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The Evolution of Cerebrotypes in Birds

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Birds · Wulst · Nidopallium · Brainstem · Cerebellum · Evolution · Prey capture · Cognition

Abstract
Multivariate analyses of brain composition in mammals, amphibians and fish have revealed the evolution of 'cerebrotypes' that reflect specific niches and/or clades. Here, we present the first demonstration of similar cerebrotypes in birds. Using principal component analysis and hierarchical clustering methods to analyze a data set of 67 species, we demonstrate that five main cerebrotypes can be recognized. One type is dominated by galliforms and pigeons, among other species, that all share relatively large brainstems, but can be further differentiated by the proportional size of the cerebellum and telencephalic regions. The second cerebrotype contains a range of species that all share relatively large cerebellar and small nidopallial volumes. A third type is composed of two species, the tawny frogmouth *(Podargus strigoides)* and an owl, both of which share extremely large Wulst volumes. Parrots and passerines, the principal members of the fourth group, possess much larger nidopallial, mesopallial and striatopallidal proportions than the other groups. The fifth cerebrotype contains species such as raptors and waterfowl that are not found at the extremes for any of the brain regions and could therefore be classified as 'generalist' brains. Overall, the clustering of species does not directly reflect the phylogenetic relationships among species, but there is a tendency for species within an order to clump together. There may also be a weak relationship between cerebrotype and developmental differences, but two of the main clusters contained species with both altricial and precocial developmental patterns. As a whole, the groupings do agree with behavioral and ecological similarities among species. Most notably, species that share similarities in locomotor behavior, mode of prey capture or cognitive ability are clustered together. The relationship between cerebrotype and behavior/ecology in birds suggests that future comparative studies of brain-behavior relationships will benefit from adopting a multivariate approach.

Introduction

In recent years, there has been a renewed interest in using comparative studies to understand the evolution of the vertebrate brain. Whereas many early approaches were limited to an examination of allometry of individual brain regions against body mass, brain volume or other brain regions [e.g., Jerison, 1973], these more recent studies have used multivariate statistics [Ridet and Bauchot, 1991; Huber et al., 1997; Barton and Harvey, 2000; Clark et al., 2001; de Winter and Oxnard, 2001; Wagner, 2001a, b; Doré et al., 2002; Barton et al., 2003; Whiting and Barton, 2003; Iwaniuk et al., 2004]. This is a logical and

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necessary approach to understanding brain evolution for at least two reasons. First, there are contingencies among brain regions that result in correlated evolution among some areas, but not all [Barton and Harvey, 2000; de Winter and Oxnard, 2001; Barton et al., 2003; Whiting and Barton, 2003; Iwaniuk et al., 2004]. The analysis of individual brain regions can then become problematic because some of the variation in any individual region may be a product of the size of other brain regions. Second, the composition of the brain is the product of a multitude of selection pressures and constraints, which makes it unlikely that simple bivariate comparisons will reveal distinguishable evolutionary patterns.

Although most of the recent use of these multivariate methods has focused upon discriminating between developmental constraints [Finlay and Darlington, 1995; Finlay et al., 2001] and mosaic models of evolutionary change in brain composition [e.g., Barton and Harvey, 2000; Clark et al., 2001; de Winter and Oxnard, 2001; Iwaniuk et al., 2004], an equally important outcome of multivariate approaches is the recognition of 'cerebrotypes' [Clark et al., 2001]. Clark et al. [2001] divided the volume of each of 12 brain regions by the volume of the entire brain to create a series of volume fractions. The set of all of the volume fractions of an individual species was then defined as a cerebrotype [Clark et al., 2001, p. 189].

Although Clark et al. [2001] coined the term 'cerebrotype', a number of previous studies recognized that different groups of vertebrates possess specific patterns of brain composition that vary among clades and ecological niches. In fact, cerebrotypes have been demonstrated, in one form or another, across a range of mammals [Legendre et al., 1994; Lapointe et al., 1999; Clark et al., 2001; de Winter and Oxnard, 2001], amphibians [Doré et al., 2002] and fish [Huber et al., 1997; Wagner, 2001a, b]. The degree to which phylogeny and ecology relate to species-specific cerebrotypes varies among studies and the taxa examined.

In mammals, cerebrotypes characterize entire lineages as well as clusters of species with similar lifestyles [Legendre et al., 1994; Lapointe et al., 1999; Clark et al., 2001; de Winter and Oxnard, 2001]. For example, primates possess larger isocortex, striatum, cerebellum and diencephalon volumes relative to the medulla than other mammalian groups. In addition, species with similar lifestyles cluster together, such as fossorial and semi-aquatic insectivores. A similar comparison within urodeles revealed that significant differences in telencephalic composition were present between two families (Salamandridae and Plethodontidae), particularly in the relative size of the three parts of the olfactory bulbs [rostral and caudal granule cell layers and mitral cell layer; Doré et al., 2002]. Using discriminant function analysis, cluster analysis and principal component analysis, Ridet and Bauchot [1991] demonstrated that overall brain composition (i.e., cerebrotypes) were specific to some lineages of fish, but not necessarily to all. In fact, some cerebrotypes cut across clades and may be related to particular ecological niches. Similar results have since been reported in African cichlids [Huber et al., 1997], mesopelagic teleosts [Wagner, 2001a] and demersal teleosts [Wagner, 2001b]. In the latter two studies, the cerebrotypes related specifically to the sensory systems. Some species were classified as sensory specialists because one sensory structure (e.g., olfactory bulbs, optic tectum) was much larger than the others, whereas other species were classified as sensory generalists because the sensory regions occupied similar proportions of overall brain volume. Given that these clusters correspond to known lifestyle similarities across species, the examination of cerebrotypes in multivariate analyses provides a useful tool for examining brain evolution in light of phylogeny, behavior and ecology.

Despite the demonstration of cerebrotypes in other vertebrates, no such analyses have been performed in birds. There is, however, ample evidence to suggest that cerebrotypes are present in birds. For example, comparisons of relative forebrain size have suggested a similar overall neural architecture in corvids and parrots [Psittaciformes; Emery and Clayton, 2004]. Volumetric studies also indicate the convergent neural evolution of telencephalic composition in some aquatic species [Carezzano and Bee de Speroni, 1995], medullary nuclei in auditory specialists [Kubke et al., 2004] and overall brain composition in parrots and passerines [Iwaniuk et al., 2005]. In a recent analysis of major brain components, Burish et al. [2004] also provide some evidence for cerebrotypes in birds. In particular they demonstrated that social complexity has driven the evolution of relatively large telencephala in birds, with the notable exception of owls. Their analysis did not, however, provide any details on telencephalic composition, which has proven to be integral in defining cerebrotypes in mammals [Legendre et al., 1994; Lapointe et al., 1999; Clark et al., 2001; de Winter and Oxnard, 2001]. Given that there are numerous examples of convergent behavioral and ecological evolution in birds [Feduccia, 1999; Bennett and Owens, 2002], and a detailed multivariate study has not been performed on avian brain composition, we therefore tested whether cerebrotypes characterize lineages and/or lifestyles of birds.

The evolution of avian cerebrotypes could be related to a number of factors. First, phylogenetic constraints could largely dictate a species brain composition. If this were true, then closely related species should be close to one another in multivariate space. Alternatively, developmental constraints could exert the strongest influence on avian brain composition. Previous studies have demonstrated that there is a strong correlation between developmental differences and brain size in birds [see reviews in Bennett and Harvey, 1985; Nealen and Ricklefs, 2001; Iwaniuk and Nelson, 2003]. Therefore, species that share similar developmental traits, such as developmental state of hatchlings, incubation period, etc., may cluster together in multivariate space. Third, avian brain composition might be a product of behavior/ecology such that species occupying a similar niche exhibit a similar brain composition. This was found in mammals and fish (see above) and it is reasonable to assume that it could also occur in birds. Using a multi-species data set and multivariate statistics, we explored the evolution of species differences in avian brain composition.

Materials and Methods

Data

The volumetric composition of the brains of 67 bird species was derived from Boire [1989], Iwaniuk et al. [2004], Ebinger [1995], Ebinger and Lohmer [1984, 1987], Rehkämper et al. [1991] and previously unpublished data (table 1). The measurement methods were similar across these studies and are provided in detail elsewhere [Boire, 1989; Boire and Baron, 1994; Iwaniuk et al., 2004, 2005]. Briefly, the brains were paraffin embedded, serially sectioned in the transverse plane, mounted, Nissl stained and a series of 70–80 digital photographs taken per brain. Area measurements of each section were made with NIH Image and the volumes of each structure reconstructed by multiplying the area by the slice thickness, interslice interval and a shrinkage factor calculated for each specimen.

The volumes of nine regions were analyzed in total. Four of these were non-telencephalic regions: optic tectum, diencephalon, cerebellum and brain stem. The brain stem consisted of the mesencephalon, myelencephalon and tegmentum minus the optic tectum. This corresponded to the sum of the mesencephalon and myelencephalon in Boire [1989] and Iwaniuk et al. [2004] and the tegmentum in Ebinger and Löhmer [1984, 1987] and Rehkämper et al. [1991].

