Brain, Behavior and Evolution

The Independent Evolution of the Enlargement of the Principal Sensory Nucleus of the Trigeminal Nerve in Three Different Groups of Birds

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Key Words

Somatosensory · Cutaneous · Allometry · Comparative method

Abstract

In vertebrates, sensory specializations are usually correlated with increases in the brain areas associated with that specialization. This correlation is called the 'principle of proper mass' whereby the size of a neural structure is a reflection of the complexity of the behavior that it subserves. In recent years, several comparative studies have revealed examples of this principle in the visual and auditory system of birds, but somatosensory specializations have largely been ignored. Many species rely heavily on tactile information during feeding. Input from the beak, tongue and face, conveyed via the trigeminal, facial, glossopharyngeal and hypoglossal nerves, is first processed in the brain by the principal sensory nucleus of the trigeminal nerve (PrV) in the brainstem. Previous studies report that PrV is enlarged in some species that rely heavily on tactile input when feeding, but no extensive comparative studies have been performed. In this study, we assessed the volume of PrV in 73 species of birds to present a detailed analysis of the relative size variation of PrV using both conventional and phylogenetically based statistics. Overall, our results indicate that three distinct groups of birds have a hypertrophied PrV: waterfowl (Anseriformes), beak-probing shorebirds (Charadriiformes), and parrots (Psittaciformes). These three groups have different sensory requirements from the orofacial region. For example, beak-probing shorebirds use pressure information from the tip of the beak to find buried prey in soft substrates, whereas waterfowl, especially filter-feeding ducks, use information from the beak, palate, and tongue when feeding. Parrots likely require increased sensitivity in the tongue to manipulate food items. Thus, despite all sharing an enlarged PrV and feeding behaviors dependent on tactile input, each group has different requirements that have led to the independent evolution of a large PrV.

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Introduction

In vertebrates, sensory specializations are usually correlated with increases in the brain areas associated with that specialization. This correlation is called the 'principle of proper mass' whereby the size of a neural structure is a reflection of the complexity of the behaviors that it subserves [Jerison, 1973]. Examples of this correlation are found in all sensory systems and in all vertebrates [e.g., somatosensory: Pubols et al., 1965; Pubols and Pubols, 1972; visual: Barton, 1998; Iwaniuk and Wylie, 2007; gustatory: Finger, 1975; auditory: Kubke et al., 2004]. Some

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of the best-studied examples of this correlation between sensory systems and behavior come from examinations of the trigeminal system in small mammals and its representation in the primary somatosensory cortex [Catania and Henry, 2006]. For example, a comparison between Norway rats *(Rattus norvegicus)* and naked mole-rats *(Heterocephalus glaber)* revealed a large representation of the vibrissae in the somatosensory cortex of the former, but a large representation of the incisor in the latter [Henry et al., 2006]. Similarly, Catania [2000, 2005] compared the representation of the trigeminal system in the somatosensory cortex of several species of insectivores and found that the cortical representation of the vibrissae and the rhinarium was a reflection of species' differences in both facial morphology and ecology. For example, the masked shrew *(Sorex sinereus)* hunts above ground during the night for small invertebrates and has a large representation of the vibrissae in the somatosensory cortex, but a very small representation of the rhinarium. In contrast, the eastern mole *(Scalopus aquaticus)*, which has an enlarged rhinarium and hunts underground, has equal representations of both the vibrissae and the rhinarium. Finally, the star-nose mole *(Condylura cristata)* has a large representation of the rhinarium and little of the vibrissae, related to the complex rhinarium comprised of 22 fleshy appendages used for detecting prey [Catania, 2005].

The correlated evolution of the trigeminal system and ecology has been studied in some detail in mammals, but there is relatively little information for other vertebrate groups, particularly for birds. Even though birds do have a well-developed trigeminal system [Dubbeldam, 1998], studies have been restricted to the anatomy and physiology in pigeons [*Columba livia*; Zeigler and Witkovsky, 1968; Silver and Witkovsky, 1973; Dubbeldam and Karten, 1978] and the mallard duck [*Anas platyrhynchus*; Dubbeldam, 1980; Arends et al., 1984; Kishida et al., 1984]. In addition, comparative studies of sensory specializations in birds have focused on other sensory systems [e.g., visual: Iwaniuk and Wylie, 2006, 2007; Iwaniuk et al., 2008; auditory: Kubke et al., 2004; Iwaniuk et al., 2006] and thus a detailed comparative analysis of the correlation between trigeminal system specialization and behavior is completely lacking in birds.

One of the unique characteristics of birds is the presence of a beak, and the form and size of the beak is strongly correlated with species-specific feeding behaviors. This correlation between beak morphology and feeding behavior even extends to the number and distribution of mechanoreceptors in the beak and tongue [Gottschaldt,

1985]. For example, in shorebirds (Charadriiformes, such as snipe and sandpipers) that use their beak for probing, mechanoreceptors are numerous and concentrated in the tip of the beak [Bolze, 1968; Pettigrew and Frost, 1985]. In ducks and geese (Anseriformes) mechanoreceptors are concentrated in the tip and ridges of the beak, as well as on their large, fleshy tongue [Berkhoudt, 1980]. Even in grain-feeding songbirds, which have relatively low numbers of mechanoreceptors in the beak, they are located exactly in the parts of the beak involved in seed-opening [Krulis, 1978]. Not only does the overall number of mechanoreceptors vary among species, but also the abundance of specific types of mechanoreceptors. In the domestic goose *(Anser anser)*, Grandry corpuscles, which are velocity detectors, are ten times more abundant than Herbst corpuscles, which detect pressure [Gottschaldt and Lausmann, 1974; Gottschaldt, 1985]. In contrast, Herbst corpuscles are much more abundant than Grandry corpuscles in shorebirds [Bolze, 1968; Piersma et al., 1998]. Finally, the presence and degree of development of the bill tip organ also varies among bird groups. The bill tip organ itself is a complex sensory structure at the tip of the beak that is covered by a horny plate and contains several touch papillae, with both Grandry and Herbst corpuscles [Iggo and Gottschald, 1974]. The bill tip organ is highly developed in waterfowl, shorebirds and parrots (Psittaciformes) and is completely lacking in most other birds [Gottschaldt and Lausmann, 1974; Gottschaldt, 1985].

The mechanoreceptors in the beak are innervated by the three branches of the trigeminal nerve [Dubbeldam and Karten, 1978]. These nerves also convey nociceptive information from the beak and proprioceptive information from jaw muscles to the gasserian ganglion [Bout and Dubbeldam, 1991]. From there, trigeminal efferents reach three main targets: the mesencephalic nucleus of the trigeminal nerve, which receives information exclusively from the proprioceptive component; the descending tract of the trigeminal nerve (TTD); and the principal sensory nucleus of the trigeminal nerve (PrV). Both PrV and TTD receive projections from the three branches of the trigeminal nerve, but differ in the type of information they receive. Although the TTD receives proprioceptive and nociceptive information, PrV is the main target of mechanoreceptive afferents [Zeigler and Witkovsky, 1968; Silver and Witkovsky, 1973; Kishida et al., 1985; Dubbeldam, 1998]. The trigeminal nerve is not, however, the only afferent of PrV. Information from the tongue is conveyed to PrV via afferents from the facial [Bout and Dubbeldam, 1985], glossopharyngeal [Dubbeldam et al.,

1979; Wild, 1981] and hypoglossal nerves [Wild, 1981, 1990].

Previous studies found that PrV is enlarged in some species that rely heavily on tactile input when feeding. For example, Stingelin [1961, 1965] found that the common snipe *(Gallinago gallinago)* and Fisher's lovebird *(Agapornis fisheri)* have relatively larger PrVs than the carrion crow *(Corvus corone)*, European bee-eater, *(Merops apiaster)* and the tawny owl *(Strix aluco)*. Similarly, using the ratio between the volume of PrV and the nucleus rotundus, as a measure of tactile versus visual specialization, Dubbeldam [1998] found that the mallard and the snipe had high ratios and the budgerigar *(Melopsittacus undulatus)* had a ratio between that of the tactile and visual specialists. Finally, Boire [1989] compared the size of PrV in 27 species and found high values in the mallard, a sandpiper *(Limnodromus griseus)* and the budgerigar. Thus, there is some evidence that PrV is hypertrophied in at least three groups of birds, waterfowl, shorebirds and parrots, but a broad systematic analysis across species has not been performed. The use of a large sample could not only reveal differences among groups, but also within groups in relation to feeding behavior and/or beak morphology. In the present study we build on previous analyses of PrV by measuring PrV volume in dozens of additional species and present a detailed analysis of size variation of PrV across 73 species using both conventional and phylogenetically based statistics.

