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Allometric Scaling of the Tectofugal Pathway in Birds

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Key Words
Allometry · Comparative method · Entopallium · Nucleus rotundus · Optic tectum

Abstract
Recent studies have shown that the relative sizes of visual regions in the avian brain are correlated with behavioral differences among species. Despite the fact that the tectofugal pathway is the primary source of visual input to the avian brain, detailed interspecific comparisons of the relative size of nuclei within the pathway, the optic tectum, nucleus rotundus and entopallium, are wanting. Here, we examine the allometric scaling relationships of each of these brain regions relative to the brain as a whole using conventional and phylogenetically based statistics across 113 species. Our results show that the relative size of tectofugal regions of the avian brain varies significantly among avian orders. More specifically, waterfowl (Anseriformes), parrots (Psittaciformes) and owls (Strigiformes) have significantly smaller tectofugal brain regions than other birds. At the opposite end of the spectrum, we found little evidence for the significant enlargement of any tectofugal region among the orders that we sampled. The lack of such hypertrophy likely reflects the heterogeneous organization of the optic tectum, nucleus rotundus and entopallium. We therefore speculate that if neural adaptations do exist in the avian tectofugal pathway that are correlated with behavior, they occur at a more refined level than simple volumetrics.

Introduction

Birds are highly dependent on vision, perhaps more so than many other vertebrates; their eyes are larger, absolutely and relative to body size, than any other terrestrial vertebrates [Walls, 1942; Ritland, 1982; Ali and Klyne, 1985; Martin, 1985; Kiltie, 2000; Land and Nilsson, 2002; Howland et al., 2004; Hall and Ross, 2007]. Although birds, as a general rule, are highly visual, their visual abilities vary tremendously among species. For example, eagles and falcons have visual acuity that is double that of primates [Shlaer, 1972; Fox et al., 1976; Reymond, 1985; Gaffney and Hodos, 2003]. Owls, in contrast, have relatively poor visual acuity [Fite, 1973; Martin and Gordon, 1974], but high sensitivity and global stereopsis similar to that of primates [Pettigrew, 1979; van der Willigen et al., 1998; Nieder and Wagner, 2001]. Budgerigars *(Melopsittacus undulatus)* have excellent color discrimination [Goldsmith and Butler, 2005] and a wide range of species are capable of detecting UV wavelengths [Odeen and

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Hastad, 2003]. Even the commonly used pigeon *(Columba livia)* exhibits an extensive array of visual abilities including the detection of static and dynamic stimuli in noise [Kelly et al., 2001], biological motion [Watanabe and Troje, 2006] and other forms of complex motion [Frost et al., 1994; Sun and Frost, 1998] as well as color discrimination and UV sensitivity [Remy and Emmerton, 1989; Palacios and Varela, 1992] and stereopsis [McFadden and Wild, 1986].

This variation in visual abilities among avian species likely places different processing requirements on visual regions of the brain. According to Jerison's [1973] 'principle of proper mass', if a species requires greater information processing to accomplish a task, there is a corresponding increase in the size of the brain region responsible for processing that information. Recent studies have demonstrated such a relationship between specific visual behaviors and the regions of the brain responsible for those behaviors. One such example is provided by owls. As mentioned previously, owls have global stereopsis akin to that found in primates. This visual specialization has placed significant demands on the processing capacity of the Wulst, the brain region responsible for mediating stereopsis in owls [Pettigrew, 1979, 1986; Nieder and Wagner, 2001]. To compensate for these increased demands, the Wulst has become significantly enlarged in owls compared to other birds [Iwaniuk and Wylie, 2006; Iwaniuk et al., 2008]. In two additional families that have frontally oriented eyes and are thought to possess global stereopsis, the frogmouths (Podargidae) and owlet-nightjars (Aegothelidae), the Wulst has also become enlarged [Iwaniuk and Wylie, 2006]. Although this might suggest that Wulst size and stereopsis are causally related, the fact that pigeons and diurnal raptors (hawks and falcons) also have stereoscopic abilities [Fox et al., 1977; McFadden and Wild, 1986] and do not have an enlarged Wulst remains problematic.

A second example is provided by the pretectum of hummingbirds. The pretectal nucleus lentiformis mesencephali of the avian brain plays a critical role in processing optic flow and the generation of the optokinetic response [Gioanni et al., 1983; McKenna and Wallman, 1985; Winterson and Brauth, 1985; Wylie and Crowder, 2000]. The function of the optokinetic reflex is to stabilize the retinal image [Waespe and Henn, 1987]. Because maintaining a stable position during hovering flight is critical to the feeding success of hummingbirds, significant demands are placed on optic flow processing in the hummingbird brain. To accomplish this task, hummingbirds have significantly enlarged the nucleus lentiformis mesencephali, relative to the rest of the brain [Iwaniuk and Wylie, 2007]. Furthermore, species that occasionally hover, such as the Belted Kingfisher *(Ceryle alcyon)*, have a moderately enlarged nucleus lentiformis mesencephali. Thus, we have ample evidence in birds that different demands on the visual system are correlated with increases in the size of specific visual regions of the brain. The pretectal and thalamofugal pathways are not, however, the sole source of visual input to the brain. In fact, the tectofugal pathway processes the majority of retinal input in birds [Shimizu and Karten, 1991; Bischof and Watanabe, 1997].

The tectofugal pathway is comprised of three main structures: optic tectum (TeO), nucleus rotundus (nRt) and entopallium (E). These regions are involved in processing of several different aspects of visual information including brightness, color, pattern discrimination, simple motion and looming stimuli [Wang et al., 1993; Bischof and Watanabe, 1997; Sun and Frost, 1998; Husband and Shimizu, 2001; Nguyen et al., 2004]. Despite the wide range of visual stimuli that are processed by the tectofugal pathway, relatively little is known about how the size of each of the components of the pathway, and the entire pathway itself, varies among birds. Given the visual requirements of different lifestyles and the range of visual abilities expressed among avian orders, one would expect that variation in the relative size of the tectofugal system is in some way related to behavioral and/or ecological differences among species.

Based on previous analyses [Boire, 1989; Boire and Baron, 1994; Iwaniuk and Hurd, 2005; Iwaniuk and Wylie, 2007; Iwaniuk et al., 2008] and what is known about the functional organization of the tectofugal pathway [Wang et al., 1993; Bischof and Watanabe, 1997; Sun and Frost, 1998; Husband and Shimizu, 2001; Nguyen et al., 2004], two main predictions can be made about interspecific differences in the relative size of the tectofugal pathway. First, species that have a relatively small TeO, such as parrots and owls [Boire and Baron, 1994; Iwaniuk et al., 2005; Iwaniuk and Hurd, 2005; Martin et al., 2007b; Iwaniuk et al., 2008; Striedter and Charvet, 2008], will also have relatively small nRt and E volumes because both nRt and E are dependent upon tectal input. Second, predatory species that rely heavily on vision, apart from owls, should have larger tectofugal regions. These species include kingfishers, hawks, falcons and herons, all of which rely heavily on vision for detecting prey [Wallman and Pettigrew, 1985; Katzir and Intrator, 1987; Moroney and Pettigrew, 1987; Martin and Katzir, 1994; Tucker et al., 2000]. The rationale for selecting these groups is that all

of them rely on rapid object localization and identification, both of which are accomplished by the tectofugal pathway [Bischof and Watanabe, 1997; Husband and Shimizu, 2001]. In addition, Iwaniuk and Hurd [2005] identified these groups as potentially sharing similar visual adaptations based on foraging behavior and similarities in eye movements and visual fields. Here, we test these two predictions as well as provide an analysis of interspecific allometry of the tectofugal pathway with a broad comparative data set of 113 species.

Materials and Methods

Measurements

We measured the volumes of 90 specimens representing 72 species of birds collected from wildlife sanctuaries and veterinary clinics and sent to us from other researchers (table 1). The heads of these specimens were immersion fixed in formaldehyde for one to several weeks, the brains extracted, weighed to the nearest milligram and stored in formaldehyde until processing. For all specimens, tissue processing was identical. The fixed brains were placed into 30% sucrose in 0.1 M phosphate-buffered saline (pH = 7.4) 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. Digital photographs were taken of nRt and E of every second section throughout the brain of each specimen. Similarly, photographs of the TeO were taken of every fourth section. The volumes of these three brain regions (see below) were measured with the public domain NIH image program ImageJ [Rasband et al. 1997–2008].

