammalia 51:305–320

Porciatti V, Fontanesi G, Raffaelli A, Bagnoli P (1990) Binocularity in the little owl, *Athena noctua* II. Properties of visually evoked potentials from the Wulst in response to monocular and binocular stimulation with sine wave gratings. Brain Behav Evol 35:40–48

Preuss TM (2001) The discovery of cerebral diversity: an unwelcome scientific revolution. In: Falk D, Gibson K (eds) Evolutionary anatomy of the primate cerebral cortex. A feitschrift for Harry Jerison. Cambridge University Press, Cambridge, pp 138–164

Rehkämper G, Frahm HD, Zilles K (1991) Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (insectivores and primates). Brain Behav Evol 37:125–143

Reiner A, Perkel DJ, Bruce LL, Butler AB, Csillag A, Kuenzel W, Medina L, Paxinos G, Shimizu T, Striedter G, Wild M, Ball GF, Durand S, Güntürkun O, Lee DW, Mello CV, Powers A, White SA, Hough G, Kubikova L, Smulders TV, Wada K, Dugas-Ford J, Husband S, Yamamoto K, Yu J, Siang C, Jarvis ED (2004) Revised nomenclature for avian telencephalon and some related brainstem nuclei. J Comp Neurol 473:377–414

Reiner A, Yamamoto K, Karten HJ (2005) Organization and evolution of the avian forebrain. Anat Rec 287A:1080–1102

Sheldon FH, Jones CE, McCracken KG (2000) Relative patterns and rates of evolution in heron nuclear and mitochondrial DNA. Mol Biol Evol 17:437–450

Sherry DF, Vaccarino AL, Buckenham K, Herz HS (1989) The hippocampal complex of food-storing birds. Brain Behav Evol 34:308–317

Shimizu T, Karten HJ 1993 The avian visual system and the evolution of the neocortex. In: Zeigler HP, Bischof HJ (eds) Vision, brain and behavior in birds. MIT Press, Cambridge, pp 103–114

Shimizu T, Cox K, Karten HJ (1995) Intratelencephalic projections of the visual wulst in pigeons (*Columba livia*). J Comp Neurol 359:551–572

Sibley CG, Ahlquist JE (1990) Phylogeny and classification of birds. Yale University Press, New Haven

Stephan H, Pirlot P (1970) Volumetric comparisons of brain structures in bats. Z Zool Syst Evol Forsch 8:200–236

Stingelin W (1958) Vergleichend morphologische Untersuchungen am Vorderhirn der Vögel auf cytologischer und cytoarchitektonischer Grundlage. Verlag Helbing & Lichtenhahn, Basel

Striedter GF (2005) Principles of brain evolution. Sinauer, Sunderland

van der Willigen RF, Frost BF, Wagner H (1998) Stereoscopic depth perception in the owl. NeuroReport 9:1233–1237

Wagner H, Frost B (1993) Disparity-sensitive cells in the owl have a characteristic disparity. Nature 364:796–798

Wallman J, Pettigrew JD (1985) Conjugate and disjunctive saccades in two avian species with contrasting oculomotor strategies. J Neurosci 5:1418–1428

Wild JM (1997) The avian somatosensory system: the pathway from wing to Wulst in a passerine (*Chloris chloris*). Brain Res 759:122–134

Wilson P (1980) The organization of the visual hyperstriatum in the domestic chick. I. Topology and topography of the visual projection. Brain Res 188:319–332

Wink M, Sauer-Gürth H, Fuchs M (2004) Phylogenetic relationship in owls based on nucleotide sequences of mitochondrial and nuclear marker genes. In: Chancelor RD, Meyburg B-U (eds) Raptors worldwide. WWGBP, Berlin, pp 517–526

Wylie DR, Shaver SW, Frost BJ (1994) The visual response properties of neurons in the nucleus of the basal optic root of the northern saw-whet owl (*Aegolius acadicus*). Brain Behav Evol 43:15–25