Materials and Methods

Specimens

We measured PrV in 47 specimens representing 46 species (table 1). For all specimens, the head was immersion-fixed in 4% paraformaldehyde in 0.1 M phosphate buffer (PB). The brain was then extracted, weighed to the nearest milligram, cryoprotected in 30% sucrose in PB, embedded in gelatin and sectioned in the coronal or sagittal plane on a freezing stage microtome at a thickness of 40 μm. Sections were collected in 0.1 M phosphate buffered saline, mounted onto gelatinized slides, stained with thionin and coverslipped with Permount.

The olfactory bulbs were intact in all of the specimens that we collected and sectioned. In the case of the spinal cord, all brains were cut following bird brain atlases [e.g., Pigeon: Karten, 1967], in which the brainstem ends at the same rostro-caudal point as the cerebellum. As a result, brain weight measurements were consistent among our specimens.

Photomicrographs of every second section were taken throughout the rostrocaudal extent of PrV using a Retiga EXi *FAST* Cooled mono 12-bit camera (Qimaging, Burnaby, B.C., Canada) and OPENLAB Imaging system (Improvision, Lexington, Mass., USA) attached to a compound light microscope (Leica DMRE, Richmond Hill, Ont., Canada). Measurements of the PrV were taken directly from these photos with ImageJ, (NIH, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/) and volumes were calculated by multiplying the area in each section by the thickness of the section (40 μm) and the sampling interval.

Additional data for 31 specimens was obtained from several sources [table 1; Boire, 1989; Carezzano and Bee-de-Speroni, 1995; Pistone et al., 2002]. This included 27 additional species. In the event that there was more than one specimen for our measurements or there was data from both studies, the number used was the average of both measurements. A paired t test between the four species that coincided between Boire [1989] and our measurements (see table 1) showed no significant differences (p > 0.05). Because neither Dubbeldam [1998] nor Stingelin [1965] used brain volume to standardize their results, we could not include their data in the current analysis.

Defining PrV

The limits of PrV were established using the descriptions of Dubbeldam and Karten [1978], Boire [1989] and Dubbeldam [1980]. In birds with small PrV volumes (e.g., Passeriformes, Columbiformes), PrV can be identified as a round or oval mass of large cells in the dorsolateral part of the anterior brainstem (fig. 1D). It lies dorsal to the root of the fifth nerve and the motor nuclei of the fifth nerve (mV). The dorsal border of PrV is defined by the brachium conjunctivum (BC) and the caudo-lateral borders are defined by the TTD.

In waterfowl, PrV lies more lateral than in other birds, just above the root of the trigeminal nerve (fig. 1A). Dubbeldam [1980] describes three cell groups that form part of PrV in the mallard, but show differences in the connections with the main part of the PrV: nucleus paraprincipalis (pP), nucleus sensorius of nIX (sIXd) and nucleus supratrigeminalis (sT). The pP lies ventral to the rostral part of the PrV and receives few projections from the gasserian ganglion. sIXd lies dorsal and medial to the caudal PrV and receives projections from the glossopharyngeal nerve. Finally, sT is a small round group of cells that is located dorsomedial to PrV and receives projections from the mesencephalic nucleus of the trigeminus. Because these three groups cannot be distinguished easily with a Nissl stain, they were all included in our measurements.

In beak-probing shorebirds, PrV size and position is similar to waterfowl (fig. 1C). Some subdivisions are apparent, but we cannot confirm if they correspond with the ones found in waterfowl. As in waterfowl, the entire cell mass was included in the measurements. In parrots, PrV has several subdivisions and appears to extend more caudally than in other birds (fig. 2A–C). Because there is no detailed description of PrV in parrots, we used coronal and sagittal sections through the brainstem of the galah *(Eolophus roseicapillus)* to aid in determining the extent and limits of the PrV in parrots.

Statistical Analyses

To test for significant differences in the relative size of PrV, we performed analyses of covariance between log_{10}-transformed PrV volumes and log_{10}-transformed brain volume minus PrV volume [Deacon, 1990; Iwaniuk et al., 2005, 2006; Iwaniuk and Wylie, 2007]. The species were separated into four categories; waterfowl, parrots, beak-probing shorebirds and non-specialists.

Because comparative analyses using species as independent data points are subject to inflated type II error [Harvey and Pagel,

Table 1. List of the species surveyed, sample size and volumes (in mm³) of the brain and the principal sensory nucleus of the trigeminal nerve (PrV)

Order	Common name	Species	n	Brain (mm³)	PrV (mm³)	Source
Anseriformes	green-winged teal	*Anas carolinensis*	1	9.43	3,165.83	this study
	chestnut teal	*Anas castanea*	1	10.138	3,424.71	this study
	Northern shoveler	*Anas clypeata*	1	8.117	3,288.51	this study
	blue-winged teal	*Anas discors*	1	7.573	2,895.75	this study
	mallard	*Anas platyrhynchos*	2	15.882	6,343.98	this study; Boire, 1989
	Australian black duck	*Anas superciliosa*	1	13.496	4,973.94	this study
	lesser scaup	*Aythya affinis*	1	10.186	4,141.89	this study
	redhead	*Aythya americana*	1	12.194	5,245.17	this study
	Canada goose	*Branta canadensis*	1	14.091	11,346.91	this study
	bufflehead	*Bucephala albeola*	1	6.045	4,122.97	this study
	common goldeneye	*Bucephala clangula*	1	10.153	5,961.39	this study
	Australian wood duck	*Chenonetta jubata*	1	3.568	4,329.15	this study
	red-breasted merganser	*Mergus serrator*	1	4.872	4,754.34	this study
	ruddy duck	*Oyura jamaicensis*	1	15.637	3,993.73	this study
Apodiformes	chimney swift	*Chaetura pelagica*	1	0.068	342.66	Boire, 1989
Caprimulgiformes	nightjar	*Caprimulgus* sp.	1	0.228	733.59	Boire, 1989
	spotted nightjar	*Eurostopodus argus*	1	0.197	1,012.55	this study
Charadriiformes	least sandpiper[a]	*Calidris minutilla*	1	1.885	472.01	Boire, 1989
	killdeer	*Charadrius vociferus*	1	0.629	1,073.36	Boire, 1989
	short-billed dowitcher[a]	*Limnodromus griseus*	2	4.59	1,230.79	this study; Boire, 1989
	common tern	*Sterna hirundo*	1	0.316	1,592.66	Boire, 1989
	Southern lapwing	*Vanellus chilensis*	1	0.492	2,461.00	Pistone et al., 2002
Ciconiiformes	grey heron	*Ardea cinerea*	1	1.504	8,445.95	Boire, 1989
	cattle egret	*Bubulcus ibis*	1	0.348	4,025.10	this study
	snowy egret	*Egretta thula*	1	0.722	3,610.00	Carezzano and Bee-de-Speroni, 1995
Columbiformes	rock dove	*Columba livia*	2	0.523	2,219.55	this study; Boire, 1989
	peaceful dove	*Geopelia placida*	1	0.296	776.06	this study
	superb fruit-dove	*Ptilinopus superbus*	1	0.242	1,052.12	this study
	ringneck dove	*Streptopelia risoria*	1	0.291	1,140.93	Boire, 1989
Coraciiformes	laughing kookaburra	*Dacelo novaeguineae*	1	0.644	3,970.08	this study
Falconiformes	Swainson's hawk	*Buteo swainsoni*	1	0.800	8,099.42	this study
	American kestrel	*Falco sparverius*	1	0.163	1,017.00	this study
Galliformes	chukar	*Alectoris chukar*	1	0.563	2,500.00	Boire, 1989
	ruffed grouse	*Bonasa umbellus*	2	0.255	3,146.72	this study
	golden pheasant	*Chrysolophus pictus*	1	0.795	3,368.73	Boire, 1989
	Northern bobwhite	*Colinus virginianus*	1	0.374	1,090.73	Boire, 1989
	common quail	*Coturnix coturnix*	1	0.34	810.81	Boire, 1989
	chicken	*Gallus domesticus*	1	1.120	2,993.00	Boire, 1989
	turkey	*Meleagris gallopavo*	1	2.839	6,096.95	Boire, 1989
	helmeted guineafowl	*Numida meleagris*	1	1.231	3,950.77	Boire, 1989
	chaco chachalaca	*Ortalis canicollis*	1	1.209	3,373.55	Boire, 1989
	Indian peafowl	*Pavo meleagris*	1	2.258	7,355.21	Boire, 1989
	ring-necked pheasant	*Phasianus colchicus*	1	0.641	2,761.58	Boire, 1989
Gruiformes	American coot	*Fulica americana*	1	1.249	2,875.00	this study
	red-gartered coot	*Fulica armillata*	1	0.402	4,015.00	Carezzano and Bee-de-Speroni, 1995

Table 1 (continued)