The remaining five regions were various subdivisions of the telencephalon that follow the criteria employed in Timmermans et al. [2000] and Lefebvre et al. [2002]. This resulted in a consistency between these two studies and the present study as well as the inclusion of data from sources that differed in the delineation of telencephalic regions. We follow the recently updated nomenclature for the telencephalic structures [Reiner et al., 2004], despite the use of alternative names in earlier studies. The nidopallial measurement included all of the nidopallial subregions (e.g., nucleus basorostralis pallii, entopallium and arcopallium) as well as area temporo-parieto-occipitalis. The mesopallium included both the dorsal and ventral subdivisions. The Wulst included the hyperpallium densocellulare, hyperpallium intercalatum, hyperpallium apicale, and nucleus interstitialis hyperpallii apicalis. The striatopallidal complex included most structures found between the lamina pallio-subpallialis and the diencephalon. This includes the striatum mediale and striatum laterale [Reiner et al., 2004] and corresponded to the paleostriatum augmentatum, paleostriatum primitivum and basal telencephalon of Boire [1989]. Lastly, we also included a telencephalon remainder volume, which included the olfactory bulbs, hippocampal formation (i.e., area parahippocampalis and hippocampus), septum and piriform cortex. Although these structures perform disparate functions in the avian brain, they constitute small proportions individually which could bias the analysis. Furthermore, the sizes of all of these structures were not available for all species. By considering the

Table 1. The sample sizes and proportions of each of the nine brain structures measured across all 67 bird species. The proportions were calculated by dividing the volume of each individual structure by that of the entire brain

Order	Species		n	N	W	M	SPC	OTe	OT	CB	DI	BSt	Source[1]
Anseriformes	Mallard	*Anas platyrhynchos*	8	0.3330	0.0900	0.1114	0.1077	0.0590	0.0464	0.0935	0.0366	0.1224	1
	Greylag goose	*Anser anser*	8	0.3139	0.0965	0.1245	0.0843	0.0669	0.0370	0.1282	0.0385	0.1103	2
	Plumed whistling-duck	*Dendrocygna eytoni*	1	0.3069	0.1068	0.1093	0.0957	0.0639	0.0353	0.1246	0.0414	0.1162	3
Apodiformes	Chimney swift	*Chaetura pelagicus*	1	0.1961	0.0455	0.0684	0.1093	0.0188	0.0835	0.1814	0.0445	0.2525	4
Caprimulgiformes	Nightjar	*Caprimulgus sp.*	1	0.1901	0.0654	0.0608	0.0654	0.0526	0.0997	0.1486	0.0524	0.2650	4
	Tawny frogmouth	*Podargus strigoides*	1	0.3454	0.2377	0.0780	0.0390	0.0394	0.0563	0.0754	0.0373	0.0896	3
Charadriiformes	Least sandpiper	*Calidris minutilla*	1	0.2212	0.0249	0.0783	0.1213	0.0565	0.0852	0.1229	0.0478	0.2419	4
	Killdeer	*Charadrius vociferus*	1	0.2123	0.0168	0.0674	0.0953	0.0550	0.1115	0.1242	0.0483	0.2692	4
	Short-billed dowitcher	*Limnodromus griseus*	1	0.2968	0.0291	0.1127	0.1318	0.0521	0.0476	0.1187	0.0397	0.1715	4
	Common tern	*Sterna hirundo*	1	0.2088	0.0334	0.0886	0.1036	0.0385	0.0886	0.1735	0.0383	0.2266	4
	Masked lapwing	*Vanellus miles*	1	0.3247	0.0505	0.1059	0.0797	0.0507	0.0802	0.1430	0.0484	0.1170	3
Ciconiiformes	Grey heron	*Ardea cinerea*	1	0.2676	0.0581	0.1134	0.0631	0.0594	0.0779	0.1206	0.0399	0.2000	4
	Nankeen night heron	*Nycticorax caledonicus*	1	0.3092	0.0700	0.0708	0.0732	0.0792	0.0844	0.1375	0.0391	0.1367	3

Table 1 (continued)