Shrinkage factors were calculated by comparing brain volumes prior to processing with brain volumes calculated by measuring serial sections on the slides. The areas of entire coronal sections were measured throughout the brain and multiplied by section thickness (40 mm) and the sampling interval (every fourth section). The difference between this measurement and the original brain volume yielded a shrinkage factor, which was subsequently applied to all of our measurements [as in Boire, 1989; Rehkamper et al., 1991; Boire and Baron, 1994; Ebinger, 1995; Iwaniuk et al., 2005; Iwaniuk and Wylie, 2007].

In terms of delineating the three regions, we adhered to descriptions in the literature (see below) as well as to several stereotaxic atlases [Karten and Hodos, 1967; Stokes et al., 1974; Matochik et al., 1991, Puelles et al., 2007, www.bsos.umd.edu/psyc/Brauthlab/atlas.htm]. We defined the TeO as all laminated layers of the tectum (fig. 1a), excluding the optic tract, as in previous studies [Rehkamper et al., 1991; Iwaniuk et al., 2005; Iwaniuk and Wylie, 2006, 2007; Iwaniuk et al., 2008].

nRt is readily distinguished from the adjacent tractus tectothalamicus, isthmo-optic tract, nucleus intercalates thalami and nucleus dorsolateralis anterior thalami, pars lateralis by the presence of relatively large, intensely Nissl-stained cells of relatively low density (fig. 1b). Although nRt is composed of several subdivisions [Mpodozis et al., 1996; Martinez-de-la-Torre et al., 1990], including nucleus triangularis, the boundaries of these subdivisions cannot be delineated in Nissl-stained sections. Thus, our measurement of nRt includes all of the subdivisions described in Mpodozis et al. [1996], including nucleus triangularis.

To define the borders of E, the telencephalic target of the tectofugal pathway [Husband and Shimizu, 2001], we followed the description of Nissl-stained coronal sections of E in Krützfeldt and Wild [2004, 2005]. The ventro-medial borders are defined by the pallial-subpallial lamina and frontal arcopallial tract (fig. 1c). The dorso-lateral borders are slightly indistinct, but can be defined by the presence of loosely packed cells in the E compared to the surrounding nidopallium and the more darkly stained central part of E. Although it was possible to discern the core (E former-

Table 1. List of the species surveyed, sample size and volumes (in mm^3) of the brain, telencephalon (Tel), optic tectum (TeO), nucleus rotundus (nRt) and entopallium (E), and the source of the data

Order	Common name	Species	n	Brain	Tel	TeO	nRt	E	Source
Anseriformes	Chestnut teal	*Anas castanea*	1	3,424	–	98.74	3.710	–	This study
	Northern shoveler	*Anas clypeata*	1	3,289	–	97.93	4.320	–	This study
	Green-winged teal	*Anas crecca*	1	3,166	–	123.92	3.969	–	This study
	Blue-winged teal	*Anas discors*	1	2,896	–	95.47	3.715	–	This study
	Mallard	*Anas platyrhynchos*	8	5,738	3,720.47	251.48	–	16.52	Ebinger, 1995
	Australian black duck	*Anas superciliosa*	1	4,974	–	119.49	5.772	–	This study
	Greylag goose	*Anser anser*	8	12,124	7,586.90	393.7	–	83.99	Ebinger and Lohmer, 1987
	Lesser scaup	*Aythya affinis*	1	4,142	–	131.66	5.063	–	This study
	Redhead	*Aythya americana*	1	5,245	–	131.70	5.554	–	This study
	Bufflehead	*Bucephala albeola*	1	4,123	–	127.91	7.203	–	This study
	Common goldeneye	*Bucephala clangula*	1	5,961	–	210.87	11.723	–	This study
	Australian wood duck	*Chenonetta jubata*	1	4,329	–	150.79	6.774	–	This study
	Plumed whistling duck	*Dendrocygna eytoni*	1	4,850	3,185.84	164.81	5.400	24.46	This study
	Red-breasted merganser	*Mergus serrator*	1	4,754	–	188.89	7.764	–	This study
Apodiformes	Common swift	*Apus apus*	1	668	374.57	42.36	1.480	7.51	This study
	Chimney swift	*Chaetura pelagica*	1	343	159.92	30.47	0.601	2.02	Boire, 1989; Boire and Baron, 1994

Table 1 (continued)

Order	Common name	Species	n	Brain	Tel	TeO	nRt	E	Source
Capri-mulgiformes	Nightjar	*Caprimulgus* spp.	1	734	342.75	58.81	1.847	2.40	Boire, 1989; Boire and Baron, 1994
	Spotted nightjar	*Eurostopodus argus*	1	1,013	426.73	60.97	1.647	–	This study
	Tawny frogmouth	*Podargus strigoides*	1	5,311	3,826.81	290.88	8.948	38	This study
Charadriiformes	Least sandpiper	*Calidris minutilla*	1	472	255.50	43.34	1.592	3.46	Boire, 1989; Boire and Baron, 1994
	Killdeer	*Charadrius vociferus*	1	1,073	523.69	130.65	3.646	10.18	Boire, 1989; Boire and Baron, 1994
	Short-billed dowitcher	*Limnodromus griseus*	1	1,231	725.11	51.12	1.877	5.62	Boire, 1989; Boire and Baron, 1994
	Common tern	*Sterna hirundo*	1	1,593	808.53	121.49	4.589	12.25	Boire, 1989; Boire and Baron, 1994
	Southern lapwing	*Vanellus chilensis*	1	2,461	1,440.65	331.30	8.369	29.78	Pistone et al., 2002; Carezzano and Bee de Speroni, 1995
	Masked lapwing	*Vanellus miles*	1	2,686	1,573.48	206.30	8.620	41.25	This study
Ciconiiformes	Grey heron	*Ardea cinerea*	1	8,446	5,028.04	697.78	24.190	97.83	Boire, 1989; Boire and Baron, 1994
	Cattle egret	*Bubulcus ibis*	1	4,025	1,939.45	213.76	11.797	57.43	This study
	Snowy egret	*Egretta thula*	1	3,612	1,973.35	443.74	10.476	42.62	Pistone et al., 2002; Carezzano and Bee de Speroni, 1995
	Nankeen night heron	*Nycticorax caledonicus*	1	3,360	1,921.54	269.32	8.070	52.45	This study
Columbiformes	White-headed pigeon	*Columba leucomela*	1	2,206	1,056.22	201.9	7.190	26.35	This study
	Rock dove	*Columba livia*	1	2,307	1,245.72	198.29	6.965	27.68	Boire, 1989; Boire and Baron, 1994
	Peaceful dove	*Geopelia placida*	1	776.1	413.78	64	2.251	2.96	This study
	Common bronzewing	*Phaps elegans*	1	1,743	872.53	154.58	5.190	16.24	This study
	Superb fruit-dove	*Ptilinopus superbus*	1	1,052.1	588.43	66.15	1.940	–	This study
	Ringneck dove	*Streptopelia risoria*	1	1,141	630.98	123.37	3.213	12.68	Boire, 1989; Boire and Baron, 1994
Coraciiformes	Laughing kookaburra	*Dacelo novaeguineae*	3	4,046	2,451.75	355.42	9.524	36.03	This study
	Sacred kingfisher	*Todiramphus sanctus*	1	967	578.09	83.07	3.205	10.95	This study
Falconiformes	Brown goshawk	*Accipiter fasciatus*	1	5,009	2,713.31	406.96	12.320	48.36	This study
Falconiformes	Swainson's hawk	*Buteo swainsoni*	1	8,099	–	450.07	21.284	–	This study
	Brown falcon	*Falco berigora*	1	6,007	3,646.70	387.05	–	–	This study
	Nankeen kestrel	*Falco cenchroides*	1	3,211	1,847.78	211.11	11.752	30.54	This study
	Australian hobby	*Falco longipennis*	2	3,248	1,728.66	221.72	7.828	20.21	This study
	Peregrine falcon	*Falco peregrinus*	1	6,187	3,370.54	338.26	13.930	41.31	This study
Galliformes	Chukar	*Alectoris chukar*	1	2,500	1,406.39	213.36	6.185	26.73	Boire, 1989; Boire and Baron, 1994
	Ruffed grouse	*Bonasa umbellus*	2	3,136	1,900.00	182.33	11.820	19.08	This study
	Golden pheasant	*Chrysolophus pictus*	1	3,369	1,726.01	316.06	10.830	28.52	Boire, 1989; Boire and Baron, 1994
	Northern bobwhite	*Colinus virginianus*	1	1,091	569.85	112.3	4.043	14.04	Boire, 1989; Boire and Baron, 1994
	Common quail	*Coturnix coturnix*	1	811	369.40	91.27	3.108	10.44	Boire, 1989; Boire and Baron, 1994
	Chicken	*Gallus domesticus*	1	2,889	1,242.46	279.55	8.067	30.71	Boire, 1989; Boire and Baron, 1994
	Turkey	*Meleagris gallopavo*	8	7,597	4,123.55	655.71	21.285	76.47	Ebinger and Rohrs, 1997
	Helmeted guineafowl	*Numida meleagris*	1	3,951	2,223.28	328.46	9.397	45.08	Boire, 1989; Boire and Baron, 1994
	Chaco chachalaca	*Ortalis canicollis*	1	3,374	1,829.65	271.27	8.128	24.56	Boire, 1989; Boire and Baron, 1994
	Indian peafowl	*Pavo meleagris*	1	7,355	4,264.04	493.97	17.327	76.02	Boire, 1989; Boire and Baron, 1994
	Grey partridge	*Perdix perdix*	10	1,849	956.57	150.03	–	–	Rehkamper et al., 1991
	Ring-necked pheasant	*Phasianus colchicus*	1	3,865	1,579.09	304.91	7.345	37.28	Boire, 1989; Boire and Baron, 1994
Gruiformes	American coot	*Fulica americana*	1	2,719	1,842.69	127.65	8.274	22.36	This study
	Red-gartered coot	*Fulica armillata*	1	4,015	2,738.46	260.11	7.228	38.15	Pistone et al., 2002; Carezzano and Bee de Speroni, 1995
Passeriformes	Brown thornbill	*Acanthiza pusilla*	1	434	233.00	34.81	1.683	4.62	This study
	Eastern spinebill	*Acanthorhynchus tenuiros-tris*	1	489	294.40	29.46	0.919	3.70	This study
	Carrion crow	*Corvus corone*	7	9,382	7,019.03	349.86	–	–	Rehkamper et al., 1991
	Blue-faced honeyeater	*Entomyzon cyanotis*	1	2,227	1,580.07	96.99	3.13	13.17	This study
	Eastern yellow robin	*Eopsaltria australis*	1	839	512.70	40.52	2.700	7.19	This study
	Gouldian finch	*Erythrura gouldiae*	1	428	238.95	20.94	1.026	1.81	This study
	European jay	*Garrulus glandarius*	3	3,943	2,596.73	248.9	–	–	Rehkamper et al., 1991
	Australian magpie	*Gymnorhina tibicen*	1	4,017	2,922.12	219.43	8.630	16.08	This study
	White-plumed honeyeater	*Lichenostomus perspicilla-tus*	1	917	603.80	47.94	1.807	9.19	This study
	Noisy miner	*Manorina melanocephala*	1	2,279	1,547.58	88.5	4.168	11.93	This study
	Superb lyrebird	*Menura novaehollandiae*	1	10,163	–	384.66	7.462	–	This study