Order	Common name	Species	n	Brain (mm³)	PrV (mm³)	Source
Passeriformes	brown thornbill	*Acanthiza pusilla*	1	0.11	434.36	this study
	Eastern spinebill	*Acanthorhynchus tenuirostris*	1	0.092	395.75	this study
	gouldian finch	*Erythrura gouldiae*	1	0.139	427.61	this study
	Australian magpie	*Gymnorhina tibicen*	1	0.310	4,017.37	this study
	noisy miner	*Manorina melanocephala*	1	0.254	2,278.96	this study
	spotted pardalote	*Pardalotus punctatus*	1	0.058	400.58	this study
	double-barred finch	*Taeniopygia bichenovii*	1	0.328	409.27	this study
	zebra finch	*Taeniopygia guttata*	1	0.214	368.73	Boire, 1989
Pelecaniformes	double-crested cormorant	*Phalacrocorax auritus*	1	1.728	7,323.36	Boire, 1989
Podicipedi-formes	white-tufted grebe	*Rollandia rolland*	1	0.411	2,056.00	Carezzano and Bee-de-Speroni, 1995
Psittaciformes	Australian king parrot	*Alisterus scapularis*	1	3.27	4,478.76	this study
	long-billed corella	*Cacatua tenuirostris*	1	6.001	11,777.99	this study
	galah	*Eolophus roseicapillus*	2	8.404	7,083.98	this study
	purple-crowned lorikeet	*Glossopsitta porphyrocephala*	1	1.753	1,939.19	this study
	budgerigar	*Melopsittacus undulatus*	2	1.760	1,185.77	this study; Boire, 1989
	cockatiel	*Nymphicus hollandicus*	1	1.97	2,111.00	this study
	blue-headed parrot	*Pionus menstruus*	1	4.230	5,282.82	Boire, 1989
	crimson rosella	*Platycercus elegans*	1	4.082	3,628.38	this study
	superb parrot	*Polytelis swainsonii*	1	2.248	2,996.14	this study
	rainbow lorikeet	*Trichoglossus haematodus*	2	3.805	3,333.98	this study
Rheiformes	greater rhea	*Rhea americana*	1	0.242	1,052.12	Boire, 1989
Sphenisciformes	Magellanic penguin	*Spheniscus magellanicus*	1	3.412	16,756.76	Boire, 1989
Strigiformes	great horned owl	*Bubo virginianus*	1	2.012	17,994.21	this study
	boobook owl	*Ninox boobook*	1	0.936	6,338.80	this study
	barn owl	*Tyto alba*	1	1.075	7,142.86	this study
Tinamiformes	red-winged tinamou	*Rhynchotus rufescens*	1	1.620	3,377.41	Boire, 1989
Trochiliformes	Anna's hummingbird	*Calypte anna*	1	0.040	183.88	this study
	blue-tailed emerald	*Chlorostilbon melisugus*	1	0.032	118.73	Boire, 1989

[a] Beak-probing shorebirds.

1991], we also used phylogenetic generalized least squares (PGLS) regressions [Garland and Ives, 2000; Garland et al., 2005]. PGLS assumes that residual variation among species is correlated, with the correlation given by a process that acts like Brownian motion evolution along the phylogenetic tree. Analyses were performed using the MATLAB program Regressionv2.m [available from T. Garland, Jr., on request; Ives et al., 2007, Lavin et al., 2008]. Currently, there is no consensus regarding the phylogenetic relationships among most orders of birds. To account for phylogenetic relatedness in our analyses, we therefore used five different phylogenetic trees that all differed in their inter-ordinal and inter-familial relationships: Sibley and Ahlquist [1990], Cracraft et al. [2004], Livezey and Zusi [2007], Davis [2008] and Hackett et al. [2008]. Resolution at the species level within orders and families was derived from additional taxon-specific studies [Johnson and

Sorenson, 1999; Donne-Goussé et al., 2002; Barker et al., 2004; Thomas et al., 2004; Pereira et al., 2007; Kimball and Braun, 2008; Wink et al., 2008; Wright et al., 2008]. Phylogenetic trees, character matrix and phylogenetic variance-covariance matrix were constructed using Mequite/PDAP:PDTREE software [Midford et al., 2002; Maddison and Maddison, 2009] and the PDAP software package (available from T. Garland upon request). Because the phylogeny was constructed from multiple sources, branch lengths were all set at 1 to provide adequately standardized branch lengths [Garland et al., 1992]. We applied two models of evolutionary change as implemented in Regressionv2.m: Brownian motion (phylogenetic generalized least-squares or PGLS) and Ornstein-Uhlenbeck [Lavin et al., 2008; Swanson and Garland, 2009]. Akaike Information Criterion was then used to determine which model best fit the data [Lavin et al., 2008].
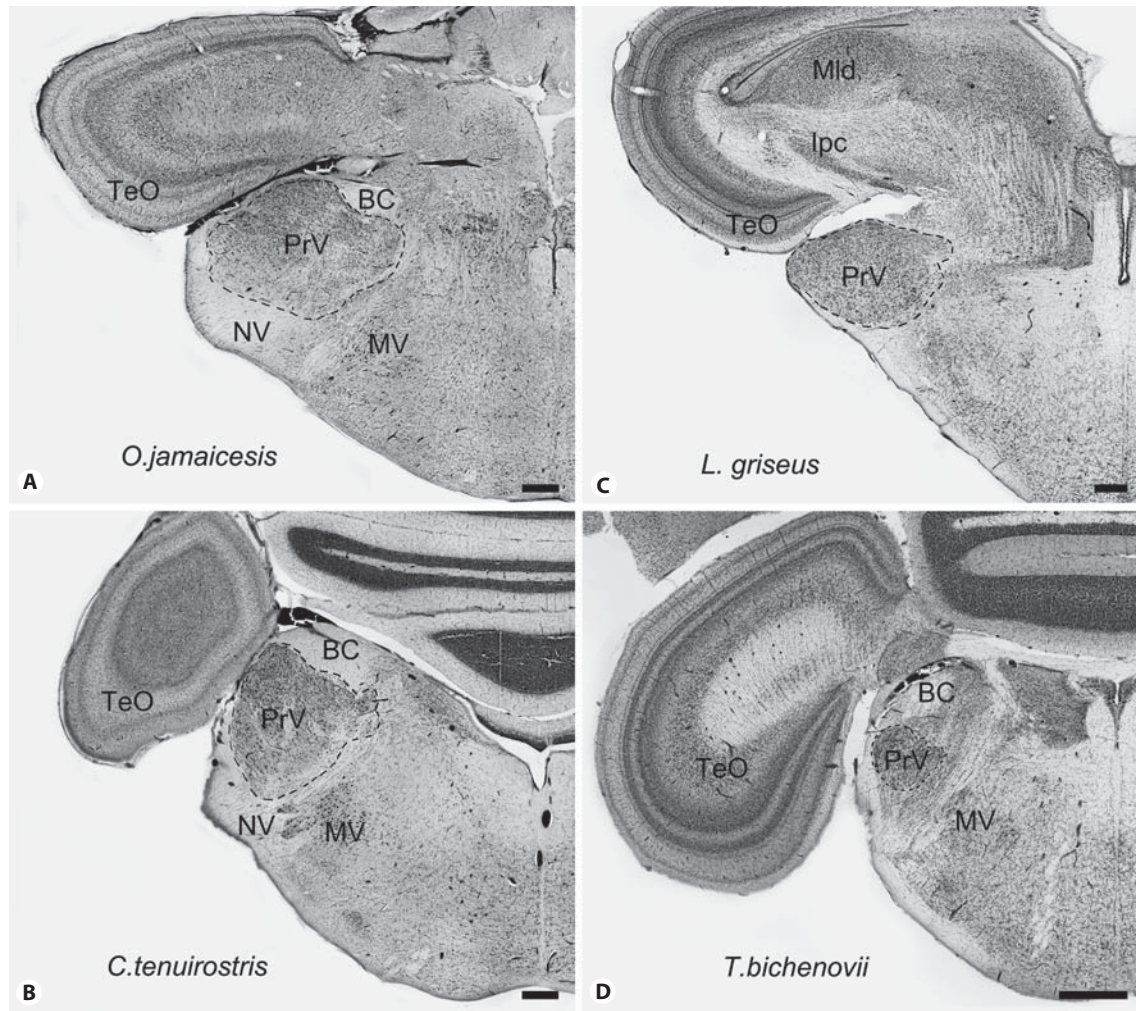
Fig. 1. Photomicrographs of coronal sections through the principal sensory nucleus of the trigeminal nerve (PrV) of four species of birds, the three somatosensory specialists (**A–C**) and a non-specialist (**D**). Pictures were taken approximately midway along the antero-posterior extent. The dotted black lines indicate the borders of PrV. **A** Ruddy duck (*Oxyura jamaicesis)*; **B** Long-billed corella *(Cacatua tenuirostris)*; **C** Short-billed dowitcher *(Limnodromus griseus)*; **D** the double-barred finch *(Taeniopygia bichenovii)*. Abbreviations are as follows: TeO = optic tectum; BC = brachium conjunctivum; NV = root of the trigeminal nerve; MV = motor nucleus of the trigeminal nerve; Mld = nucleus mesencephalicus lateralis pars dorsalis; Ipc = nucleus isthmi parvocellularis. Scale bars = 600 μm.