Order	Species		n	N	W	M	SPC	OTe	OT	CB	DI	BSt	Source[1]
Columbiformes	White-headed pigeon	*Columba leucomela*	1	0.2506	0.0668	0.0768	0.0594	0.0565	0.0975	0.1600	0.0563	0.1762	3
	Rock dove	*Columba livia*	6	0.2471	0.0516	0.1022	0.0907	0.0623	0.0861	0.1680	0.0503	0.1416	5
	Common bronzewing	*Phaps elegans*	1	0.2104	0.0738	0.0829	0.0734	0.0889	0.0938	0.1659	0.0537	0.1573	3
	Ring dove	*Streptopelia risoria*	1	0.2234	0.0389	0.0847	0.0991	0.0666	0.1002	0.1117	0.0472	0.2281	4
Coraciiformes	Laughing kookaburra	*Dacelo novaeguineae*	1	0.3298	0.0490	0.1138	0.0638	0.0368	0.1036	0.1267	0.0411	0.1355	3
	Sacred kingfisher	*Todiramphus sanctus*	1	0.3209	0.0761	0.0993	0.0778	0.0437	0.0888	0.1274	0.0406	0.1254	3
Falconiformes	Brown goshawk	*Accipiter fasciatus*	1	0.3112	0.0796	0.0814	0.0665	0.0277	0.0849	0.1604	0.0509	0.1374	3
	Nankeen kestrel	*Falco cenchroides*	1	0.3220	0.0838	0.0993	0.0750	0.0192	0.0685	0.1465	0.0582	0.1276	3
	Australian hobby falcon	*Falco longipennis*	1	0.3432	0.0880	0.0609	0.0511	0.0086	0.0718	0.1861	0.0584	0.1319	3
Galliformes	Chukar	*Alectoris chukar*	1	0.2381	0.0622	0.0929	0.921	0.0462	0.0806	0.1076	0.0478	0.2325	4
	Golden pheasant	*Chrysolophus pictus*	1	0.2271	0.0489	0.0831	0.0836	0.0391	0.0882	0.1295	0.0514	0.2493	4
	Bobwhite	*Colinus virginianus*	1	0.2305	0.0591	0.0705	0.0758	0.0509	0.0959	0.1096	0.0569	0.2509	4
	Common quail	*Coturnix coturnix*	10	0.1856	0.0417	0.0713	0.0813	0.0408	0.1040	0.1217	0.0597	0.2938	6
	Chicken	*Gallus domesticus*	1	0.1947	0.0471	0.0752	0.0869	0.0386	0.0996	0.2077	0.0534	0.1967	4
	Turkey	*Meleagris gallopavo*	1	0.2282	0.0626	0.0906	0.0812	0.0396	0.1029	0.1591	0.0452	0.1906	4
	Guineafowl	*Numida meleagris*	1	0.2544	0.0535	0.0900	0.0885	0.0339	0.0769	0.1282	0.0462	0.2284	4
	Chaco chachalaca	*Ortalis canicollis*	1	0.2352	0.0571	0.0846	0.0718	0.0640	0.0760	0.1474	0.0480	0.2157	4
	Peafowl	*Pavo meleagris*	1	0.2458	0.0701	0.1130	0.0848	0.0452	0.0648	0.1382	0.0396	0.1984	4
	Grey partridge	*Perdix perdix*	10	0.2671	0.1209	0.0826	0.0690	0.0115	0.0864	0.1287	0.0737	0.1600	6
	Ring-necked pheasant	*Phasianus colchicus*	10	0.2533	0.0593	0.0906	0.1029	0.0411	0.0750	0.0968	0.0526	0.2283	6
Passeriformes	Carrion crow	*Corvus corone*	7	0.4153	0.1204	0.1537	0.0936	0.0064	0.0394	0.0847	0.0313	0.0552	6
	Blue-faced honeyeater	*Entomyzon cyanotis*	1	0.3850	0.0604	0.1382	0.1133	0.0334	0.0448	0.1053	0.0331	0.0864	3
	European jay	*Garrulus glandarius*	3	0.3474	0.1229	0.1266	0.1016	0.0122	0.0681	0.0923	0.0500	0.0787	6
	House sparrow	*Passer domesticus*	4	0.3359	0.1269	0.1084	0.1055	0.0142	0.0679	0.1008	0.0487	0.0916	6
	Grey currawong	*Strepera versicolor*	1	0.3815	0.0519	0.1828	0.0966	0.0296	0.0505	0.0943	0.0329	0.0800	3
	Zebra finch	*Taeniopygia guttata*	1	0.2820	0.0654	0.0945	0.1214	0.0323	0.0708	0.1020	0.0411	0.1906	4
Pelecaniformes	Double-crested cormorant	*Phalacrocorax auritus*	1	0.1995	0.1841	0.0911	0.0705	0.0336	0.0481	0.1516	0.0477	0.1738	4
Procellariiformes	Short-tailed shearwater	*Puffinus tenuirostris*	1	0.1871	0.0987	0.0703	0.0874	0.0794	0.0526	0.2191	0.0392	0.1662	3
Psittaciformes	Masked lovebird	*Agapornis personata*	1	0.3633	0.0749	0.1620	0.1291	0.0289	0.0302	0.0888	0.0397	0.0830	3
	Peach-faced lovebird	*Agapornis roseicollis*	1	0.3691	0.0994	0.1233	0.1195	0.0331	0.0408	0.0873	0.0504	0.0771	3
	King parrot	*Alisterus scapularis*	3	0.3098	0.1081	0.1244	0.1244	0.0271	0.0424	0.0941	0.0396	0.1302	3
	Blue-winged amazon	*Amazona aestiva*	1	0.3719	0.0999	0.1450	0.1083	0.0207	0.0360	0.0817	0.0422	0.0944	3
	Galah	*Cacatua roseicapilla*	2	0.3618	0.1036	0.1356	0.1335	0.0179	0.0314	0.0978	0.0382	0.0803	3
	Yellow-tailed black-cockatoo	*Calyptorhynchus funereus*	1	0.3887	0.1288	0.1294	0.1410	0.0231	0.0196	0.0730	0.0325	0.0639	3
	Eclectus parrot	*Eclectus roratus*	2	0.3534	0.1113	0.1308	0.1311	0.0315	0.0351	0.0751	0.0380	0.0937	3
	Musk lorikeet	*Glossopsitta concinna*	3	0.3341	0.1156	0.1180	0.1372	0.0307	0.0361	0.0967	0.0423	0.0892	3
	Budgerigar	*Melopsittacus undulatus*	1	0.3210	0.0727	0.1398	0.1406	0.0369	0.0514	0.0959	0.0361	0.1057	4
	Bourke's parrot	*Neopsephotus bourkii*	1	0.3586	0.1010	0.1130	0.1067	0.0334	0.0482	0.0963	0.0439	0.0989	3
	Cockatiel	*Nymphicus hollandicus*	3	0.3571	0.1085	0.1100	0.1258	0.0244	0.0350	0.0930	0.0381	0.1080	3
	Blue-headed pionus	*Pionus menstruus*	1	0.3551	0.0785	0.1350	0.1454	0.0259	0.0495	0.0736	0.0404	0.0967	4
	Crimson rosella	*Platycercus elegans*	3	0.3401	0.0931	0.1197	0.1312	0.0348	0.0429	0.0919	0.0411	0.1051	3
	Eastern rosella	*Platycercus eximius*	4	0.3349	0.1004	0.1261	0.1457	0.0279	0.0410	0.0921	0.0398	0.0921	3
	Superb parrot	*Polytelis swainsonii*	2	0.3200	0.0931	0.1155	0.1494	0.0210	0.0556	0.0969	0.0481	0.1004	3
	Red-rumped parrot	*Psephotus haematonotus*	2	0.3540	0.0919	0.1295	0.1378	0.0252	0.0387	0.0912	0.0461	0.0858	3
	Alexandrine parrot	*Psittacula eupatria*	1	0.3840	0.0898	0.1624	0.1253	0.0350	0.0260	0.0787	0.0304	0.0685	3
	Indian ring-necked parrot	*Psittacula krameri*	1	0.3513	0.1367	0.1358	0.1337	0.0326	0.0291	0.0715	0.0376	0.0716	3
	African grey parrot	*Psittacus erithacus*	1	0.3835	0.1069	0.1400	0.1057	0.0199	0.0248	0.0963	0.0408	0.0820	3
	Green-cheeked conure	*Pyrrhura molinae*	1	0.3329	0.1103	0.1170	0.0914	0.0413	0.0517	0.1120	0.0564	0.0871	3
	Rainbow lorikeet	*Trichoglossus haematodus*	2	0.3370	0.1129	0.1366	0.1356	0.0265	0.0339	0.0973	0.0392	0.0810	3
Sphenisciformes	Magellanic penguin	*Spheniscus magellanicus*	1	0.2486	0.1381	0.1186	0.1016	0.0296	0.0393	0.1535	0.0283	0.1424	4
Strigiformes	Boobook owl	*Ninox boobook*	1	0.2860	0.2651	0.0887	0.0429	0.0401	0.0310	0.1135	0.0312	0.1015	3
Struthioiniformes	Rhea	*Rhea americana*	1	0.2009	0.1184	0.0934	0.0669	0.0509	0.0664	0.1534	0.0340	0.2157	4
Tinamiformes	Red-winged tinamou	*Rhynchotus rufescens*	1	0.2370	0.0603	0.0926	0.0839	0.0597	0.1024	0.0967	0.0356	0.2317	4
Trochiliformes	Blue-tailed emerald	*Chlorostilbon mellisugus*	1	0.1866	0.0440	0.0624	0.0977	0.0442	0.0957	0.1817	0.0492	0.2385	4

N = Nidopallium; M = mesopallium; W = Wulst; SPC = striatopallidal complex; Ote = other telencephalic structures; OT = optic tectum; CB = cerebellum; DI = diencephalon; BSt = brain stem. Details of how these structures were delineated can be found in the text.

[1] The sources of the data are as follows: 1 = Ebinger [1995]; 2 = Ebinger and Löhmer [1987]; 3 = Iwaniuk et al. [2004; this study]; 4 = Boire [1989]; 5 = Ebinger and Löhmer [1985]; 6 = Rehkämper et al. [1991].

four structures together, we were able to increase the number of species included in the analysis (67 species versus 43 species) and several taxa from divergent taxa/clades were included that were otherwise unavailable (hummingbird, swift, cormorant, penguin, sandpipers, ratites).

Statistical Analysis

Prior to statistical analysis, the volume of each brain region was divided by the overall brain volume to yield a proportion and therefore yields comparable results to previous demonstrations of cerebrotypes [Clark et al., 2001; de Winter and Oxnard, 2001; table 1]. In addition, by expressing the relative size of each region as a proportion of brain volume, potentially confounding sources of error, such as variable section thickness or tissue distortion, are less likely to have an effect than if the structures are examined as absolute volumes, compared directly against one another or compared to body mass. Two sets of statistical analyses were performed. First, we performed a principal component analysis (PCA) of the proportions. This is a useful method for examining the evolution of cerebrotypes because it reduces the number of variables to a number that is amenable to bivariate analyses. PCA's do, however, tend to minimize the distance between clusters that are not widely separated while maintaining the representation of widely separated clusters [Rohlf, 1970]. Therefore, we also performed a cluster analysis, which enables the examination of groups of species (i.e., clusters) that are not widely separated. Although cluster analyses are not supported by extensive statistical reasoning, they are a useful heuristic in data exploration and can be used to both generate and test hypotheses [Aldenderfer and Blashfield, 1984]. With respect to the present study, the cluster analysis provides a representation of the similarity and dissimilarity among species in multivariate space that is easier to interpret than the PCA and includes all of the variation in all of the structures.

All statistical analyses were performed in R [Ihaka and Gentleman, 1996]. We determined the principal component loadings of the data matrix using the princomp function of the mva library [Venables and Ripley, 1999]. Cluster analyses were performed using the hierarchical cluster function, hclust, algorithm [Murtagh, 1985]. We used the unweighted pair group method with arithmetic means (UPGMA) for the cluster analysis. Unlike other linkage methods (e.g., Ward's, single linkage, complete linkage), the UPGMA method is robust to alterations in the order of species in the data set, does not have a tendency to produce long or spherical dendrograms and is not prone to elevational biases [Aldenderfer and Blashfield, 1984].

Domestication has a significant effect upon not only relative brain size, but also its composition in birds [Ebinger and Löhmer, 1984, 1987; Ebinger, 1995; Ebinger and Röhrs, 1995]. For this reason, we ran the analyses both including all species and with the domesticated species removed. We considered species to be domesticated if they were obtained from known laboratory or other long-term captive bred stock and have undergone significant behavioral [Price, 1984, 1999], neural [Ebinger and Löhmer, 1984, 1987; Ebinger 1995; Ebinger and Röhrs, 1995], or other morphological changes [Sossinska, 1982] relative to a wild ancestor. Using these criteria, the following species were excluded from the re-analysis: chicken *(Gallus domesticus)*, common quail *(Coturnix coturnix)*, grey partridge *(Perdix perdix)*, turkey *(Meleagris gallopavo)*, peafowl *(Pavo meleagris)*, zebra finch *(Taeniopygia guttata)*, ringed dove *(Streptopelia risoria)* and budgerigar *(Melopsittacus undulatus)*.