Table 1 (continued)

Order	Common name	Species	n	Brain	Tel	TeO	nRt	E	Source
Passeriformes	Spotted pardalote	*Pardalotus punctatus*	1	401	190.72	19.69	1.367	3.80	This study
	House sparrow	*Passer domesticus*	4	989	637.56	62.69	–	–	Rehkamper et al., 1991
	Mountain chickadee	*Poecile gambeli*	1	624.8	418.7	35.62	2.044	5.39	This study
	Pied currawong	*Strepera versicolor*	1	5,425	3,984.13	270.86	13.50	32.08	This study
	Double-barred finch	*Taeniopygia bichenovii*	1	409	228.4	28.19	0.880	3.13	This study
	Zebra finch	*Taeniopygia guttata*	1	328	207.83	24.69	0.796	1.42	Boire, 1989; Boire and Baron, 1994
Pelecaniformes	Double-crested cormorant	*Phalacrocorax auritus*	1	7,323	4,341.73	361.21	14.626	42.67	Boire, 1989; Boire and Baron, 1994
Podici-pediformes	White-tufted grebe	*Rollandia rolland*	1	2,059	1,183.89	209.99	4.736	20.39	Pistone et al., 2002; Carezzano and Bee de Speroni, 1995
Procellariiformes	Short-tailed shearwater	*Puffinus tenuirostris*	1	4,658	2,334.24	235.01	8.670	29.33	This study
Psittaciformes	Masked lovebird	*Agapornis personata*	1	2,824	2,069.65	82.57	–	–	This study
	Peach-faced lovebird	*Agapornis roseicollis*	1	2,008	1,454.88	79.74	2.785	3.101	This study
	Australian king parrot	*Alisterus scapularis*	3	4,794	3,271.457	202.14	6.318	16.42	This study
	Blue-headed Amazon parrot	*Amazona aestiva*	1	7,955	5,672.01	273.47	11.213	21.31	This study
	Blue-crowned conure	*Aratinga acuticaudata*	1	5,222	4,325.91	114.88	–	–	Fernandez et al., 1997
	Sulphur-crested cockatoo	*Cacactua galerita*	1	14,515	11,292.48	322.11	9.580	47.59	This study
	Yellow-tailed black cockatoo	*Calyptorhynchus funereus*	1	16,111	12,823.58	309.66	11.947	42.23	This study
	Eclectus parrot	*Eclectus roratus*	2	6,248	4,583.16	221.10	7.960	23.30	This study
	Galah	*Eolophus roseicapilla*	2	6,600	4,908.67	211.06	7.103	22.26	This study
	Musk lorikeet	*Glossopsitta concinna*	3	3,159	2,272.74	98.76	5.294	8.60	This study
	Budgerigar	*Melopsittacus undulatus*	1	1,220	825.12	59.64	1.882	3.93	Boire, 1989; Boire and Baron, 1994
	Monk parakeet	*Myopsitta monachus*	1	3,697	2,733.19	156.38	–	–	Fernandez et al., 1997
	Bourke's parrot	*Neopsephotus bourkii*	1	1,213	834.24	56.42	–	3.08	This study
	Cockatiel	*Nymphicus hollandicus*	2	2,339	1,676.78	80.82	4.195	11.37	This study
	Blue-headed parrot	*Pionus menstruus*	1	5,283	3,851.82	257.95	9.297	16.12	Boire, 1989; Boire and Baron, 1994
	Crimson rosella	*Platycercus elegans*	3	3,822	2,687.57	160.24	6.404	7.66	This study
	Eastern rosella	*Platycercus eximius*	4	3,258	2,326.68	129.84	4.721	10.57	This study
	Superb parrot	*Polytelis swainsonii*	2	3,157	2,163.20	134.88	4.130	–	This study
	Red-rumped parrot	*Psephotus haematonotus*	2	1,940	1,402.55	73.47	3.437	7.67	This study
	Alexandrine parrot	*Psittacula eupatria*	1	6,327	4,942.37	160.94	–	19.304	This study
	Indian ring-necked parrot	*Psittacula krameri*	1	4,243	3,269.62	120.45	–	–	This study
	African grey parrot	*Psittacus erithacus*	1	6,405	4,726.89	155.14	7.412	15.49	This study
	Green-cheeked conure	*Pyrrhura molinae*	1	4,656	3,123.51	232.93	8.259	–	This study
	Rainbow lorikeet	*Trichoglossus haematodus*	2	3,728	2,726.62	123.42	4.890	9.99	This study
Rheiformes	Greater rhea	*Rhea americana*	1	19,228	10,281.31	1286.55	49.130	191.38	Boire, 1989; Boire and Baron, 1994
Sphenisciformes	Magellanic penguin	*Spheniscus magellanicus*	1	16,757	10,890.21	672.29	24.661	147.93	Boire, 1989; Boire and Baron, 1994
Strigiformes	Northern saw-whet owl	*Aegolius acadicus*	1	2,343	2,009.90	64.49	3.6470	6.127	This study
	Burrowing owl	*Athene cunicularia*	1	5,878	4,816.43	148.71	–	–	Alma and Bee de Speroni, 1992
	Great horned owl	*Bubo virginianus*	1	17,994	–	322.05	9.056	–	This study
	Boobook owl	*Ninox boobook*	1	4,913	3,464.78	148.60	5.503	15.80	This study
	Barn owl	*Tyto alba*	1	6,149	4,108.76	136.51	–	–	Alma and Bee de Speroni, 1992
Tinamiformes	Tataupa tinamou	*Crypturellus tataupa*	1	1,583	–	159.25	7.440	23.43	Bee de Speroni and Carezzano, 1995
	Red-winged tinamou	*Rhynchotus rufescens*	1	3,377	1,971.68	327.43	13.051	46.87	Boire, 1989; Boire and Baron, 1994
Trochiliformes	Anna's hummingbird	*Calypte anna*	1	183	86.93	14.28	0.453	0.95	This study
	Blue-tailed emerald	*Chlorostilbon melisugus*	1	119	56.17	12.36	0.279	0.62	Boire, 1989; Boire and Baron, 1994
	Rufous hummingbird	*Selasphorus rufus*	1	121	57.83	11.75	0.329	0.63	This study

ly known as Ec) from the surrounding perientopallium (Ep) in some specimens, this was not true for most of our material and the reports from which we gleaned additional data (see below) did not distinguish between Ec and Ep. Therefore, the measurements reported for E in this study comprise both Ec and Ep.