Results

Figure 1 shows coronal sections through the PrV of a waterfowl, the ruddy duck (A; *Oxyura jamaicensis*); a parrot, the long-billed corella (B; *Cacatua tenuirostris*); a beak-probing shorebird, the short-billed dowitcher (C; *Limnodromus griseus*); and the double-barred finch (D, *Taeniopygia bichenovii*). This last one represents a non-specialist bird. PrV looks similar in all the species: an oval cell mass dorsal to the root of the V nerve and ventral to

the BC [for detailed description in pigeons see Dubbeldam and Karten, 1978]. In the three specialist groups, PrV is greatly expanded, both laterally and rostro-caudally. In waterfowl and beak-probing shorebirds, the lateral part of the nucleus is expanded against the brainstem wall, forming a protuberance ventrally and caudally to the optic tectum (fig. 1A, C). In these groups, the anterior part PrV continues rostrally to the root of the V nerve and BC and can be followed to the level of isthmo-optic nucleus. The most caudal parts of the nucleus extend to

the level of the root of the VII nerve and lie laterally to the nucleus vestibularis medialis (VeM) [see Dubbeldam, 1980, for detailed description in the mallard].

In parrots, PrV is also expanded, but presents some differences when compared to the waterfowl and shorebirds. Figure 2 shows three sagittal sections at different mediolateral planes (medial to lateral, A–C) and three coronal sections at different rostro-caudal planes (anterior to posterior, D–F) from the galah (*Eolophus roseicapillus*). In parrots, PrV does not extend as far laterally (fig. 2B) or rostrally as in the other two groups (fig. 2A). The caudal portion extends to a similar extent in waterfowl and beak-probing shorebirds, dorsally to the root of the VII nerve (fig. 2C), but lies in a much more dorsal position, inside the cerebellar peduncle and dorsal to the VeM (fig. 2C). Sagittal sections show that this most caudal portion of PrV is separated from the main part of PrV by a bundle of fibers that course from the posterior part of the brainstem to join the BC (fig. 2A–C). Because this group of cells is of similar size and organization to the main part of the PrV, we considered it to be part of the nucleus and divided PrV in parrots into superior and inferior components (PrVi, PrVs). These two components could be distinguished in the coronal section of all the parrots examined, but not in any other species (see fig. 1, 2).

Our statistical analysis showed that the three somatosensory specialists have a significantly larger PrV, relative to brain volume, than the non-specialist birds. The regression lines describing the relation between PrV volume and brain volume for the three specialist taxa are significantly higher than those for the non-specialists (fig. 3; table 2), with waterfowl and beak-probing shorebirds having the largest PrV and parrots falling between these two groups and the non-specialists. ANCOVA shows a significant effect for the group (F = 111.06, d.f. = 3, 68, p < 0.0001) on the size of PrV relative to brain size. Tukey HSD post-hoc comparisons revealed that all three specialist groups, the waterfowl, beak-probing shorebirds and parrots, have significantly larger relative PrV volumes compared to non-specialists. In addition, the beak-probing shorebirds and waterfowl have significantly larger relative PrV volumes than the parrots.

These results were corroborated by the PGLS approach. We detected a significant effect of group on the relative size of PrV for all five phylogenies and both models of evolutionary change (table 2). Thus, even though our categorization of species is largely based on taxonomy, a phylogenetically based approach also detects a significant difference between the specialists and non-specialists. Based on the lower Akaike Information Criteri-

on, ordinary least square regressions fit the data better than both models of evolutionary change (table 2).

The hypertrophy of PrV in these three groups is also evident when comparing the average volume occupied by the PrV relative to total brain size for each group (fig. 4). Beak-probing shorebirds show the highest average (0.3864 ± 0.0183), almost twice that for waterfowl (0.2229 ± 0.0867) and four times that for parrots (0.0957 ± 0.0282).

Waterfowl show the largest variation among the three specialist groups (fig. 5). The ruddy duck has the largest PrV relative to brain size, followed by species within the genera *Anas* and *Aythya*. At the low end, the red-breasted merganser (*Mergus serrator*) and the Australian wood duck (*Chenonetta jubata*) have the smallest PrV volumes, more similar to the volumes we observed in parrots. Thus, although waterfowl all have relatively large PrV volumes, there appears to be considerable variation among species within the order, which might reflect differences in feeding behavior.

Discussion

Our results showed that at least three groups of birds possess a hypertrophied PrV: waterfowl, beak-probing shorebirds and, to a lesser degree, parrots. Although this was suggested by Stingelin [1965], Dubbeldam [1998] and Boire [1989] only one or two species of each specialist group and a few non-specialists were used in these studies. Our study therefore corroborates previous observations, but adds to these studies by analyzing a broader range of species and using sophisticated analytical techniques to test for differences among groups.

Fig. 2. Photomicrograph of the principal sensory nucleus of the trigeminal nerve (PrV) in the Galah (*Eolophus roseicapillus*). Coronal sections at three different antero-posterior levels through are shown in **A** (anterior) to **C** (posterior), and sagittal sections at three different medio-lateral levels are shown in **D** (medial) to **F** (lateral). The dotted black lines indicate the borders of PrV. Abbreviations are as follows: PrVi = inferior part of principal sensory nucleus of the trigeminal nerve; PrVs = superior part of the principal sensory nucleus of the trigeminal nerve; TeO = optic tectum; BC = brachium conjunctivum; NV = root of the trigeminal nerve; MV = motor nucleus of the trigeminal nerve; Cb = cerebellum; VeM = nucleus vestibularis medialis. Scale bars = 600 μm.
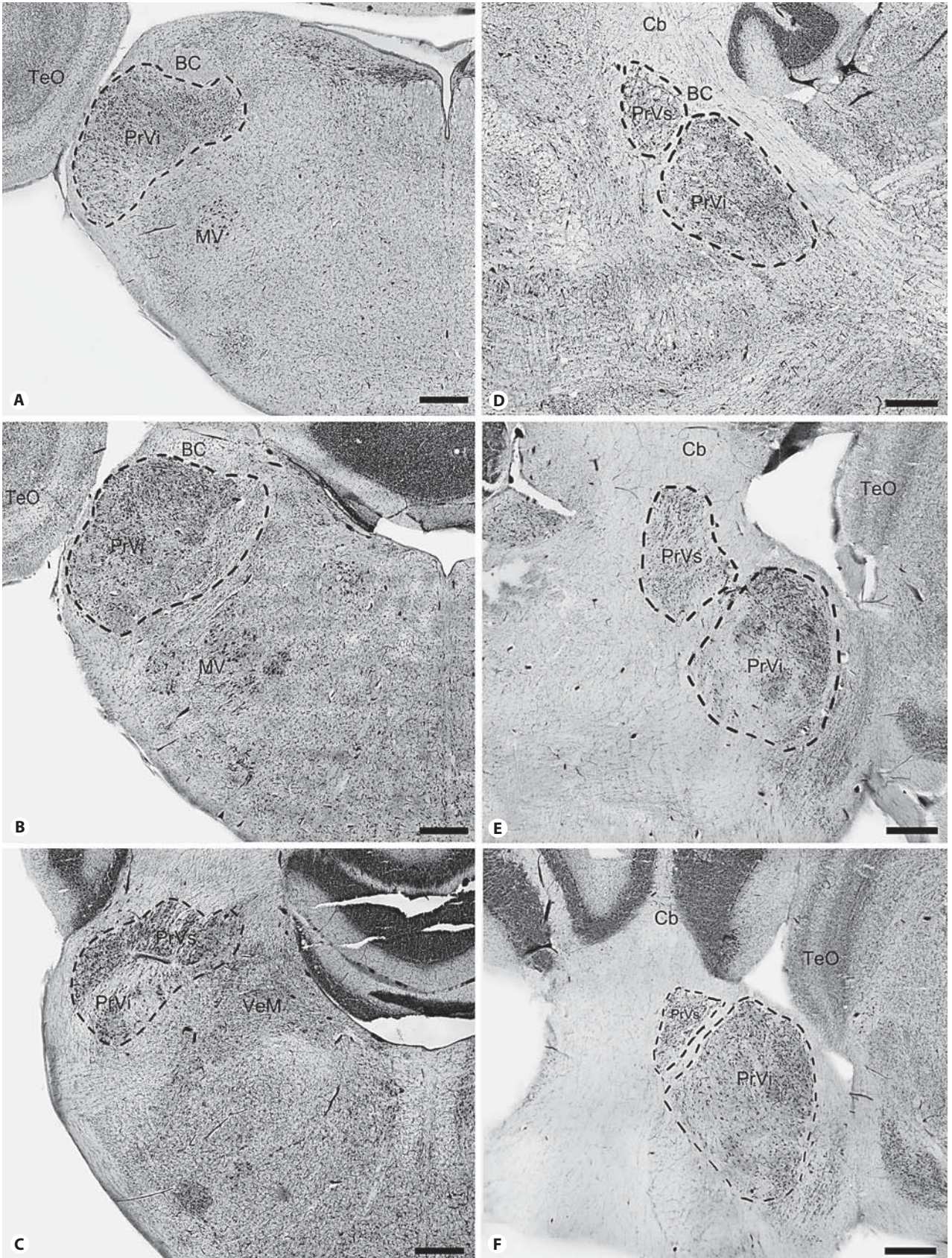
Fig. 3. Scatterplot of the volume of principal sensory nucleus of the trigeminal nerve (PrV) volume plotted as a function of brain minus PrV volume for all species examined (see table 1). Waterfowl are indicated by black triangles, beak-probing shorebirds by white triangles, parrots by white circles and non-specialists by black circles. The solid lines indicate the least squares linear regression line for all species, and the dotted lines are the 95% confidence interval around the regression line.
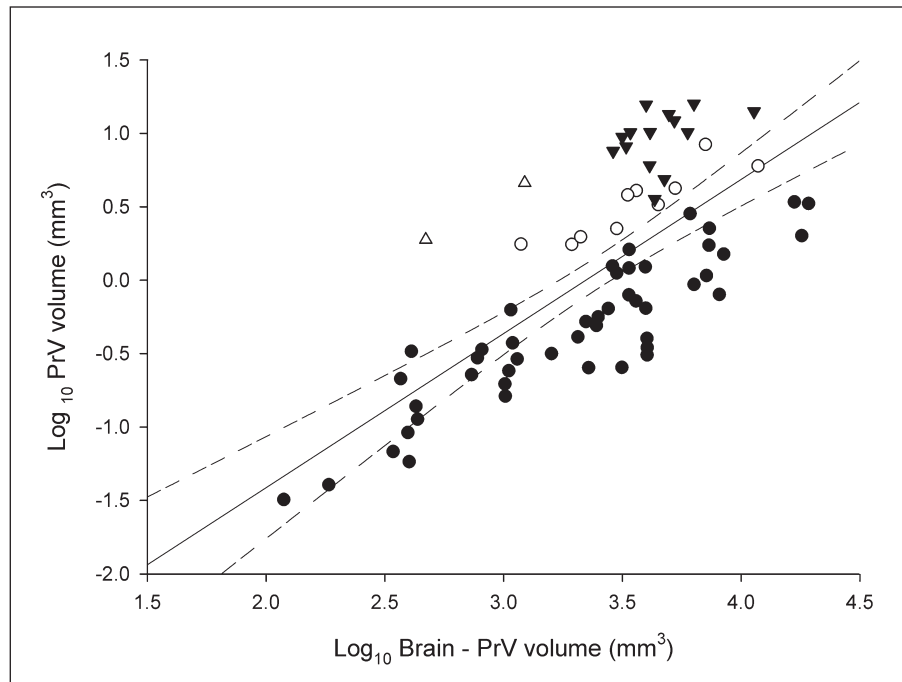
Table 2. Results of least-squares linear regression performed on species as independent data points ('No phylogeny') and generalized least square with five different phylogenetic trees and two models of evolutionary change, Brownian motion and Ornstein-Uhlenbeck [Lavin et al., 2008; Swanson and Garland, 2009]