Results

Principal Component Analyses (PCA)

Principal component analyses performed on the correlation matrix of the relative size of the nine structures yielded eight principal components (table 2). Of these eight, the first three explained more than 90% of the

Table 2. The loadings and cumulative amount of variation explained by each of the nine principal components (PC's) obtained from a principal component analysis of the nine brain regions across all 67 bird species

Structure[1]	Principal component loadings							
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
N	0.621	−0.263	−0.171	0.471	−0.151	–	0.381	0.114
W	0.227	0.834	0.347	–	–	–	–	0.116
M	0.225	−0.202	0.101	−0.217	0.286	0.701	−0.407	–
SPC	0.128	−0.349	0.342	−0.604	−0.286	−0.397	–	0.167
Other TE	–	–	–	–	0.834	−0.319	0.271	–
OT	−0.212	–	−0.198	0.371	–	−0.312	−0.652	0.369
CB	−0.241	0.201	−0.707	−0.359	−0.245	0.201	0.221	0.116
DI	–	–	–	–	−0.176	−0.174	−0.158	−0.889
Brainstem	−0.619	−0.158	0.419	0.293	−0.139	0.282	0.340	–
Cumulative % of variation	0.721	0.851	0.911	0.954	0.973	0.987	0.997	1.000

N = Nidopallium; W = Wulst; M = mesopallium; SPC = striatopallidal complex; Other TE = remainder of the telencephalon; OT = optic tectum; CB = cerebellum; DI = diencephalon.

Details of how these brain regions were defined are provided in the text.

observed variation in the scores. Principal component 1 (PC1) is largely a function of nidopallium and brainstem proportions, PC2 mostly reflects the proportions of the Wulst and SPC, whereas PC3 is primarily composed of brainstem and cerebellum proportions.

The exclusion of the domesticated species did not have an appreciable effect on the PCA (table 3). Although not shown, there was also no significant change in the scatter of species in bivariate plots of PC1 and PC2, PC1 and PC3, and PC2 and PC3. Because the PCA was not significantly affected by the inclusion/exclusion of the domesticated species, only the analyses that included all 67 species are discussed any further.

In the plot of PC2 against PC1, there is a heavy clustering of species at both the bottom left and bottom right

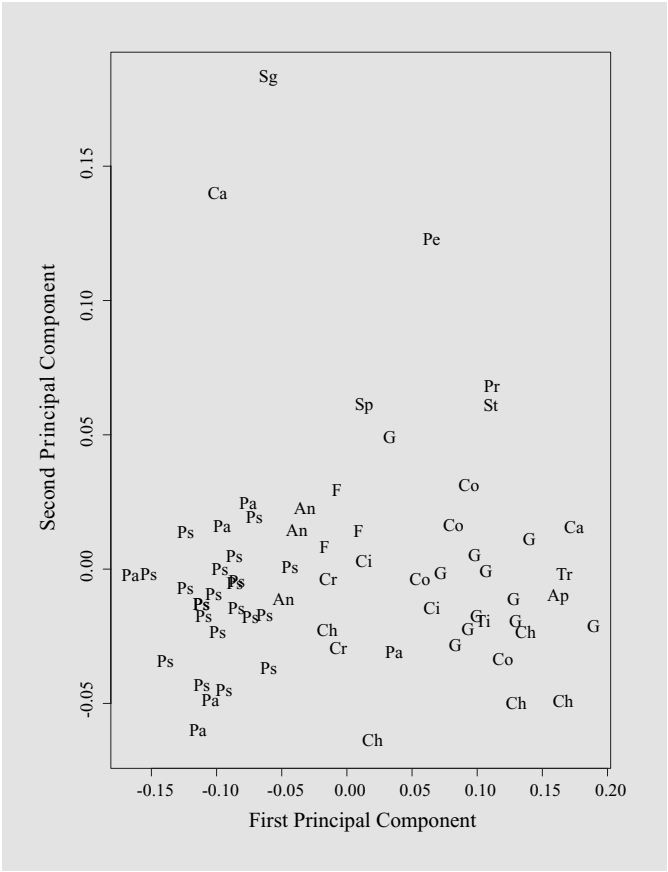

Fig. 1. A scatterplot of principal components 2 vs. 1, both obtained from a principal component analyses (PCA) of the nine brain regions measured across all 67 bird species. Abbreviated order names refer to the orders and species listed in table 1 and are as follows: An = Anseriformes; Ap = Apodiformes; Ca = Caprimulgiformes; Ch = Charadriiformes; Ci = Ciconiiformes; Co = Columbiformes; Cr = Coraciiformes; F = Falconiformes; G = Galliformes; Pa = Passeriformes; Pe = Pelecaniformes; Pr = Procellariiformes; Ps = Psittaciformes; Sg = Strigiformes; Sp = Sphenisciformes; St = Struthioniformes; Ti = Tinamiformes, and Tr = Trochiliformes.

Table 3. The loadings and cumulative amount of variation explained by each of the nine principal components (PC's) obtained from a principal component analysis of the nine brain regions, excluding domesticated species (for abbreviations see table 1)

Structure[1]	Principal component loadings							
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
N	0.621	–0.275	–0.259	0.415	–0.193	–	0.368	0.122
W	0.222	0.885	0.282	–	–	–	–	–
M	0.227	–0.191	0.165	–0.179	0.371	0.696	–0.344	–
SPC	0.132	–0.319	0.491	–0.514	–0.288	–0.387	–	0.174
Other TE	–0.101	–	–	–	0.783	–0.368	0.337	–
OT	–0.203	–	–0.260	0.337	–	–0.286	–0.687	0.322
CB	–0.249	0.156	–0.613	–0.505	–0.278	0.221	0.172	0.128
DI	–	–	–	–	–0.134	–0.167	–0.128	–0.904
Brainstem	–0.618	–0.144	0.358	0.381	–0.157	0.269	0.336	–
Cumulative % of variation	0.721	0.851	0.911	0.954	0.973	0.987	0.997	1.000

N = Nidopallium; W = Wulst; M = mesopallium; SPC = striatopallidal complex; Other TE = remainder of the telencephalon; OT = optic tectum; CB = cerebellum; DI = diencephalon.

Details of how these brain regions were defined are provided in the text.

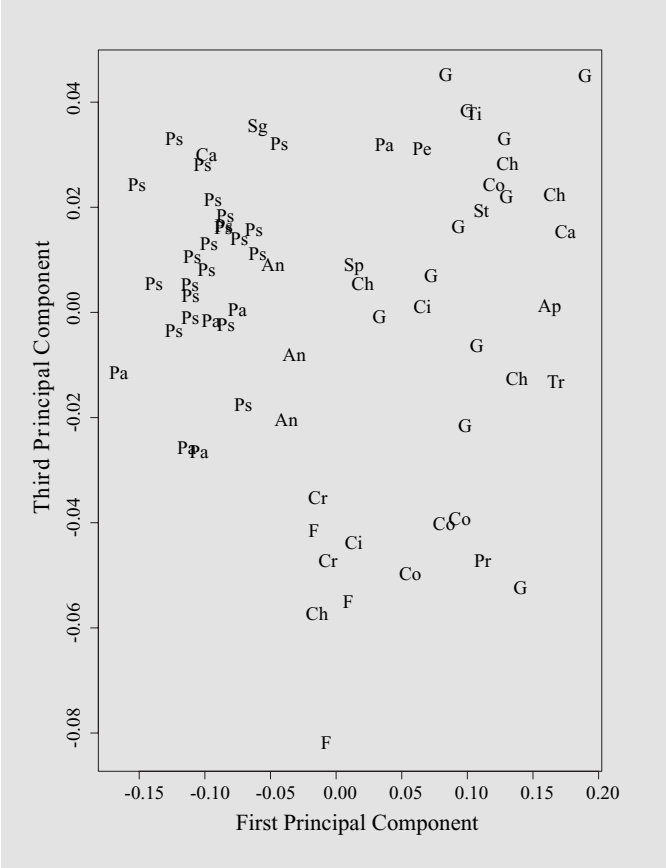

Fig. 2. A scatterplot of principal components 3 versus 1, both obtained from a principal component analyses (PCA) of the nine brain regions measured across all 67 bird species. Abbreviated order names refer to the orders and species listed in table 1 and are provided in the legend for figure 1.