It should be noted that due to variations in staining intensity, not all structures could be measured in all species. Thus, there are some species for which we do not currently have data for some structures (table 1). Similarly, sample sizes and brain region volumes differ for some species in this study compared to previous studies [Iwaniuk and Hurd, 2005; Iwaniuk et al., 2005, 2008; Iwaniuk and Wylie, 2006, 2007] because we selected those individuals from which we could reliably measure as many of the three brain regions as possible.

In addition to our own data, we gleaned brain region volumes from the literature for an additional 41 species [Ebinger and Löhmer, 1987; Boire, 1989; Rehkamper et al., 1991; Alma and Bee de Speroni, 1992; Bee de Speroni and Carezzano, 1995; Carezzano and Bee de Speroni, 1995; Ebinger, 1995; Ebinger and Röhrs, 1995; Fernandez et al., 1997; Pistone et al., 2002]. In all cases, similar borders were used to define each of the three regions.

Statistical Analysis

To examine scaling relationships, we plotted the volume of each of the three tectofugal brain regions against brain volume minus the volume of each specific region [Deacon, 1990]. Thus, to examine relative TeO volume, we plotted TeO volume against brain volume minus TeO volume. In addition, we examined the scaling relationships between E and telencephalon volume because previous analyses of the Wulst indicated some differences in allometric scaling depending upon whether Wulst was related to whole brain or telencephalic volume [Iwaniuk and Wylie, 2006; Iwaniuk et al., 2008]. As with brain volume, we subtracted the volume of E from the telencephalon. Finally, we summed the volumes of TeO, nRt and E to yield the volume of the entire tectofugal pathway and subtracted this from whole brain volume to examine allometric scaling of the entire pathway.

Allometric equations were calculated using linear least-squares regressions using: (1) species as independent data points, and (2) independent contrasts to account for phylogenetic relatedness. Since the publication of Sibley and Ahlquist [1990], several alternative topologies of avian inter-ordinal and inter-familial relationships have become available. Because different phylogenetic trees can yield different results [Iwaniuk, 2004], we therefore tested four models based on the trees provided in Sibley and Ahlquist [1990], Livezey and Zusi [2007], Davis [2003], and Hackett et al. [2008]. Resolution within each order was provided by order- and family-specific studies [Brown and Toft, 1999; Johnson and Sorenson, 1999; Donne-Goussé et al., 2002; Barker et al., 2004; Driskell and Christidis, 2004; Wink and Sauer-Gürth, 2004; Pereira et al., 2007; Kimball and Braun, 2008; Wink et al., 2008; Wright et al., 2008], although this still left several nodes unresolved.

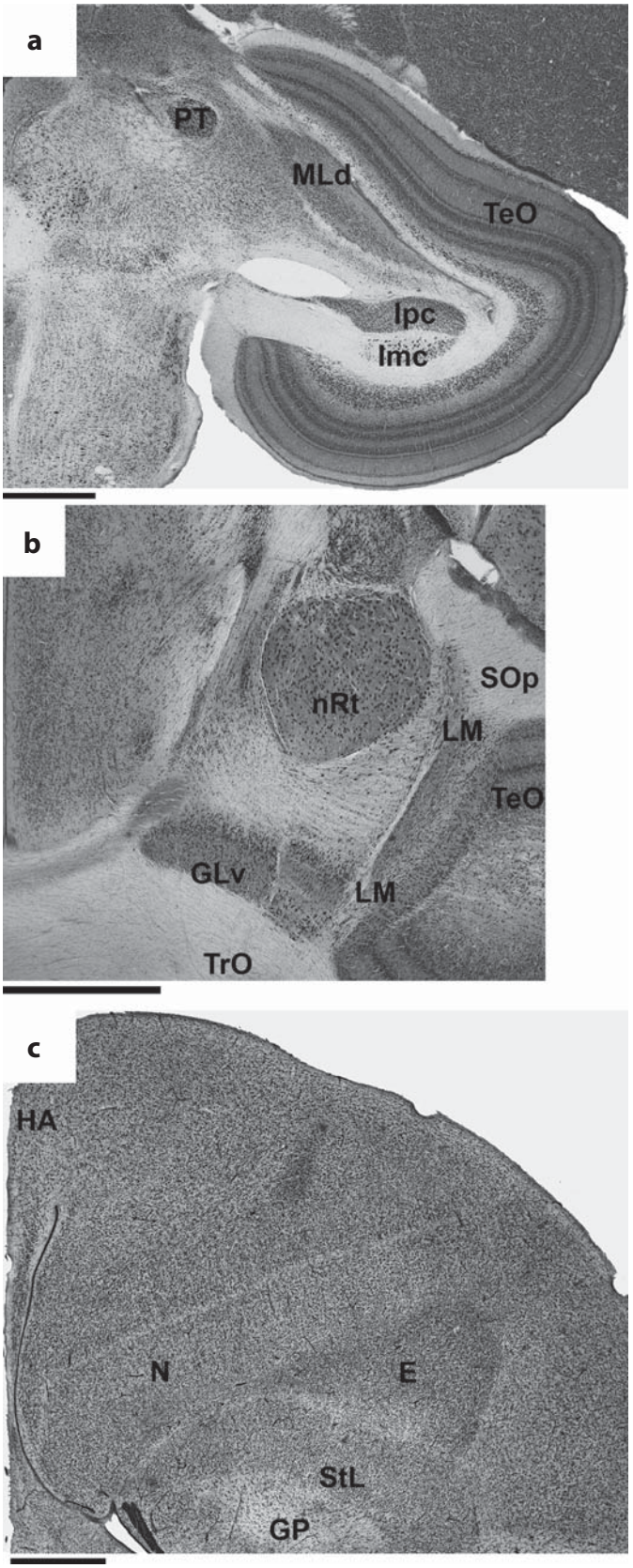

Fig. 1. a Coronal section taken through the optic tectum of an eastern yellow robin *(Eopsaltria australis)*. **b** Coronal section through the nucleus rotundus of an eastern yellow robin. **c** Coronal section taken through the entopallium approximately midway along its medio-lateral extent of a short-billed dowitcher *(Limnodromus griseus)*. E = Entopallium; GLv = ventral leaflet of the lateral geniculate nucleus; GP = globus pallidus; HA = hyperpallium apicale; Imc = nucleus isthmi magnocellularis; Ipc = nucleus isthmi parvocellularis; LM = nucleus lentiformis mesencephali; MLd = nucleus mesencephalicus lateralis, pars dorsalis; N = nidopallium; nRt = nucleus rotundus; PT = nucleus pretectalis; SOp = stratum opticum; StL = lateral striatum; TeO = optic tectum; TrO = optic tract. Note that LM is labeled twice in **b** to illustrate that in this section, lentiformis mesencephali has a dorsal and ventral component, but it is not continuous from the dorsal through to the ventral aspect. Scale bars = 1 mm.

The trees and log_{10}-transformed data were entered into the PDAP module [Midford et al., 2005] of the comparative analysis software package Mesquite [Maddison and Maddison, 2009]. Arbitrary branch length models were used to standardize the contrasts because the relationships were derived from different sources using different methods (e.g. morphology, nuclear genes, mitochondrial DNA). Each model was tested for adequate standardization of the contrasts following the procedures outlined in Garland et al. [1992]. Allometric equations based on the independent contrasts calculated for each of the four trees are provided for each of the three brain regions as well as the tectofugal pathway as a whole.