PrV	Evolution-ary change models	F	d.f.	Slope	r^2	AIC
No phylogeny		111.06	3,68	0.82	0.919	–21.04
Sibley and Ahlquist, 1990	PGLS	15.78	3,68	0.725	0.695	1.04
	OU	80.76	3,68	0.801	0.883	–19.43
Davis, 2003	PGLS	14.23	3,68	0.746	0.698	–1.52
	OU	70.27	3,68	0.805	0.882	–19.35
Livezey and Zusi, 2007	PGLS	16.17	3,68	0.716	0.690	–0.51
	OU	70.13	3,68	0.796	0.881	–19.3
Hackett et al., 2008	PGLS	16.71	3,68	0.718	0.699	–3.84
	OU	60.86	3,68	0.795	0.868	–19.7
Cracraft et al., 2004	PGLS	16.67	3,68	0.724	0.699	–2.16
	OU	74.57	3,68	0.797	0.884	–19.44

OU = Ornstein-Uhlenbeck; PGLS = phylogenetic generalized least squares.

We found that the PrV in parrots has a unique anatomical feature whereby the posterior part continues more caudally than other species, lying dorsally to the VeM and separated from the main part by a bundle of fibers (fig. 2D–F). We named this the superior part of PrV (PrVs). In all the parrot species analyzed PrVs and the main part of PrV had similar cell shape and size. Wild [1981] considered PrVs to be part of the nucleus vestibularis superior in the galah, but we found that this nucleus lies more caudally and can be distinguished from PrVs due to very different cytoarchitectonic features. Furthermore, Stingelin [1965] also considered this cell mass to be part of PrV. Also, Boire's [1989] measurement of the volume of PrV in the budgerigar is very similar to ours, and thus Boire [1989] must have considered this cell mass to be part of PrV. Tracer studies, however, would be necessary to confirm this as part of PrV.

As noted previously (see introduction), PrV receives projections not only from the trigeminal nerve, which innervates the upper and lower beak, but also from the facial [Bout and Dubbeldam, 1985], glossopharyngeal [Dubbeldam et al., 1979; Wild, 1981] and hypoglossal nerves [Wild, 1981, 1990]. PrV therefore gathers information from the beak, palate, tongue and pharynx. This convergence of sensory information from the orofacial region into PrV is clear in waterfowl and parrots [Dub-

Fig. 4. Bar graph of the relative size of PrV expressed as a percentage of total brain volume. The solid line indicates the mean for all non-specialists (0.0239) and the error bars indicate standard deviations.
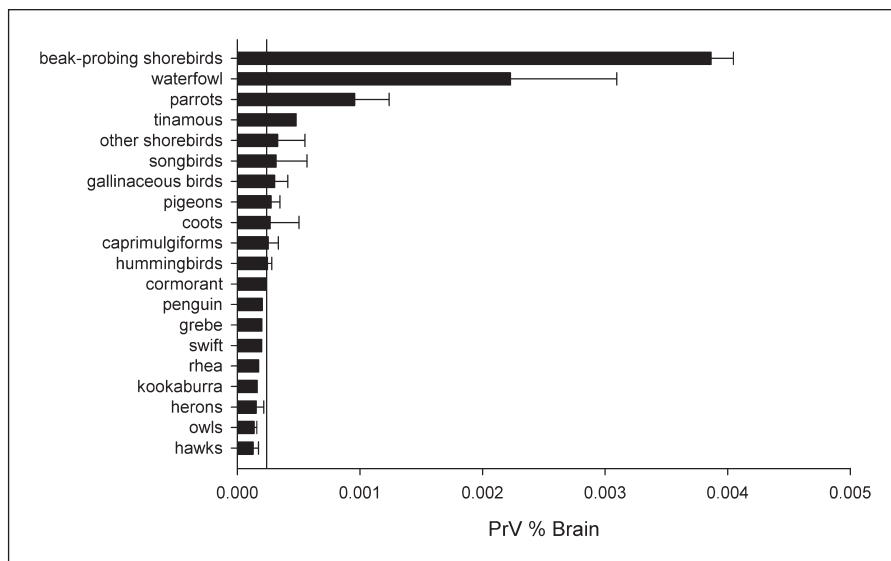
Fig. 5. Scatterplot of the volume of principal sensory nucleus of the trigeminal nerve (PrV) volume plotted as a function of brain minus PrV volume for all waterfowl (Anseriformes) species examined. Abbreviations are as follows: O.ja = *Oxyura jamaicensis*; An.pl = *Anas platyrhynchus*; An.su = *Anas superciliosa*; An.ca = *Anas castanea*; An.cl = *Anas clypeata*; An.di = *Anas discors*; An.cr = *Anas carolinensis*; At.am = *Aythya americana*; At.cl = *Aythya affinis*; Br.ca = *Branta canadensis*; Bu.cl = *Bucehala clangula*; Bu.al = *Bucephala albeola*; M.se = *Mergus serrator*; C.ju = *Chenonetta jubata.*
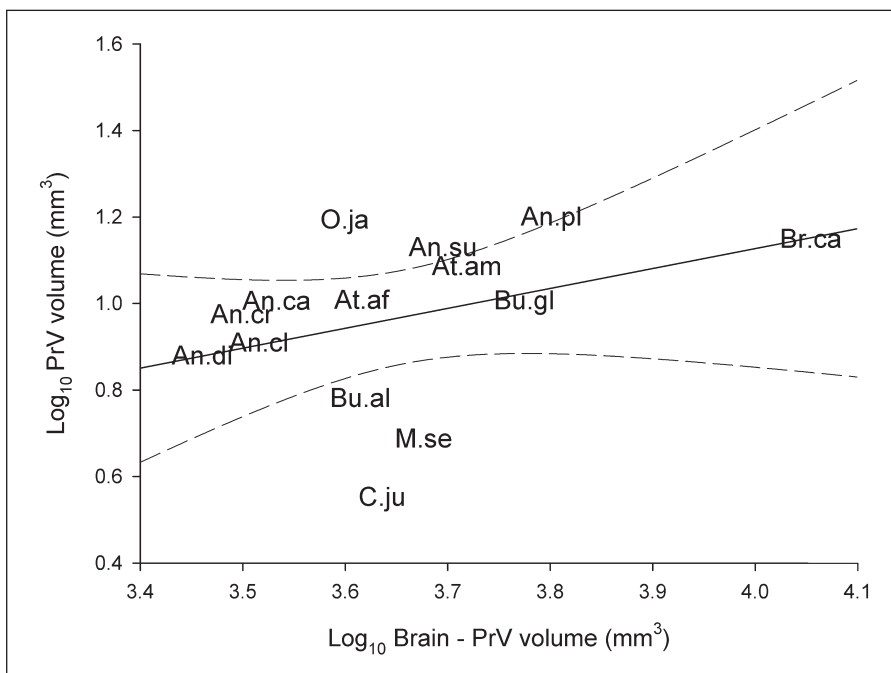
beldam et al., 1979; Wild, 1981], but seems to be lacking in the pigeon [Arends et al., 1984, 1998]. Dubbeldam [1992] proposed that these differences in the innervation of PrV among species are correlated with the functional demands of specific feeding behaviors. The alternative is that non-trigeminal afferents to PrV are present in the pigeons, but are too small to be detected, and therefore the relative contribution of each nerve to PrV would vary in concert with different feeding behaviors.