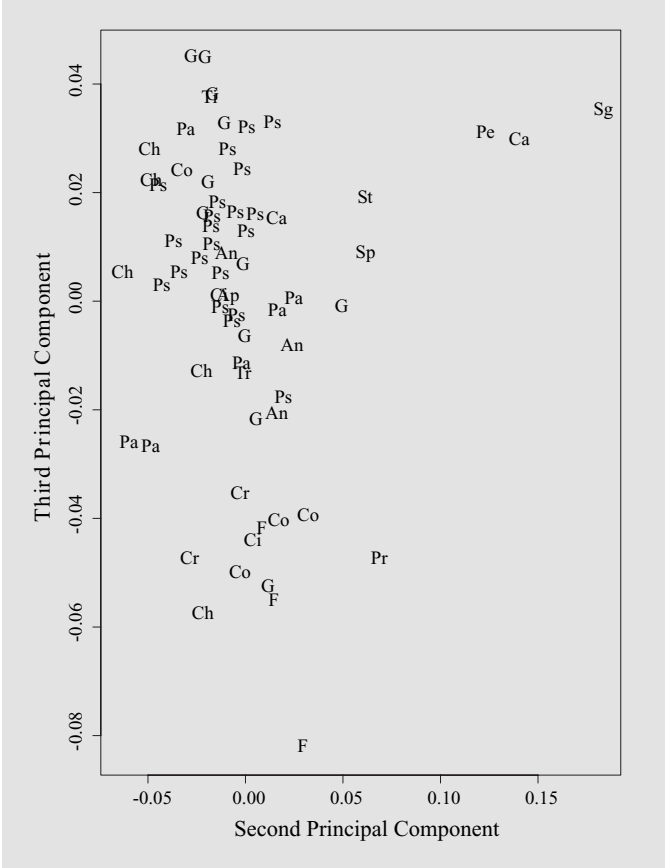

Fig. 3. A scatterplot of principal components 3 vs. 2, both obtained from a principal component analyses (PCA) of the nine brain regions measured across all 67 bird species. Abbreviated order names refer to the orders and species listed in table 1 and are provided in the legend for figure 1.

sides of the scatterplot (fig. 1). The left side group is composed of primarily parrots and passerines with large nidopallial and small brainstem proportions, whereas the right side is predominately gallinaceous birds (e.g., quail, pheasant, chicken, etc.) with small nidopallial and large brainstem proportions. In the middle of the PC1 axis, there are relatively few species and there are few species above 0.05 on the PC2 axis. It should be noted that there are two significant outliers with high PC2 values, and hence large Wulst and low nidopallial and SPC proportions: the boobook owl *(Ninox boobook)* and the tawny frogmouth *(Podargus strigoides)*. A third outlier is the double-crested cormorant *(Phalacrocorax auritus)* because it too possesses a relatively high PC2 value, but is more similar in brainstem and/or nidopallial volume to birds with higher PC1 values.

Clusters are less prominent in the plot of PC3 against PC1 (fig. 2). The scatter along PC1 is of course identical, but there is some separation along PC3. In particular, there is an assemblage of species at the lower end of PC3 that possess relatively large cerebella. This group includes: the short-tailed shearwater *(Puffinus tenuirostris)*, both kingfishers, all three raptors, chicken, common tern *(Sterna hirundo)*, three pigeons and one of the herons *(Nycticorax caledonicus)*.

Lastly, the plot of PC3 against PC2 reveals similar groupings to the previous two plots (fig. 3). For example, the frogmouth and owl are outliers at the upper right hand corner of the plot and they are accompanied by the double-crested cormorant. There is also a cluster near the bottom left hand corner that is composed of the same large cerebellum species noted in the plot of PC1 and PC3 (see

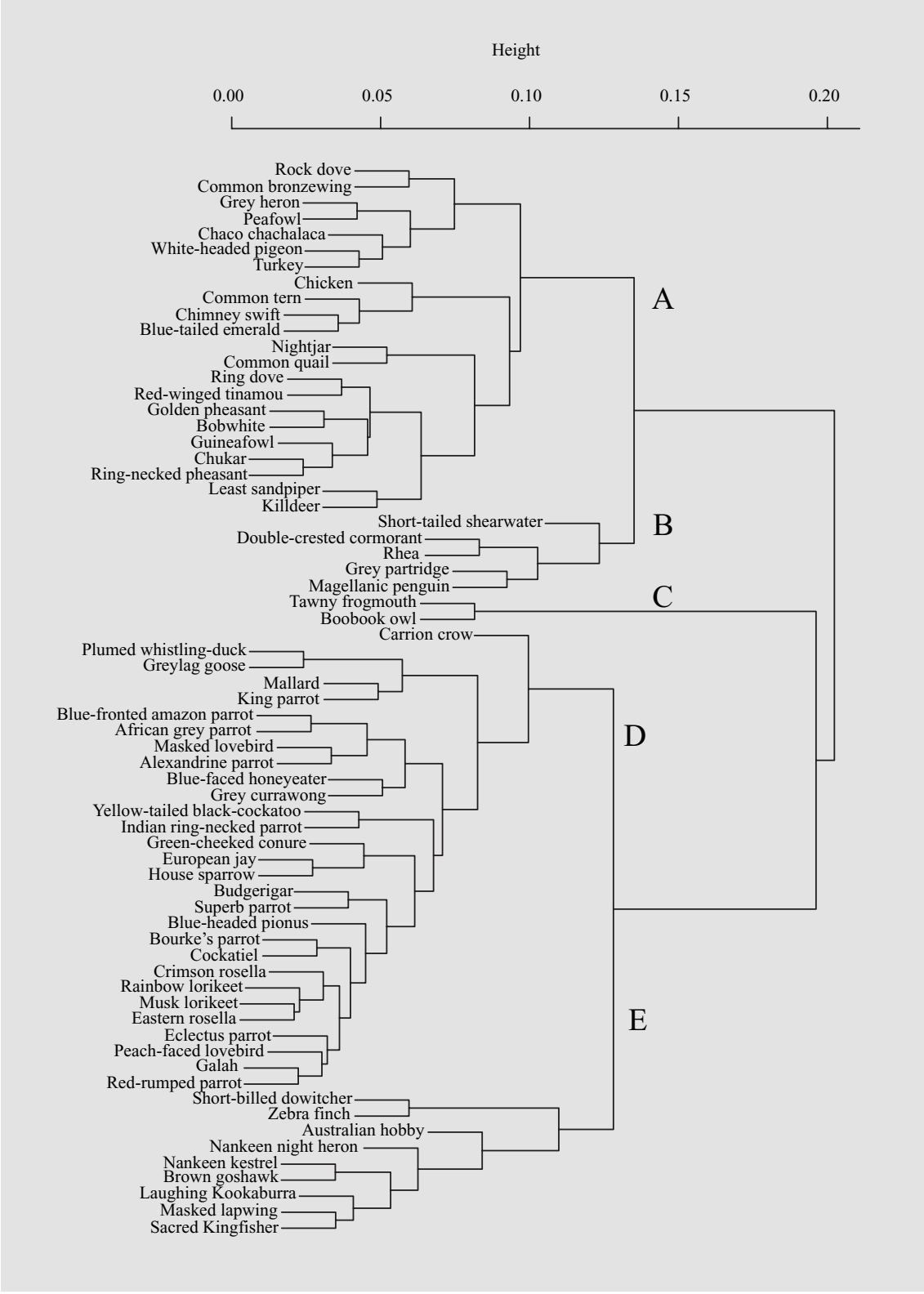

Fig. 4. A dendrogram resulting from a UPGMA hierarchical cluster analysis performed across all 67 bird species. The height of the dendrogram refers to the similarity index calculated across all nine brain regions. Five distinct clusters are indicated by the capital letters, A, B, C, D, and E.

Table 4. The mean proportions for each of the nine brain regions shown for each of the five clusters identified in the cluster analyses of all species (figure 4)

Cluster	N	W	M	SPC	OTe	OT	CB	DI	BSt
A	0.2368 (0.1995–0.2486)	0.0557 (0.1184–0.1841)	0.0833 (0.0911–0.1186)	0.0841 (0.0669–0.1016)	0.0462 (0.0296–0.0509)	0.0884 (0.0393–0.0664)	0.1438 (0.1516–0.1535)	0.0493 (0.0283–0.0477)	0.2124 (0.1424–0.2157)
B	0.2207 (0.2148–0.2367)	0.1320 (0.0470–0.0640)	0.0912 (0.0765–0.0903)	0.0791 (0.0792–0.0939)	0.0410 (0.0453–0.0595)	0.0586 (0.0796–0.0919)	0.1613 (0.1294–0.1574)	0.0446 (0.0443–0.0499)	0.1716 (0.2011–0.2351)
C	0.3157 (0.2860–0.3454)	0.2514 (0.2377–0.2651)	0.0843 (0.0798–0.0887)	0.0409 (0.0390–0.0429)	0.0398 (0.0395–0.0402)	0.0437 (0.0310–0.0563)	0.0945 (0.0754–0.1135)	0.0342 (0.0312–0.0373)	0.0956 (0.0896–0.1015)
D	0.3517 (0.3475–0.3664)	0.1005 (0.0937–0.1093)	0.1316 (0.1264–0.1399)	0.1206 (0.1153–0.1292)	0.0305 (0.0232–0.0292)	0.0410 (0.0363–0.0457)	0.0933 (0.0866–0.0943)	0.0405 (0.0383–0.0433)	0.0909 (0.0811–0.0935)
E	0.3106 (0.3114–0.3264)	0.0567 (0.0610–0.0871)	0.0955 (0.0864–0.1102)	0.0913 (0.0715–0.0962)	0.0492 (0.0341–0.0574)	0.0792 (0.0538–0.0810)	0.1259 (0.1231–0.1494)	0.0416 (0.0406–0.0497)	0.1461 (0.1217–0.1404)

The 95% confidence intervals for each structure are shown in parentheses. Abbreviations of the brain regions can be found in table 1.

above). Lastly, there is a dense conglomeration of the remaining species, such as the parrots, passerines and galliforms, in the upper left-hand side of the plot.