Lastly, to test for significant differences in relative brain region size among orders, we performed ANOVAs of residuals derived from the regression analysis using species as independent data points. Although this analysis was not phylogenetically 'corrected', it provides a test of whether orders are indeed different from one another in terms of the relative size of the three brain regions and the tectofugal pathway as a whole in a similar fashion to previous analyses [e.g. Iwaniuk et al. 2007].

Results

Optic Tectum

The TeO scales with negative allometry against brain volume (table 2, fig. 2a). Relative to brain volume, a parrot, the green-cheeked conure *(Aratinga acuticaudata)*, has the smallest and a shorebird, the Southern Lapwing *(Vanellus chilensis)*, the largest TeO volumes. A plot of residuals derived from a conventional least-squares linear regression indicates that there is considerable overlap amongst orders (fig. 3a), but an ANOVA yielded a significant effect of order ($F = 13.21$, d.f. = 19, 93, $p < 0.0001$, $r^2 = 0.67$). Pairwise comparisons using Tukey's HSD test indicated that parrots (Psittaciformes), waterfowl (Anseriformes) and owls (Strigiformes) have significantly smaller relative TeO volumes than most other orders. At the opposite end of the spectrum, gallinaceous birds (Galliformes) and herons (Ciconiiformes) have relatively large TeO volumes, but this was only significant relative to songbirds (Passeriformes), hummingbirds (Trochiliformes), parrots, waterfowl and owls. Thus, although gallinaceous birds have relatively large TeO volumes, this is only significant when compared to a handful of other orders.

Nucleus Rotundus

nRt also scales with negative allometry against brain volume (table 2, fig. 2b). Relative to brain volume, the great-horned owl *(Bubo virginianus)* has the smallest and the tinamous *(Crypturellus tata* and *Rhynchotus rufescens)* have the largest nRt volumes. As with the TeO (fig. 3a), there is considerable overlap in the distribution of nRt residuals amongst the orders (fig. 3b). Nevertheless, an ANOVA of the residuals yielded a significant difference among orders ($F = 8.91$, d.f. = 19, 79, $p < 0.0001$, $r^2 = 0.61$). The tinamous (Tinamiformes) have significantly larger nRt residuals than several orders [songbirds, caprimulgiforms, parrots, waterfowl, hummingbirds, swifts (Apodiformes) and owls] and the waterfowl, parrots and owls have significantly lower nRt residuals compared to the following orders: tinamous; greater rhea (*Rhea americana*, Rheiformes); herons; falcons (Falconiformes); gallinaceous birds; kingfishers (Coraciiformes); shorebirds (Charadriiformes); and pigeons (Columbiformes).

Table 2. Results of least-squares linear regression performed on each of the three tectofugal brain regions and the sum of the three regions ('tectofugal pathway') using both species as independent data points ('no phylogeny') and independent contrasts with four different phylogenetic trees

	F	d.f.	Slope	r^2
Optic tectum				
No phylogeny	356.58	1, 111	0.7562	0.76
Sibley and Ahlquist, 1990	435.84	1, 107	0.7647	0.80
Davis, 2003	482.74	1, 101	0.7643	0.82
Livezey and Zusi, 2007	422.84	1, 106	0.7768	0.80
Hackett et al., 2008	458.76	1, 101	0.7903	0.81
Nucleus rotundus				
No phylogeny	477.13	1, 97	0.8098	0.83
Sibley and Ahlquist, 1990	464.65	1, 93	0.7399	0.83
Davis, 2003	512.76	1, 87	0.7872	0.85
Livezey and Zusi, 2007	456.75	1, 92	0.7392	0.83
Hackett et al., 2008	486.90	1, 87	0.7519	0.84
Entopallium (brain)				
No phylogeny	273.62	1, 82	0.9458	0.77
Sibley and Ahlquist, 1990	363.26	1, 78	0.9600	0.82
Davis, 2003	401.87	1, 72	0.9627	0.84
Livezey and Zusi, 2007	336.60	1, 77	0.9600	0.81
Hackett et al., 2008	356.45	1, 72	0.9640	0.82
Entopallium (telencephalon)				
No phylogeny	184.66	1, 81	0.8380	0.69
Sibley and Ahlquist, 1990	294.37	1, 77	0.8776	0.79
Davis, 2003	330.44	1, 71	0.8090	0.81
Livezey and Zusi, 2007	267.07	1, 76	0.8726	0.77
Hackett et al., 2008	286.40	1, 71	0.8835	0.79
Tectofugal pathway				
No phylogeny	361.92	1, 79	0.8302	0.82
Sibley and Ahlquist, 1990	391.84	1, 75	0.7936	0.84
Davis, 2003	429.21	1, 69	0.8020	0.85
Livezey and Zusi, 2007	392.11	1, 74	0.8197	0.84
Hackett et al., 2008	415.46	1, 69	0.8454	0.85

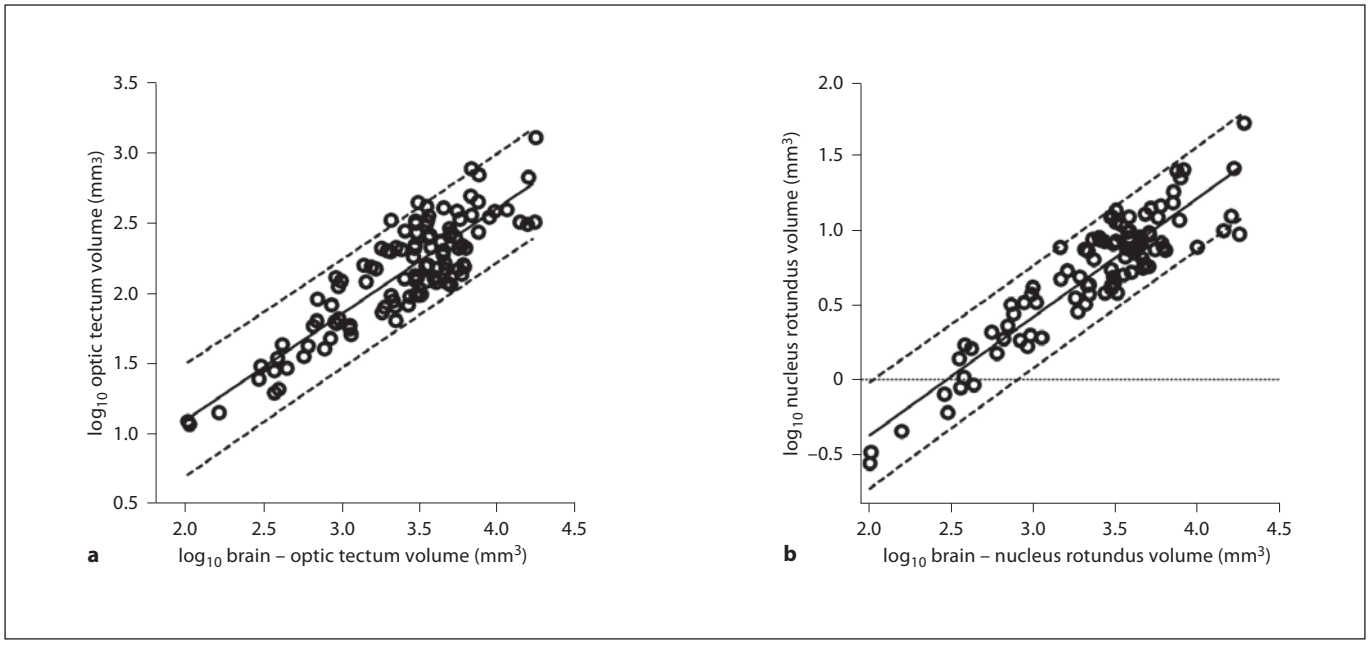

Fig. 2. Allometric scaling relationships are depicted for the optic tectum (TeO) and nucleus rotundus (nRt). **a** Scatterplot of log-transformed TeO volume plotted against log-transformed brain minus TeO volume. **b** Scatterplot of log-transformed nRt volume plotted against log-transformed brain minus nRt volume. In both graphs, the solid line indicates the least-squares linear regression line and the dotted lines represent the 95% confidence interval.