Feeding Mechanism and PrV Hypertrophy

To understand the hypertrophy of PrV in beak-probing shorebirds, waterfowl and parrots, we must consider the particular feeding behaviors of each group and the

sensory demands these behaviors place on different parts of the orofacial region. These three groups are very specialized with respect to their feeding behaviors and present several related anatomical and behavioral adaptations.

In the case of beak-probing shorebirds, we could only include two species, the least sandpiper *(Calidris minutilla)* and the short-billed dowitcher *(Limnodromus griseu),* both of which belong to the family of the Scolopacidae. Feeding behavior in most scolopacids consists of inserting the beak into a soft substrate (e.g., sand or mud) to capture invertebrates that live below the sediment surface [Barbosa and Moreno, 1999; Nebel and Thompson, 2005]. To detect their prey, they use a complex array of sensory pits in the tip of the bill, which are filled with Herbst corpuscles. These mechanoreceptors sense pressure or vibrational cues from buried invertebrate prey [Gerritsen and Meiboom, 1986; Zweers and Gerritsen, 1997; Piersma et al., 1998]. In some cases, such as the red knot *(Calidris canutus)* and sanderling *(C. alba)*, it has been suggested that the high density of mechanoreceptors is used to detect changes in pressure patterns produced by buried objects, allowing these species to detect immobile bivalves without direct contact [Gerritsen and Meiboom, 1986; Piersma et al., 1998]. Thus, scolopacids depend highly upon the trigeminal system for foraging and this has likely placed increased demands on the processing capacity of PrV thereby leading to its enlargement. Beak-probing as a feeding strategy is not, however, limited to scolopacids. Within Charadriiforms, oystercatchers (Haematopodidae) have long, narrow beaks that are used to capture buried worms and bivalves [Hulscher, 1976; Boates and Goss-Custard, 1989; Zweers et al., 1994]. Although not related to shorebirds, ibis (Threskiornithidae) also have long narrow beaks that are used to probe in mud and shallow waters in search of small invertebrates [Bildstein, 1987; Bildstein et al., 1989; Zweers et al., 1994]. Stingelin [1965] measured PrV volume in the sacred ibis *(Threskiornis aethiopica)*, using a cerebral index approach and found it was of similar relative size to a snipe *(G. gallinago)*.

Recently, Cunningham et al. [2007] found that kiwis *(Apteryx spp.)* have a large number of sensory pits in the tip of the beak and the number of Herbst corpuscles per pit was similar to beak-probing shorebirds. Based on this, they proposed that kiwis must use tactile information in a similar fashion to beak-probing shorebirds. Martin et al. [2007] analyzed the brain of kiwis and reported a 'large and well-defined' PrV, but no measurements were provided. Because kiwis also have an enlarged olfactory system [Martin et al., 2007] and there is some controversy regarding the use of olfactory versus tactile information in foraging [see Cunningham et al., 2007], a comparison of the relative size of PrV to other beak-probing birds could be useful in determining the relative importance of tactile information in the feeding behavior of kiwis.

Waterfowl exhibit a great diversity of diets and feeding behaviors, and this is reflected in a large variation in the size of PrV (fig. 5). Waterfowl from the genera *Oxyura, Anas* and *Aythya* are mostly filter feeders or search for food items in the sediment while diving [Tome and Wrubleski, 1988; Kooloos et al., 1989; Barbosa and Moreno, 1999]. The general foraging behavior of these birds consists of inserting the tip of the bill into the substrate while moving their head from side to side and opening and closing the bill. The bill movements are coordinated with tongue movements; when the bill opens, the tongue retracts and acts as a piston, sucking water and food particles inside the mouth. When the bill closes, the tongue expels the water through the sides of the bill and the lamellae that line the bill trap any food items. As the mouth opens again and the tongue is retracted, horny spines on the lateral edge of the caudal tongue are used to sweep food out of the lamellae [Zweers et al., 1977; Tome and Wrubleski, 1988; Kooloos et al., 1989]. This complex behavior is associated with a large number of mechanoreceptors in the beak and tongue of waterfowl, especially Grandry's corpuscles, which detect velocity [Gottschaldt and Lausmann, 1974; Gosttchaldt, 1985]. Mechanoreceptors in the beak, and especially in the bill tip organ, are used to detect and discriminate food items, whereas those in the tongue and palate are used for monitoring the transport and flow of water and food into the oral cavity [Zweers et al., 1977; Berckhoudt, 1980]. Given the complexity of these coordinated movements for filter feeding and their reliance on somatosensory input throughout the oral cavity, it is therefore of little surprise that the PrV is enlarged in all filter-feeding species.

Not all waterfowl, however, share an equally large PrV. As indicated in our results, there is significant variation among species. In the middle range are the bufflehead *(Bucephala albeola)*, the common goldeneye *(Bucephala clangula)* and the Canada goose *(Branta canadiensis)*. Bufflehead and goldeneye feed by diving and actively trapping small invertebrates [Goodman and Fisher, 1962; Pehrsson, 1976] whereas Canada geese are terrestrial grazers [Goodman and Fisher, 1962]. At the lower end of PrV size among the waterfowl are the red-breasted merganser and the Australian wood duck. The former is a diving duck with an elongated narrow beak and it feeds

exclusively on fish mainly using visual cues [Goodman and Fisher 1962; Sjöberg, 1988], whereas the Australian wood duck has a short beak and is a terrestrial grazer, feeding mostly on grass and occasionally on insects [Dawson et al., 1989; Marchant and Higgins, 1990]. Previously, Dubbeldam [1998] used the ratio between PrV volume and the volume of a visual nucleus, the nucleus rotundus, as a measurement of somatosensory specialization in nine species of waterfowl and found a similar degree of variation. The ratio was high in filtering species in the genera *Anas* and *Aythya*, and low in the Mandarin duck *(Aix galericulata)*, a short-billed duck that feeds on small invertebrates [Delacour, 1954]. Filter feeding is thought to represent the ancestral feeding method of Anseriformes and all other feeding behaviors are secondarily derived [Olson and Feduccia, 1980; Zweers and Vandenberg, 1996]. This suggests that the expansion of PrV in all waterfowl is probably an ancestral feature that also reflects the consequences of enhanced somatosensory processing for filter feeding, and that smaller PrV sizes are due to the loss of this behavior. Why non-filter feeding waterfowl retain relatively large PrV volumes compared to other avian taxa is, however, unclear. One possible explanation is that a larger PrV can be used for other feeding strategies too, such as enhanced sensitivity in the bill tip of mergansers which would probably aid in the capturing of fish. It should also be noted that just as probe feeding is not exclusive to scolopacid shorebirds, filter feeding has also evolved in other groups of birds [Zweers et al., 1994]. For example, both flamingos [Phoenicopteridae; Zweers et al., 1995] and Antarctic prions [Procellariidae; Morgan and Ritz, 1982; Harper, 1987; Klages and Cooper, 1992] have evolved some form of filtering that involves straining water through lamellae in the sides of their beaks, but the species differ greatly in the form of the beak, how they use it, and in their water pumping mechanism [Zweers et al., 1994]. These differences should be reflected in the sensory requirements from the orofacial region during feeding and, ultimately, in the size of PrV.