Cluster Analysis

The cluster analyses yielded a tree with five distinct clusters labeled A, B, C, D and E (fig. 4). We identified only these five clusters because they possessed much longer branches than any of the other groupings and were clearly separated from other groups at a distance of between 0.15 and 0.10. With the exclusion of the domesticated species, the overall composition of the dendrogram changed slightly, but these same five major clusters could still be recognized (fig. 5). Because the overall composition of the dendrograms was virtually identical in both cases, only the analysis that included all species is discussed further.

Cluster 'A' consists primarily of galliform birds, pigeons and doves and a few species from other orders. Specifically, these were: grey heron *(Ardea cinerea)*, common tern, chimney swift *(Chaetura pelagica)*, blue-tailed emerald *(Chlorostilbon mellisugus)*, a nightjar (*Caprimulgus* sp.), least sandpiper *(Calidris minutilla)*, killdeer *(Charadrius vociferus)* and red-winged tinamou. This cluster is characterized by proportionately larger optic tectum, diencephalon and brainstem volumes than the other clusters (table 4). In fact, the mean brainstem proportion of this cluster is almost three times that of clusters B and C. Cluster A also has the smallest Wulst and mesopallial volumes, although the Wulst is not that much smaller than cluster E and the mesopallium is similar to that of cluster C. A closer examination of this cluster reveals that it can be subdivided into three smaller clusters. The first of these contains the heron, pigeons and some galliforms, the second contains the tern, swift, hummingbird and chicken and the third is an assortment of the remaining species (i.e., killdeer, sandpiper, nightjar, galliforms, dove and tinamou). ANOVAs indicated significant differences between these three sub-clusters for seven of the nine regions (nidopallium: $F = 6.53$, df = 2, 19, $P = 0.01$; Wulst: $F = 0.03$, df = 2, 19, $P = 0.03$; mesopallium: $F = 4.47$, df = 2, 19, $P = 0.03$; striatopallidal complex: $F = 5.01$, df = 2, 19, $P = 0.02$; other telencephalon: $F = 5.05$, df = 2, 19, $P = 0.02$; optic tectum: $F = 0.80$, df = 2, 19, $P = 0.46$; cerebellum: $F = 29.16$, df = 2, 19, $P < 0.01$; diencephalon: $F = 0.47$, df = 2, 19, $P = 0.63$; brainstem: $F = 16.43$, df = 2, 19, $P < 0.01$). Post-hoc Tukey-Kramer tests revealed that the first sub-cluster had significantly larger nidopallial and 'other telencephalon' volumes and smaller SPC volumes than the second sub-cluster. The second sub-cluster also had significantly larger cerebella than both of the other sub-clusters and smaller brainstems than the third sub-cluster. In fact, the second sub-cluster has proportionately the largest mean cerebellum of any of the groups identified (mean = 0.1861), which is larger than that of cluster B (table 4). Overall, cluster A is characterized by larger brainstems, diencephala and optic tecta than other clusters and the sub-clusters are separated by nidopallial, SPC, 'other telencephalon', cerebellar and brainstem size.

The 'B' cluster is composed of an assortment of species belonging to different orders that includes: Magellanic

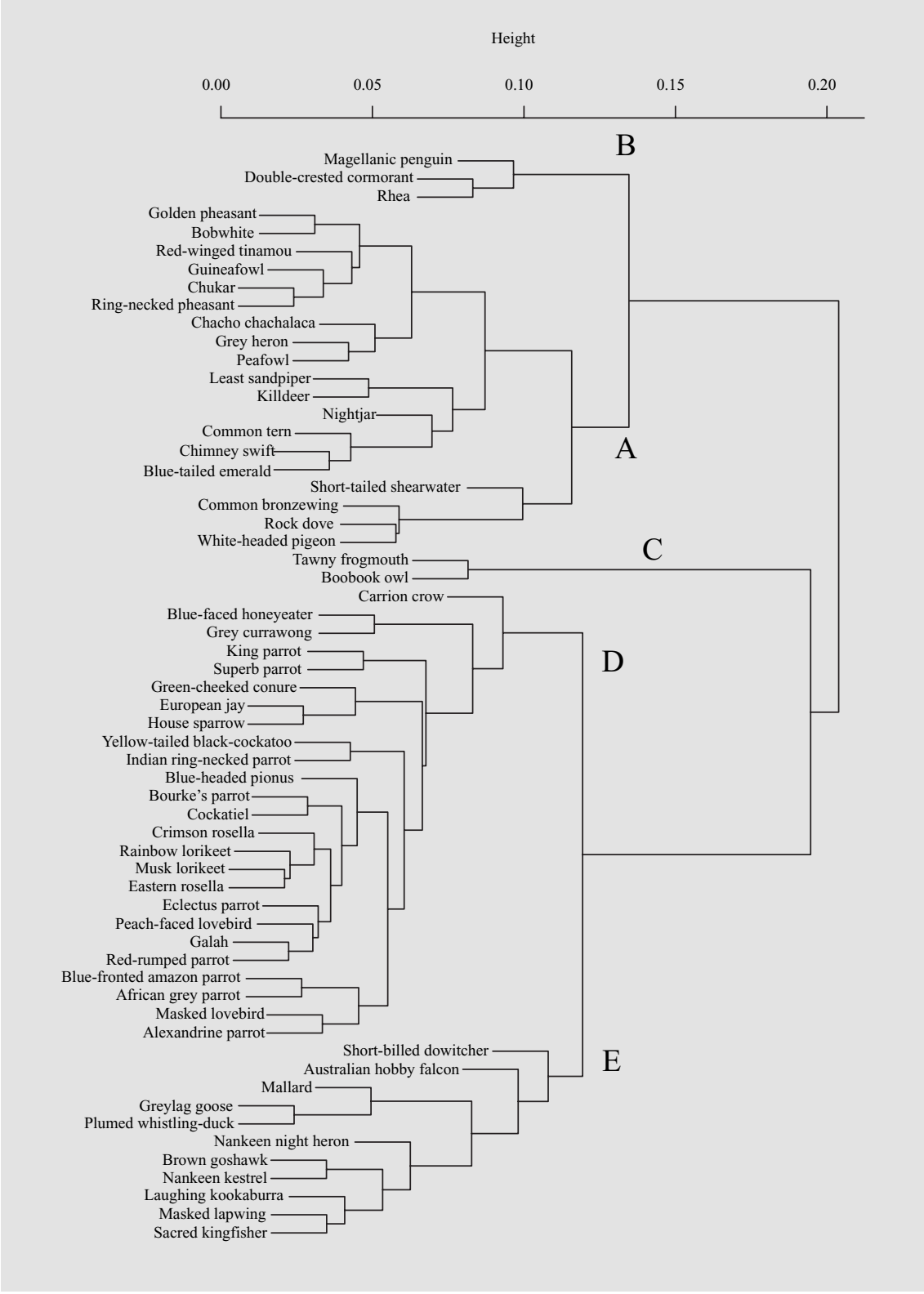

Fig. 5. A dendrogram resulting from a UPGMA hierarchical cluster analysis that excluded the seven domesticated species (n = 60). As with figure 4, the height of the dendrogram refers to the similarity index calculated across all nine brain regions and the five distinct clusters are indicated by the capital letters, A, B, C, D, and E.

penguin *(Spheniscus magellanicus)*, double-crested cormorant, short-tailed shearwater, rhea *(Rhea americana)* and grey partridge. This cluster of species has much larger cerebella and smaller nidopallial volumes than the other clusters (table 4). The only exception to this is the subcluster within A that has larger cerebella discussed above. Apart from the cerebellum and nidopallium, cluster B also has relatively large brainstem and diencephalic proportions, although neither of these is as large as that of cluster A. A large cerebellum and small nidopallium therefore distinguish cluster B from the other clusters.

The only two species in cluster 'C' are the frogmouth and the owl. As indicated in the PCA (see above), these two species possess much larger Wulst volumes than any other birds measured (table 4). Proportionally, the volume of the Wulst is five times that of the lower value (cluster A) and over twice that of the next largest value (cluster D). Perhaps offsetting this large Wulst are smaller mesopallial and striatopallidal volumes in the frogmouth and the owl (table 4). In fact, the striatopallidal complex occupies one third the brain volume space as that of species in cluster D. In addition, the owl and the frogmouth have a smaller diencephalic volume than other clusters, but the range of variation in the size of the diencephalon across all the clusters is much less than that of the other structures (0.0312–0.0373). A massive Wulst therefore distinguishes the frogmouth and owl from the other clusters.