Entopallium

Unlike TeO and nRt, the E scaled with negative allometry to isometry, depending upon what method was used to calculate the regression line (table 2). As shown by the confidence intervals in figure 4, isometry with both brain (fig. 4a) and telencephalic (fig. 4b) volume cannot be ruled out, but there is a tendency towards negative allometry. Relative to both brain and telencephalic volume, the peach-faced lovebird *(Agapornis roseicollis)* has the smallest E and the Nankeen night heron *(Nycticorax caledonicus)* has the largest E. Again, there is considerable overlap in relative E volume among orders (fig. 3c). An ANOVA of the residuals yielded a significant difference among orders regardless of whether E was related to brain volume ($F = 10.91$, d.f. = 19, 64, $p < 0.0001$, $r^2 = 0.69$) or telencephalic volume ($F = 12.60$, d.f. = 19, 63, $p < 0.0001$, $r^2 = 0.73$). Post hoc tests revealed that parrots have significantly smaller relative E volumes compared to most other orders [tinamous, herons, rhea, gallinaceous birds, kingfishers, coots (Gruiformes), pigeons, shorebirds, falcons and swifts]. The herons exhibited significantly larger relative E volumes, but only with respect to several orders at the low end of the spectrum, namely owls, waterfowl, parrots, hummingbirds, songbirds and caprimulgiforms.

Scaling of the Entire Tectofugal Pathway

Finally, the tectofugal pathway as a whole (the sum of TeO, nRt and E volumes) also scaled with negative allometry (table 2) relative to brain volume (fig. 5). The southern lapwing has the largest and the yellow-tailed black cockatoo *(Calyptorhynchus funereus)* the smallest tectofugal pathway, relative to brain volume. Plots of the tectofugal pathway residuals again yielded substantial overlap among many orders (fig. 3d), but the tinamous and owls stood out as having particularly high and low residuals, respectively. An ANOVA of the residuals yielded a significant difference among orders ($F = 10.55$, d.f. = 19, 61, $p < 0.0001$ $r^2 = 0.69$). Post hoc tests corroborated our observations of the distribution. At the one end of the spectrum, tinamous have significantly larger relative tectofugal pathway volumes than songbirds, waterfowl, owls and parrots. At the other end of the spectrum, both owls and parrots have significantly smaller tectofugal pathway volumes than the tinamous, white-tufted grebe *(Rollandia rolland)*, rhea, herons, galliforms, kingfishers, pigeons, shorebirds and falcons.

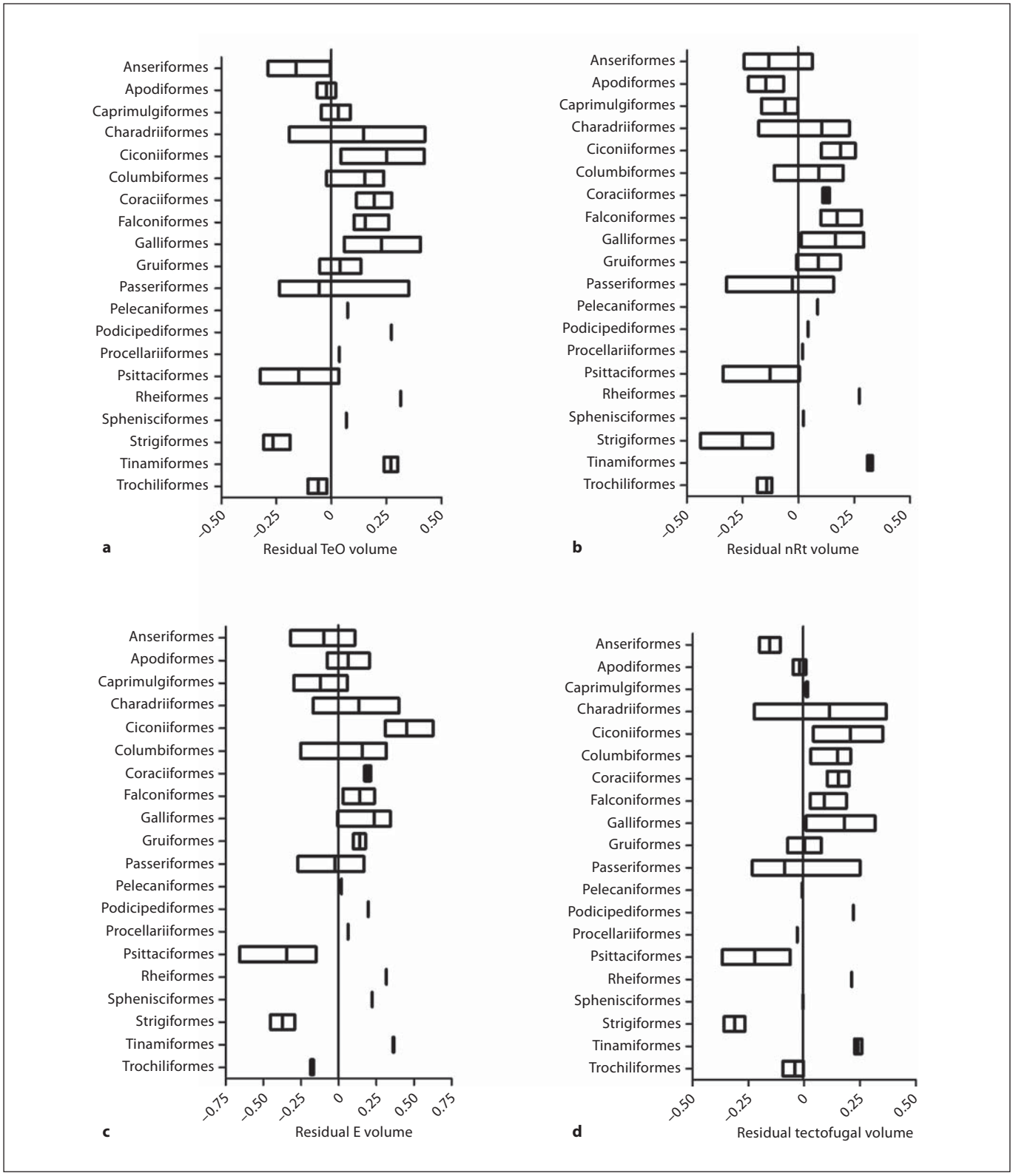

Fig. 3. Boxplots illustrating differences in relative size of the three tectofugal regions across the 19 avian orders examined. **a** Optic tectum. **b** Nucleus rotundus. **c** Entopallium (values shown are the means of the residuals derived from both graphs shown in figure 4). **d** Sum of the three tectofugal regions.