Lastly, we found parrots have a hypertrophied PrV, but not as large as waterfowl or beak-probing shorebirds (fig. 3, 4). Contrary to the other two specialist groups, parrots do not rely on mechanosensory information from the beak to find their food. Instead, they use mechanosensory information in the processing of food items, such as seeds, nuts and fruit. Indeed, the feeding apparatus (i.e., beak, palate and tongue) of parrots is highly adapted to seed husking in all species, irrespective of diet [Homberger, 1980a]. The tongue is specially adapted to the

seed-husking task and possesses a series of cavernous bodies and a large number of muscles, making it fleshy and highly mobile [Homberger, 1980a, b, 1986; Zweers et al., 1994]. When husking seeds and fruits, parrots use the tip of their tongue to constantly rotate and position the food item against the palate, and use coordinated movements of the lower jaw and tongue to break and remove the husk [Homberger, 1980b, 1983; Zweers et al., 1994]. The distribution of mechanoreceptors in the parrot orofacial region corresponds to this feeding mechanism, with a high concentration of touch papillae in the tip of the lower beak [Gottschaldt, 1985] and in the tip of the tongue [Zweers et al., 1994]. Parrots also use the tongue to drink water by shaping the tip of their tongue to resemble a spoon, to pick up small seeds against the upper jaw, and even in the control of vocalizations [Homberger, 1980b, 1983; Zweers et al., 1994; Beckers et al., 2004]. Mechanoreceptors in the dorsal part of the tongue are innervated by the lingual branch of the glossopharyngeal nerve, whereas receptors in the ventral and lateral parts are innervated by the lingual branch of the hypoglossal nerve [Wild, 1981]. Wild [1981] found that in the galah *(E. roseicapillus)*, both nerves send projections to PrV, but contrary to the situation in the mallard duck [Dubbeldam et al., 1979], this projection overlaps with that from the trigeminal nerve. Wild [1981] proposed that this particular organization serves as the anatomical substrate for sensory integration during seed-husking behavior. The relatively large PrV of parrots therefore seems to be directly correlated with the evolution of the sensory and morphological specializations for seed husking. What is surprising, however, is that nectar-feeding species, such as the rainbow *(Trichglossus haematodus)* and purple-crowned lorikeets *(Glossopsitta porphyrocephala)* have a PrV that is similar in size to all of the species feeding on seeds and nuts. Perhaps these species require similar somatosensory processing for tongue-feeding in flowers or for climbing around thin branches using the beak as an additional 'limb'.

Conclusions

Enlargement of the PrV in birds appears to be related to at least three very specific feeding behaviors: beak-probing, filtering and seed husking. Even though each specific feeding strategy is restricted to a separate taxonomic group in our study, each has evolved several times within birds. Analyses of the relative size of PrV in some of these groups (e.g., flamingos in the case of filtering or

oystercatchers in the case of beak-probing) could reveal further convergence of somatosensory specializations related to feeding behaviors. Furthermore, other birds might present other specialized feeding mechanisms that require an increased amount of somatosensory information from the orofacial region. PrV enlargement could therefore have evolved independently several times in response to the somatosensory requirements of a range of feeding behaviors in birds.

References

Arends JJ, Woelders-Blok A, Dubbeldam JL (1984) The efferent connections of the nuclei of the descending trigeminal tract in the mallard *(Anas platyrhynchos L.)*. Neuroscience 13:797–817.

Barbosa A, Moreno E (1999) Evolution of foraging strategies in shorebirds: an ecomorphological approach. Auk 116:712–725.

Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J (2004) Phylogeny and diversification of the largest avian radiation. Proc Nat Acad Sci USA 101:11040–11045.

Barton RA (1998) Visual specialization and brain evolution in primates. Proc Biol Sci 265:1933–1937.

Beckers GJ, Nelson BS, Suthers RA (2004) Vocaltract filtering by lingual articulation in a parrot. Curr Biol 14:1592–1597.

Berkhoudt H (1980) The morphology and distribution of cutaneous mechanoreceptors (Herbst and Grandry corpuscles) in bill and tongue of the mallard *(Anas platyrhynchos L.)*. Neth J Zool 50:1–34.

Bildstein KL (1987) Energetic consequences of sexual size dimorphism in white ibises *(Eudocimus albus)*. Auk 104:771–775.

Bildstein KL, McDowell SG, Brisbin IL (1989) Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predation. Anim Behav 37:133–139.

Boates JS, Goss-Custard JD (1989) Foraging behaviour of oystercatchers *Haematopus ostralegus* during a diet switch from worms *Nereis diversicolor* to clams *Scrobicularia plana*. Can J Zool 67:2225–2231.

Boire D (1989) Comparaison quantitative de l'encéphale de ses grades subdivisions et de relais visuals, trijumaux et acoustiques chez 28 espèces. PhD Thesis, Université de Montréal, Montréal.

Bolze G (1968) Anordnung und Bau der Herbstchen Körperchen in Limicolenschnabeln im Zusammenhang mit der Nahrungsfindung. Zool Anz 181:313–355.

Bout RG, Dubbeldam JL (1985) An HRP study of the central connections of the facial nerve in the mallard *(Anas platyrhynchos L.)*. Acta Morphol Neerl Scand 23:181–193.

Bout RG, Dubbeldam JL (1991) Functional morphological interpretation of the distribution of muscle spindles in the jaw muscles of the mallard *(Anas platyrhynchos)*. J Morphol 210:215–226.

Carezzano F, Bee-de-Speroni N (1995) Composición volumétrica encefálica e índices cerebrales en tres aves de ambiente acuático (Ardeidae, Podicipedide, Rallidae). Facena 11:75–83.

Catania KC (2000) Cortical-organization in moles: evidence of new areas and a specialized S2. Somatosens Mot Res 17:335–347.

Catania KC (2005) Evolution of sensory specializations in insectivores. Anat Rec 287:1038–1050.

Catania KC, Henry EC (2006) Touching on somatosensory specializations in mammals. Curr Opin Neurobiol 16:467–473.

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

Cunningham S, Castro I, Alley M (2007) A new prey-detection mechanism for kiwi *(Apteryx* spp.) suggests convergent evolution between paleognathous and neognathous birds. J Anat 211:493–502.

Davis KE (2008) Reweaving the tapestry: a supertree of birds. PhD Thesis, University of Glasgow, UK.

Dawson TJ, Johns AB, Beal AM (1989) Digestion in the Australian wood duck *(Chenonetta jubata)*: a small avian herbivore showing selective digestion of the hemicellulose component of fiber. Physiol Zool 62:522–540.

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

Delacour J (1954) The waterfowl of the world. London: Country Life.

Donne-Goussé C, Laudet V, Hänni C (2002) A molecular phylogeny of anseriformes based on mitochondrial DNA analysis. Mol Phylogenet Evol 23:339–356.

Dubbeldam JL (1980) Studies on the somatotopy of the trigeminal system in the mallard, *Anas platyrhynchos* L. II. Morphology of the principal sensory nucleus. J Comp Neurol 191:557–571.

Dubbeldam JL (1992) Nerves and sensory centres – a matter of definition? Hypoglossal and other afferents of the avian sensory trigeminal system. Zool JB Anat 122:179–186.

Dubbeldam JL (1998) The sensory trigeminal system in birds: input, organization and effects of peripheral damage. A review. Arch Physiol Biochem 106:338–345.

Dubbeldam JL, Karten HJ (1978) The trigeminal system in the pigeon *(Columba livia)*. I. Projections of the gasserian ganglion. J Comp Neurol 180:661–678.

Dubbeldam JL, Brus ER, Menken SB, Zeilstra S (1979) The central projections of the glossopharyngeal and vagus ganglia in the mallard, *Anas platyrhynchos* L. J Comp Neurol 183:149–168.

Finger TE (1975) Feeding patterns and brain evolution in ostariophysean fishes. Acta Physiol Scand Suppl 638:59–66.

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

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

Garland T Jr, Bennett AF, Rezende EL (2005) Phylogenetic approaches in comparative physiology. J Exp Biol 208:3015–3035.

Gerritsen AFC, Meiboom A (1986) The role of touch in prey density estimation by *Calidris alba*. Neth J Zool 36:530–562.

Goodman DC, Fisher HI (1962) Functional anatomy of the feeding apparatus in waterfowl (Aves: Anatidae). Carbondale, IL: Southern Illinois University Press.

Gottschaldt KM (1985) Structure and function of avian somatosensory receptors. In: Form and function in birds Vol. 3. (King AS, McLelland J, eds), pp 375–461. London: Academic Press.