Cluster 'D' is composed of all the parrots, all the passerines, except for the zebra finch, and the waterfowl *(Anas platyrhynchos*, *Anser anser*, *Dendrocygna eytoni)* in one of the cluster analyses (fig. 4). This cluster possesses the largest nidopallial, mesopallial and striatopallidal volumes of any other clusters (table 4), thus indicating that the telencephalon occupies a much larger proportion of the brain in parrots and passerines than most other species. On average, the telencephalon occupies over 70% of total brain volume and approaches 80% in several parrot species. At the other end of the spectrum, cluster D also has proportionately smaller 'other telencephalon', optic tectum, cerebellum and brainstem volumes than the other clusters. Thus, a large nidopallium, mesopallium and striatopallidal complex and small non-telencephalic regions typify the parrots and passerines.

Finally, cluster 'E' is composed of kingfishers *(Dacelo novaeguineae, Todiramphus sanctus)*, raptors *(Accipiter fasciatus, Falco cenchroides, F. longipennis)*, a heron *(Nycticorax caledonicus)*, two shorebirds *(Limnodromus griseus, Vanellus miles)*, the zebra finch and waterfowl (fig. 5 only). The only exceptionally large structure is the 'other telencephalon', but even this is quite similar to the average volume of species in cluster A. For the remaining structures, the average for each of the brain structures was not the highest or lowest of all five clusters. The relative lack of a brain structure(s) that characterizes this cerebrotype suggests that these species could be considered 'neural generalists' in comparison to the other clusters.

Discussion

In a similar fashion to multivariate analyses of brain composition in other taxa [Ridet and Bauchot, 1991; Huber et al., 1997; Clark et al., 2001; de Winter and Oxnard, 2001; Wagner, 2001a, b; Doré et al., 2002], our study indicates that bird brains have evolved specific cerebrotypes that have evolved convergently in disparate taxa. In fact, some of the clusters identified appear to map onto ecological and/or behavioral similarities. It should be noted, however, that although several brain regions were measured, each brain region is, in fact, multifunctional. For example, the nidopallium is composed of regions that process auditory [field L; Bonke et al., 1979], visual [entopallium; Husband and Shimizu, 2001; Nguyen et al., 2004] and somatosensory [nucleus basalis; Wild et al., 1997] information as well as the integration of information from multiple nidopallial and non-nidopallial brain regions [Kroner and Güntürkün, 1999]. A finer level of volumetric analysis might therefore reveal not only different clustering patterns, but also more striking degrees of convergence and divergence of brain composition. In addition, there is the potential issue of the surface area of fissured structures, such as the avian cerebellum, yielding different results from volumetric data [Sultan, 2002]. We were unable to address this issue in the present study because we did not have access to the slides used by previous studies [Ebinger and Löhmer, 1985, 1987; Boire, 1989; Rehkämper et al., 1991; Ebinger, 1995]. A preliminary analysis of the avian cerebella that we have examined does indicate some grouping similarities with this study, but also some marked differences [Iwaniuk et al., unpubl. data]. Despite these potential confounds, the present analysis still provides a crucial step to understanding species differences in avian brain composition as well as correlations between the brain and behavior. This is particularly evident in a comparison of behavior and ecology within the clusters (see below).

Before discussing the relationships between cerebrotypes and phylogeny, development and ecology, it is important to note the effects that domestication has on the brain composition of birds. Studies by Ebinger and

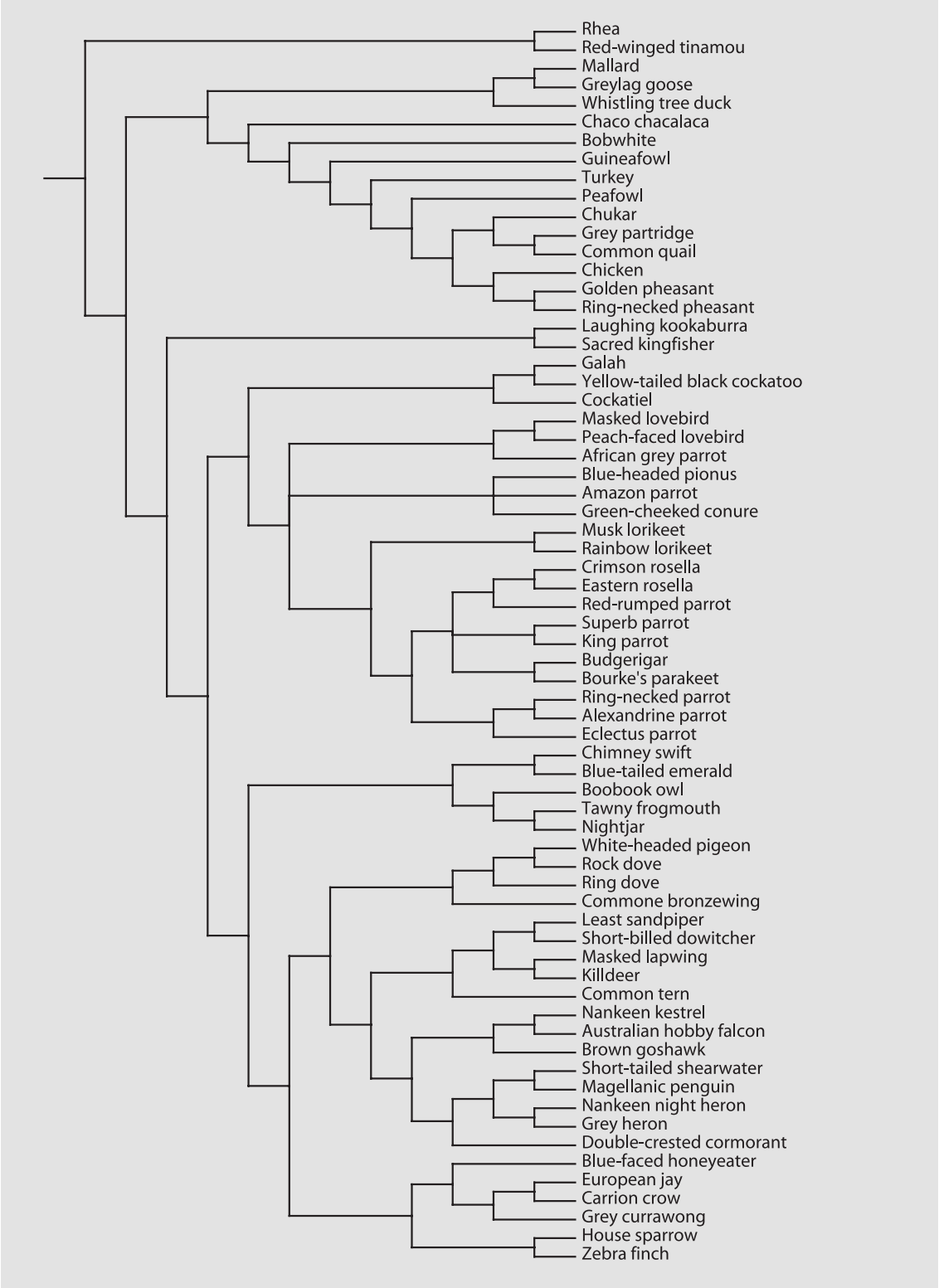

Fig. 6. A phylogenetic tree of the 67 species used in the present study. Phylogenetic relationships are primarily based upon Sibley and Ahlquist [1990], with additional resolution provided by Dimcheff et al. [2002], Kimball et al. [1999], Christidis et al. [1991] and Shapiro et al. [2002]. The topology of this phylogenetic tree is markedly different from the dendrogram produced in the cluster analysis (fig. 4).

colleagues [Ebinger and Löhmer, 1984, 1987; Ebinger, 1995; Ebinger and Röhrs, 1995] have demonstrated that the process of domestication has significant effects on brain composition in several species. The topological variations in the two clusters presented in this paper support these previous findings. In fact, the exclusion of these domesticated species resulted in some changes in the clustering of entire groups, such as the waterfowl. This difference highlights two features of this study. First, the domestication process can result in the evolution of a cerebrotype that does not resemble wild species that are closely related. For example, the composition of the domesticated zebra finch brain does not closely resemble that of other passerines (fig. 4). Second, the clusters resulting from a cluster analysis can be affected by the species included in the analysis. The addition of more species, particularly from orders not previously sampled (e.g., Gruiformes, Piciformes), could alter the composition of the identified clusters. We therefore limit our discussion of the clusters to broad patterns and clusters that were robust to the inclusion/exclusion of the domesticated species.

A comparison between the dendrograms (figs. 4 and 5) and a phylogenetic tree of the species (fig. 6), clearly demonstrates that the overall clustering pattern is not congruent with phylogeny and supports the earlier contention of Burish et al. [2004]. This is not to say that phylogeny plays no role in compositional differences of the avian brain. On the contrary, species within orders do tend to cluster with one another in multivariate space. In both the PCA and the cluster analysis, parrots, passerines, galliforms, waterfowl, kingfishers and raptors all tend to clump closer to one another than to species from other orders. The exceptions within these taxa were the domesticated species, which, as mentioned previously, have undergone significant changes in brain composition as a result of domestication [Ebinger and Löhmer, 1984, 1987; Ebinger, 1995; Ebinger and Röhrs, 1995]. Species from some of the other orders, however, are clustered in very different parts of the dendrogram. The two herons, for example, are at opposite ends of the dendrogram (clusters A and E, figs. 4 and 5). The most pronounced variation in clustering patterns occurs in the charadriiforms, which are spread out across three different clusters (A, B and E). This combination of scattered and clade-specific cerebrotypes demonstrates that avian brain composition can be constrained by phylogenetic relatedness, but that this effect does vary in strength among orders.