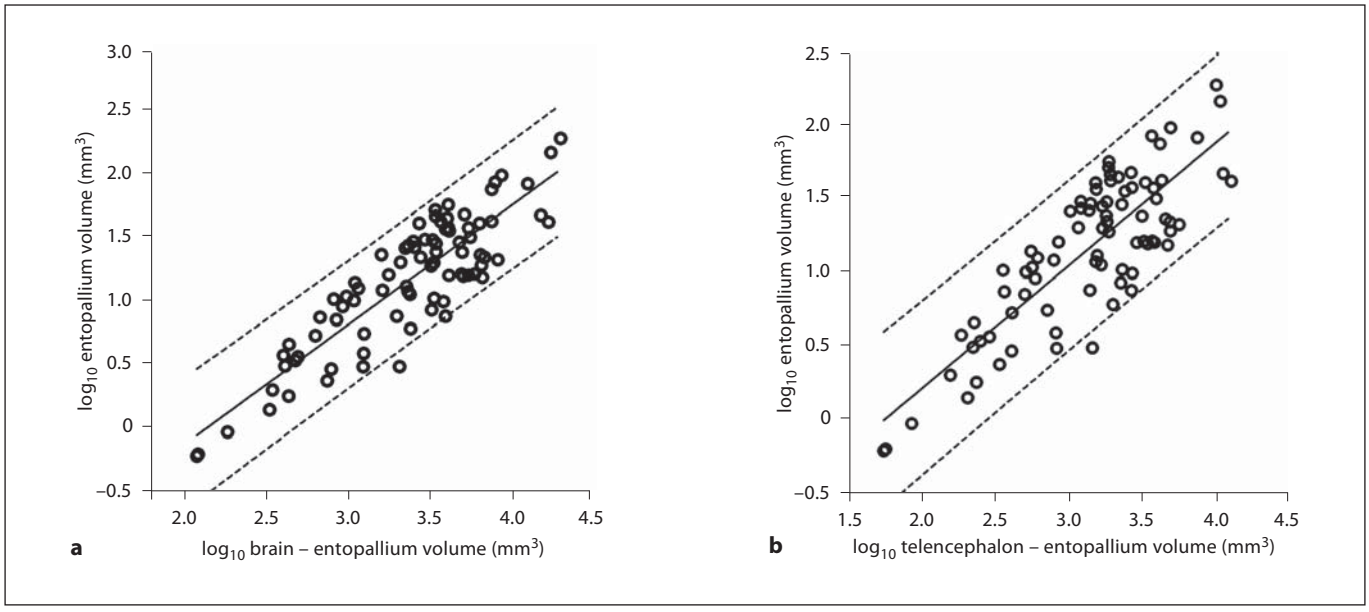

Fig. 4. Allometric scaling relationships are depicted for the entopallium. **a** Scatterplot of log-transformed entopallium volume plotted against brain minus entopallium volume. **b** Scatterplot of log-transformed entopallium volume plotted against telencephalon minus entopallium volume. In both graphs, the solid line indicates the least-squares linear regression line and the dotted lines represent the 95% confidence interval.

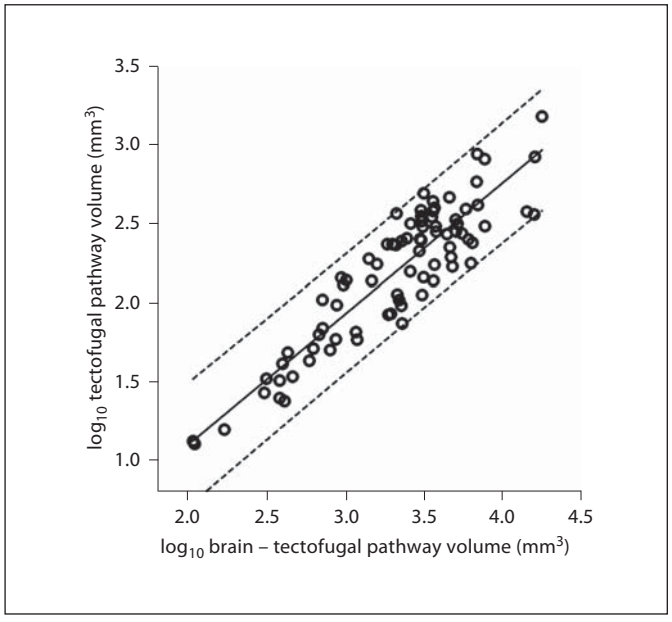

Fig. 5. Allometric scaling relationship is depicted for the entire tectofugal pathway (sum of optic tectum, nucleus rotundus and entopallium volumes) relative to brain volume minus the size of the pathway. As with the other figures, both axes are $\log_{10}$ transformed, the solid line indicates the least-squares linear regression lines and the dotted lines represent the 95% confidence interval.

Discussion

Overall, our results indicate that the tectofugal pathway generally scales with negative allometry relative to brain volume and that several groups tend to have significantly smaller tectofugal regions than most other birds. This was particularly true of the waterfowl, parrots and owls. Although our results could have been affected by species sampling, it is by far the most comprehensive sampling of the visual regions of the avian brain to date. Furthermore, we sampled from several 'highly visual' groups (i.e. visually guided vertebrate predators with relatively large eyes) including falcons and hawks, herons, kingfishers and owls to account for as much variation in the visual system as we could. That said, we cannot discount the possibility that including additional species, especially those from unsampled orders (e.g. Piciformes, Coliiformes and Cuculiformes), could affect our conclusions. Given the present data, we can, however, conclude that: (1) owls, waterfowl and parrots have significantly smaller tectofugal regions relative to brain volume than other birds; and (2) there is little evidence for grade shifts indicative of tectofugal hypertrophy.

Why Have a Smaller Tectofugal System?

As detailed above, three taxa, owls, waterfowl and parrots, all have significantly smaller tectofugal regions than other birds. From a developmental perspective, the reduction of the TeO in waterfowl and parrots arises primarily from allocating a smaller amount of tissue to the tectum during the earliest stages of neurogenesis compared to other taxa [Striedter and Charvet, 2008; Charvet and Striedter, 2009]. Although this provides a mechanistic basis for understanding these broad species differences, why these specific taxa have undergone a significant reduction in size of the tectofugal pathway has remained largely unexplored. Here we provide two possible explanations.

One possibility is that the relatively small size of the tectofugal pathway does not reflect a reduction in the tectofugal regions per se, but rather an expansion of other regions and pathways. Two features, in fact, tie waterfowl, parrots and owls together; all three have both a reduced tectofugal pathway and an enlarged telencephalon [Portmann, 1947; Iwaniuk and Hurd, 2005]. Thus, the small tectofugal pathway of these three taxa could be a result of having an enlarged telencephalon and/or other brain regions as opposed to a reduction in the size of the tectofugal structures. A closer examination of the proportional sizes of telencephalic and other brain regions provides further support for this scaling hypothesis. Owls, for example, have a grossly enlarged Wulst, the telencephalic target of the thalamofugal pathway. Waterfowl have also undergone an enlargement of the Wulst, albeit to a lesser extent than owls [Iwaniuk et al., 2008; Iwaniuk and Wylie, 2007], as well as expanding other telencephalic regions [Boire, 1989; Iwaniuk and Hurd, 2005]. Finally, parrots have expanded nidopallial and mesopallial regions relative to most other taxa [Iwaniuk, 2003; Iwaniuk and Hurd, 2005]. Outside of the telencephalon, other regions are also expanded in these three taxa, which could also contribute to the relatively small size of the tectofugal pathways. In owls, the auditory nucleus mesencephalicus lateralis, pars dorsalis is enlarged [Iwaniuk et al., 2006] and the principal nucleus of the trigeminal nerve is enlarged in both waterfowl and parrots [Gutierrez-Ibanez et al., 2009]. Although these two structures comprise a small percentage of overall brain volume, they could nevertheless contribute to calculating relatively small tectofugal regions. Thus, hypertrophy of brain regions outside of the tectofugal pathway likely contributes to the relatively small size of all tectofugal regions shown here.

A second possibility is that this reduction in the tectofugal pathway reflects some aspect(s) of the visual abilities of these three taxa. Although there are several retinorecipient regions in the avian brain, the vast majority of retinal ganglion cells terminate in the TeO [Mpodozis et al., 1995]. Thus, the relative size of the tectum could reflect the density of retinal ganglion cells or, at the very least, the number of optic nerve fibres that terminate in the tectum. Relatively little is known about the retinal morphology of waterfowl or parrots, but there is some evidence that owls have a lower density of retinal ganglion cells than other birds (table 3). Similarly, a recent study by Hall et al. [2009] demonstrated that optic foramen size, an approximation of optic nerve size, is much smaller in owls compared to most other birds. It is tempting to suggest that the tectofugal reduction and thalamofugal enlargement that are characteristic of owls and some caprimulgiform birds [Iwaniuk and Wylie, 2006], somehow reflect eye position and/or stereopsis, but correlations among these traits are confounded by at least two factors. First, falcons and pigeons have stereoscopic vision, but have a relatively small Wulst and tectofugal regions much larger than that of owls (fig. 3). Second, frontally eyed species can have a large Wulst and small tectum or vice versa [Iwaniuk et al., 2008]. With respect to owls, however, we can draw correlations between the large Wulst and small tectofugal pathway and behavior. Owls do have enhanced scotopic vision [Martin, 1977] and global stereopsis [Pettigrew, 1979, 1986; van der Willigen et al., 1998], but relatively poor visual acuity [Fite, 1973; Martin and Gordon, 1974] and color discrimination [Martin, 1974; Bowmaker and Martin, 1978]. Thus, a relatively small tectofugal pathway may be a reflection of visual abilities and retinal structure in owls, but this does not appear to extend equally to all avian taxa.