Developmental differences appear to have a weaker effect on clustering patterns than phylogeny. Modes of development, incubation periods and other developmental parameters are significantly correlated with relative brain size in birds [see reviews in Nealen and Ricklefs, 2001; Iwaniuk and Nelson, 2003] and therefore it could be expected that clustering patterns would reflect developmental differences, such as developmental modes. This did not, however, occur. Precocial species were just as likely to be clustered with other precocial species as they were with altricial species. For example, the altricial pigeons and doves were clustered with markedly more precocial species, such as galliforms. Similarly, the precocial waterfowl were clustered with significantly more altricial species, such as the raptors and kingfishers. The only exception to this was the clustering of parrots and passerines together, all of which are altricial species and tend to have longer incubation and parental dependency periods than most other altricial species [Iwaniuk, 2003]. The close association of parrots and passerines might, however, relate to their behavior and ecology just as much as any developmental similarities. Thus, developmental differences do not appear to have a strong effect on cerebrotype across the species examined.

Rather than reflecting phylogeny and development, many of the clusters reflect similarities in behavior and ecology. The relationship between clustering pattern and behavior and ecology does not appear to be as clear cut as in mammals [de Winter and Oxnard, 2001] or fish [Huber et al., 1997; Wagner, 2001a, b]. For example, the species within cluster B reflect a variety of ecological niches. What lifestyle characteristics are shared by the flightless rhea, pigeons and seabirds is not clearly evident. The same is also true for the clustering of herons in disparate groups and the ring dove and least sandpiper with the galliforms. As discussed above, some of these clustering patterns might arise from measuring relatively large, multifunctional brain regions rather than specific, functional circuits (e.g., tectofugal, thalamofugal or auditory pathways). Nevertheless, the remaining clusters (A, C, D and E) do appear to be related to broad similarities in three behavioral features: locomotion, cognition and prey capture.

The first of these, similarities in locomotor behavior, only applies to the small cluster containing the tern, swift and hummingbird (cluster A, figs. 4 and 5). All three of these species catch their prey and/or feed almost exclusively in mid-flight. Their tight clustering probably reflects the relatively large cerebella of these species compared to the rest of the brain. Why the chicken possesses a similar cerebrotype to these species is uncertain, but it is likely the product of domestication. Domestication has

differential effects on brain regions that vary from species to species [Ebinger and Löhmer, 1984, 1987; Ebinger, 1995; Ebinger and Röhrs, 1995]. Thus, the inclusion of the chicken in this group does not necessarily indicate anything about behavioral similarities. In fact, the exclusion of the chicken and other domesticated species from the cluster analysis puts the nightjar in the same cluster as the tern, swift and hummingbird (fig. 5). This lends further support to the notion that this group is representative of aerial predators because the nightjars also rely upon taking prey on the wing [Cleere, 1998].

All of the parrots and passerines (with the exception of the domesticated zebra finch) were clumped together. Both parrots and passerines are known to perform more complex cognitive tasks than most other bird species [Emery and Clayton, 2004] and they both possess relatively large telencephalic volumes [Burish et al., 2004; Iwaniuk et al., 2005]. It has therefore been suggested that the expansion of the telencephalon in passerines and parrots is correlated with the expression of complex cognitive behavior, such as social interactions [Burish et al., 2004; Iwaniuk et al., 2005]. The relatively large proportions of the nidopallium, mesopallium and striatopallidal complex further support the correlation between cognition and telencephalic expansion (table 4). As noted previously, the nidopallium is the major site of information integration in the avian brain. The nidopallium not only receives projections from sensory pathways [e.g., Bonke et al., 1979; Wild et al., 1997; Husband and Shimizu, 2001], the caudal nidopallium is essential for several aspects of learning and perception [e.g., Ribeiro et al., 1998; Braun et al., 1999; Güntürkün and Durstewitz, 2000; Plummer and Striedter, 2002] and relatively large nidopallial volumes are significantly correlated with tool use [Lefebvre et al., 2002]. The mesopallium is also involved in a variety of 'cognitive' behaviors, such as innovative feeding behaviors [Timmermans et al., 2000], social behavior [Ball and Balthazart, 2001], vocal perception/production [e.g., Gentner et al., 2000; Plummer and Striedter, 2002], and learning [Horn, 1998; Barber et al., 1999]. Lastly, the striatopallidal complex does not appear to be directly involved in the execution of cognitively complex behaviors, but areas within it are essential to learning [Scharff and Nottebohm, 1991; Csillag, 1999; Watanabe, 2001]. Thus, an expansion of all three regions would likely result in the increase in learning ability and cognitive capacity of both parrots and passerines. In contrast to locomotor or prey capture specializations then, parrots and passerines could be considered to possess a 'cognitive' cerebrotype. That is, the specialization of this cerebrotype is complex cognitive functions, such as problem solving, tool use and social behavior, rather than an ecological specialization per se. In this regard, parrots and passerines are similar to primates because all three taxa share similar cognitive abilities [Marler, 1996; Emery and Clayton, 2004] and brain composition [Emery and Clayton, 2004; Iwaniuk et al., 2005]. What remains to be determined, however, is whether the selection pressures that have resulted in this neural and cognitive convergence are the same [Iwaniuk and Arnold, 2004].

Similarities in prey capture, however, provide the strongest evidence of niche-specific cerebrotypes. For example, the kingfishers and raptors share similar predatory behaviors with one another. Both groups are visually guided predators that capture small vertebrates and large invertebrates. This type of hunting strategy has also resulted in the convergent evolution of similar eye movements and visual fields between kingfishers and some raptors [Wallman and Pettigrew, 1985; Moroney and Pettigrew, 1987]. Based upon these similarities, it is likely that the visual system is of similar relative size in kingfishers and raptors. Although there is little overlap in relative Wulst and optic tectum volume between these two groups (table 1), they have almost identical relative nidopallial volumes (kingfisher mean = 0.321, raptor mean = 0.311). This could indicate similar scaling of the entopallium, the nidopallial target of afferents originating in the nucleus rotundus of the thalamofugal visual pathway [see review in Husband and Shimizu, 2001]. A detailed comparison of raptors and kingfishers, as well as other coraciiform birds that share similar visual optics [e.g., bee-eaters; Moroney and Pettigrew, 1987] and feeding behaviors [Fry and Fry, 1992], could reveal further similarities in brain structure.

The final example of clusters correlating with behavior and ecology is the close association between the frogmouth and the owl in both the PCA and cluster analyses. Both species are nocturnal perch hunters that possess binocular vision [Pettigrew, 1986] and similar saccadic eye movements [Wallman and Pettigrew, 1985]. Burish et al. [2004] noted that owls possess large telencephala, but owls, unlike other birds with large telencephala, do not engage in complex social behavior. Clearly, the large telencephalic volumes of owls are due to the enlargement of the visual Wulst and this same feature is shared with frogmouths, another solitary species. The extent of similarity between frogmouths and owls extends even further to the morphology of the cerebellum [Iwaniuk AN, Wylie DRW, unpubl. data]. The frogmouth is, however, classified as a caprimulgiform [Monroe and Sibley, 1997], an order

composed mainly of nightjars and related species, and the relationships among frogmouths, other caprimulgiforms and owls remains controversial [see reviews in Sibley and Ahlquist, 1990; Mayr, 2002]. An analysis of brain structure and composition amongst other caprimulgiform species might therefore be informative in determining phylogenetic relationships.

Conclusions

In a similar fashion to previous studies on mammals, amphibians and fish, the present analysis demonstrates that cerebrotypes in birds relate to both phylogeny and ecology. The extent to which the cerebrotypes are related to sensory specializations [as in Wagner 2001a, b], however, must await the development of a more detailed data set on avian brain composition. Given that size correlations exist among brain regions [Iwaniuk et al., 2004] and that cerebrotypes relate primarily to behavior and ecology, future comparative investigations into brain-behavior relationships should attempt to incorporate a multivariate approach. For example, can differences in innovation rate [e.g., Lefebvre et al., 1997, 1998; Timmermans et al., 2000] or tool use [Lefebvre et al., 2002] be explained by cerebrotype as well as forebrain and mesopallial/nidopallial volume? Similarly, a cerebrotype-like approach could be used to analyze specific neural systems, such as the vocal control nuclei in vocal learning species (i.e., 'neurotypes'). A move towards multivariate and integrative comparisons will likely produce a more accurate picture of how the brain has evolved as well as functional relationships of the brain with behavior.

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