Waterfowl may represent another taxa in which tectofugal pathway size is, in some way, a reflection of retinal structure and behavior. The domestic mallard *(Anas platyrhynchos)* has a peak retinal ganglion cell density much lower than that of taxa with larger tectofugal regions, such as galliforms and pigeons (table 3). The optic foramen does not appear to closely approximate the optic nerve in waterfowl [Hall et al., 2009], so estimates of optic nerve size are not readily available, but it seems more than coincidental that two taxa in which peak retinal ganglion cell densities are fairly low also happen to have smaller tectofugal regions. The similarities between waterfowl and owls also go beyond retinal morphology; waterfowl also have an enlarged Wulst, albeit not to the same extent as owls [Iwaniuk et al., 2008]. In contrast to owls, the Wulst enlargement in waterfowl is likely due to somatosensory rather than visual requirements. All waterfowl

Table 3. Peak retinal ganglion cell densities measured in several avian taxa

Taxon	Retinal ganglion cell density (cells/mm^2)	Reference
Owls	4,000–16,000	Bravo and Pettigrew, 1981; Wathey and Pettigrew, 1989
Ostrich *(Struthio camelus)*	9,000	Boire et al., 2001
Mallard *(Anas platyrhynchos)*	15,820	Rahman et al., 2006
Seabirds	19,000	Hayes et al., 1991
Songbirds	25,600–65,000	Coimbra et al., 2006; Rahman et al., 2006
Diurnal raptors	25,000–65,000	Inunza et al., 1991
Galliforms	30,000–38,000	Erlich, 1981; Budnik et al., 1984; Hart, 2002
Pigeon *(Columba livia)*	39,000	Binggeli and Pauli, 1969
Kingfishers	120,000–180,000	Moroney and Pettigrew, 1987

have an enlarged principal trigeminal nucleus [Gutierrez-Ibanez et al., 2009] and it is likely that the rostral Wulst, which is primarily somatosensory [Pettigrew and Frost, 1985; Wild, 1997; Manger et al., 2002], is similarly enlarged. Based on the hypertrophy of the principal trigeminal nucleus and reduction of the tectofugal pathway, it could be suggested that waterfowl rely more upon somatosensory cues, specifically trigeminal input, for foraging than visual cues. Vision is, however, used by several waterfowl species to detect and capture prey [Tome and Wrubleski, 1988; Guillemain et al., 2002; Martin et al., 2007a]. Behavioral studies indicate that vision is more critical in some species than in others [Tome and Wrubleski, 1988] and there is some interspecific variation in eye movements and visual field within the order [Martin, 1986; Guilleman et al., 2002; Martin et al., 2007a]. Kalisinska [2005] reported that the optic lobes were larger in piscivorous and diving ducks than in other species and we did detect some variation in the relative size of the TeO and nRt among the species we sampled. Based on the apparent correlations among retinal morphology, tectofugal and thalamofugal brain region volumes and behavior in owls, we predict that waterfowl likely share with owls enhanced scotopic vision, but relatively poor color discrimination and visual acuity.

Parrots present the most difficult case of reduction in tectofugal brain regions to explain because of the lack of suitably detailed information on their eye morphology and visual behavior. Parrots do possess relatively small eyes [Hall, 2005], so the relatively small tectofugal pathway could be indicative of relatively small visual projections in the first place. Corroborative evidence can be found in the volumes of other visual brain regions. Both the nucleus lentiformis mesencephali, a visual region of the pretectum, and the Wulst are relatively small in parrots [Iwaniuk and Hurd, 2005; Iwaniuk and Wylie, 2007; Iwaniuk et al., 2008]. The extent to which these differences reflect the visual abilities of parrots is, however, unclear. Apart from color discrimination [Goldsmith and Butler, 2005], the visual abilities of parrots are unknown. Mate selection in most parrots is at least partially dependent on visual cues [Pearn et al., 2001; Hausmann et al., 2003] and virtually all species perform a range of visual displays [Forshaw, 1989]. Similarly, most foraging parrots locate seeds, fruit and nuts from a distance and orient their eyes to food items held in the foot or to individual seeds if foraging on the ground [Iwaniuk, pers. obs.]. These behaviors argue against 'poor' visual abilities despite the relatively small size of their eyes, optic foramen and assorted visual regions of the brain. Clearly, more information on parrot visual abilities and retinal morphology is needed to better understand the evolution of relatively small visual regions in the parrot brain.

Lack of Tectofugal Hypertrophy

Previous analyses of the pretectum and thalamofugal pathway demonstrated that some avian orders exhibit hypertrophied brain regions. For example, hummingbirds, and a few other hovering species, have a significantly enlarged nucleus lentiformis mesencephali [Iwaniuk and Wylie, 2007] and owls, frogmouths and owlet-nightjars all exhibit significantly hypertrophied Wulst volumes [Iwaniuk and Wylie, 2006; Iwaniuk et al., 2008]. In these two cases, hummingbirds and owls exhibit grade shifts relative to all other birds. That is, they have taxon-specific allometric lines that are shifted vertically a significant distance along the y-axis (i.e. larger intercepts) from other birds. No such grade shifts were, however, found in our

analyses of the tectofugal pathway. In other words, we did not detect any groups with a significantly hypertrophied tectofugal region relative to all other birds. Based on the species that we sampled, we suggest that the heterogeneous organization of the tectofugal pathway is largely responsible for the perceived lack of hypertrophy.

The hetereogeneity of the tectofugal pathway is apparent at two different levels of organization. First, cells within TeO, nRt and E are responsive to more than just visual stimuli. For example, the TeO contains neurons that respond to auditory as well as visual stimuli [Cotter, 1976; Knudsen, 1984; Lewald and Dörrscheidt, 1998; Zahar et al., 2009]. A recent study by Reches and Gutfreund [2009] has similarly demonstrated that both nRt and E also respond to non-visual stimuli. Second, even within the visual-responsive neurons of the tectofugal pathway, most cells respond best to a specific type of visual stimulus. In the TeO, many neurons respond best to moving stimuli [Frost et al., 1983, 1988, 1990], but in nRt, cells can be responsive to color, luminosity or movement and these cells are located in different parts of the nucleus itself [Wang et al., 1993; Sun and Frost, 1998]. Finally, this same pattern is repeated in E, which also exhibits heterogeneric responses to visual stimuli [Bischof and Watanabe, 1997; Nguyen et al., 2004; Xiao et al., 2006; Xiao and Frost, 2009].

In terms of understanding species differences in the relative size of tectofugal brain regions, this heterogeneous organization clearly presents at least two potential problems for detecting clades that have undergone tectofugal hypertrophy. First, species may have an enlarged tectofugal pathway in response to auditory, somatosensory and/or visual processing demands. Within our data set, if this were true, then we would expect the owls, waterfowl, parrots and beak-probing shorebirds to all share enlarged tectofugal regions. As detailed above for the first three taxa, this is clearly not the case. Thus, the presence of neurons that are not specific to visual stimuli does not appear to significantly affect allometric relationships. Second, the specificity of cells within the tectofugal regions to specific types of visual stimuli could result in species varying in the proportional size of motion, luminance and color-responsive regions. For example, some lifestyles could require more cells responsive to looming stimuli than color discrimination. The relative size of regions within nRt and E that respond to looming stimuli could then be enlarged at the expense of the color-responsive regions without having an effect on the overall size of the entire brain region. In fact, this could explain why gallinaceous birds and pigeons have tectofugal pathways of similar size to predatory species, such as kingfishers, falcons and herons. Perhaps all of them rely on the tectofugal pathway for foraging and other behaviors, but emphasize different types of visual stimuli. One could imagine predatory species being more reliant on looming stimuli to guide prey capture than pecking birds, which might emphasize rapid object identification to increase foraging efficiency. In either case, the end result in terms of the size of the tectofugal pathway would be enlargement, but for different reasons.

Conclusions

Overall, we conclude that waterfowl, parrots and owls all have significantly smaller tectofugal regions than other avian taxa, but there are no apparent cases of tectofugal hypertrophy. As discussed above, our ability to interpret these results is hampered at several levels by a dearth of comparative information on retinal morphology and visual abilities across a broad range of bird species in addition to the innate heterogeneity of the tectofugal brain regions themselves. Clearly, to gain a better understanding of how to relate species' ecology and behavior to the volumetrics of visual regions in the avian brain, these knowledge gaps need to be tackled. In particular, detailed studies of the retinal morphology and visual abilities of waterfowl and parrots would greatly aid in determining why these taxa have undergone a reduction in tectofugal brain region volumes. Similarly, future studies should also address whether there are species differences in the relative size of functional zones within nRt and E in order to test our hypothesis that the sizes of these regions vary according to lifestyle.

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