Gottschaldt KM, Lausmann S (1974) The peripheral morphological basis of tactile sensibility in the beak of geese. Cell Tissue Res 153:477–496.

Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han KL, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC, Yuri T (2008) A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768.

Harper PC (1987) Feeding behaviour and other notes on 20 species of Procellariiformes at sea. Notornis 34:169–192.

Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford, UK: Oxford University Press.

Henry EC, Remple MS, O'Riain MJ, Catania KC (2006) Organization of somatosensory cortical areas in the naked mole-rat *(Heterocephalus glaber)*. J Comp Neurol 495:434–452.

Homberger DG (1980a) Funktionell-morphologische Untersuchungen zur Radiation der Ernährungs- und Trinkmethoden der Papageien. Bonn Zool Monogr 13:1–192.

Homberger DG (1980b) Functional morphology and evolution of the feeding apparatus in parrots, with special reference to the Pesquet's parrot, *Psttrichas fuligidus* (lesson). In: Conservation of new world parrots (Pasquier RF, ed), pp 471–485. Washington, DC: Smithsonian Institution Press.

Homberger DG (1983) Nonadaptive evolution of avian drinking methods. Am Zool 23:894.

Homberger DG (1986) The lingual apparatus of the African grey parrot, *Psittacus erithacus* Linné (Aves: Psittacidae): description and theoretical mechanical analysis. Ornithol Monogr 39:1–233.

Hulscher JB (1976) Localization of cockles *(Cardium edule)* by an oystercatcher *(Haematopus ostralegus)* in darkness and daylight. Ardea 64:292–310.

Iggo A, Gottschald KM (1974) Cutaneous mechanoreceptors in simple and in complex sensory structures. In: Symposium: mechanoreception (Schwartzkopff J, ed), pp 153–176. Opladen: Westdeutscher Verlag.

Ives AR, Midford PE, Garland T Jr (2007) Within-species variation and measurement error in phylogenetic comparative methods. Syst Biol 56:252–270.

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

Iwaniuk AN, Wylie DRW (2006) The evolution of stereopsis and the wulst in caprimulgiform birds: a comparative analysis. J Comp Physiol A 192:1313–1326.

Iwaniuk AN, Clayton DH, Wylie DRW (2006) Echolocation, vocal learning, auditory localization and the relative size of the avian auditory midbrain nucleus (Mld). Behav Brain Res 167:305–317.

Iwaniuk AN, Wylie DRW (2007) Comparative evidence of a neural specialization for hovering in hummingbirds: hypertrophy of the pretectal nucleus lentiformis mesencephali. J Comp Neurol 50:211–221.

Iwaniuk AN, Heesy CP, Hall MI, Wylie DR (2008) Relative wulst volume is correlated with orbit orientation and binocular visual field in birds. J Comp Physiol A 194:267–282.

Jerison HJ (1973) Evolution of the brain and intelligence. New York: Academic Press.

Johnson KP, Sorenson MD (1999) Phylogeny and biogeography of dabbling ducks (Genus: *Anas*): a comparison of molecular and morphological evidence. Auk 116:792–805.

Kimball RT, Braun EL (2008) A multigene phylogeny of Galliformes supports a single origin of erectile ability in non-feathered facial traits. J Avian Biol 39:438–445.

Kishida R, Dubbeldam JL, Goris RC (1985) Primary sensory ganglion cells projecting to the principal trigeminal nucleus in the mallard, *Anas platyrhynchos*. J Comp Neurol 240:171–179.

Klages NTW, Cooper J (1992) Bill morphology and the diet of filter-feeding seabird: the Broad-billed Prion *Pachyptila vittata* at South Atlantic Gough Island. J Zool Lond 227:385–396.

Kooloos JGM, Kraaijeveld AR, Langenbach GEJ (1989) Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata* and *Aythya fuligula* (Aves, Anseriformes) Zoomorphology 108:269–290.

Krulis V (1978) Struktur und Verteilung von Tastrezeptoren im Schnabel-Zungenbereich von Singvögeln im besonderen der Fringillidae. Rev Suisse Zool 85:385–447.

Kubke MF, Massoglia DP, Carr CE (2004) Bigger brains or bigger nuclei? Regulating the size of auditory structures in birds. Brain Behav Evol 63:169–180.

Lavin SR, Karasov WH, Ives AR, Middleton KM, Garland T Jr (2008) Morphometrics of the avian small intestine, compared with non-flying mammals: a phylogenetic approach. Physiol Biochem Zool 81:526–550.

Livezey BC, Zusi RL (2007) Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. Zool J Linn Soc 149:1–95.

Maddison WP, Maddison DR (2009) Mesquite: a modular system for evolutionary analysis. Version 2.6 http://mesquiteproject.org

Marchant S, Higgins P (1990) Handbook of Australian, New Zealand and Antarctic birds, Vol 1. Melbourne: Oxford University Press.

Martin GR, Wilson KJ, Wild MJ, Parsons S, Kubke FM, Corfield J (2007) Kiwi forego vision in the guidance of their nocturnal activities. PLoS One 2:e198.

Midford PE, Garland T Jr, Maddison WP (2002) PDAP:PDTREE for Mesquite, version 1.00. http://mesquiteproject.org/mesquite/pdap/.

Morgan WL, Ritz DA (1982) Comparison of the feeding apparatus in the Mutton-bird, *Puffinus tenuirostris* (Temminck) and the Fairy Prion, *Pachyptila turtur* (Kuhl) in the relation to the capture of krill, *Nyctyphanes australis*. J Exp Mar Biol Ecol 59:61–76.

Nebel S, Thompson GI (2005) Foraging behaviour of Western Sandpipers changes with sediment temperature: implications for their hemispheric distribution. Ecol Res 20:503–507.

Olson SL, Feduccia A (1980) *Presbyornis* and the origin of the Anseriformes (Aves: Charadriomorphae). Smithson Contrib Zool 323:1–24.

Pehrsson O (1976) Food and feeding grounds of the Goldeneye *Bucephala clangula* (L.) on the Swedish west coast. Ornis Scand 7:91–112.

Pereira SL, Johnson KP, Clayton DH, Baker AJ (2007) Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleogene. Syst Biol 56:656–672.

Pettigrew JD, Frost BJ (1985) Tactile fovea in the *Scolopacidae?* Brain Behav Evol 26:185–195.

Piersma T, van Aelst R, Kurk K, Berkhoudt H, Maas LRM (1998) A new pressure sensory mechanism for prey detection in birds: the use of seabed-dynamic principles? Proc R Soc Lond B 265:1377–1383.

Pistone E, Carezzano F, Bee-de-Speroni N (2002) Relative encephalic size and cerebral indices of *Vanellus c. chilensis* (Aves: Charadriidae) Rev Chil Hist Nat 7:595–602.

Pubols BH, Welker WI, Johnson JI (1965) Somatic sensory representation of forelimb in dorsal root fibers of raccoon, coatimundi, and cat. J Neurophysiol 28:312–341.

Pubols BH, Pubols LM (1972) Neural organization of somatic sensory representation in the spider monkey. Brain Behav Evol 5:342–366.

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

Silver R, Witkovsky P (1973) Functional characteristics of single units in the spinal trigeminal nucleus of the pigeon. Brain Behav Evol 8:287–303.

Sjöberg K (1988) Food selection, food-seeking patterns and hunting success of captive Goosanders *Mergus merganser* and Red-breasted Mergansers *M. serrator* in relation to the behaviour of their prey. Ibis 130:79–93.

Stingelin W (1961) Grössenunterschiede des sensiblen Trigeminuskerns bei verschiedenen Vögeln. Rev Suisse Zool 68:247–251.

Stingelin W (1965) Qualitative und quantitative Untersuchungen an Kerngebieten der Medulla oblongata bei Vögeln. Bibl Anat 6:1–116.

Swanson DL, Garland T Jr (2009) The evolution of high summit metabolism and cold tolerance in birds and its impact on present-day distributions. Evolution 63:184–194.

Thomas GH, Wills MA, Székely TA (2004) Supertree approach to shorebird phylogeny. BMC Evol Biol 4:28

Tome MW, Wrubleski DA (1988) Underwater foraging behavior of canvasbacks, lesser scaups, and ruddy ducks. Condor 90:168–172.

Wild JM (1981) Identification and localization of the motor nuclei and sensory projections of the glossopharyngeal, vagus, and hypoglossal nerves of the cockatoo *(Cacatua roseicapilla)*, Cacatuidae. J Comp Neurol 203:351–377.

Wild JM (1990) Peripheral and central terminations of hypoglossal afferents innervating lingual tactile mechanoreceptor complexes in Fringillidae. J Comp Neurol 298:157–171.

Wink M, Heidrich P, Sauer-Gurth H, Elsayed AA, Gonzalez J (2008) Molecular phylogeny and systematics of owls (Strigiformes). In: Owls of the world (Konig C, Weick F, eds), pp 42–63. London: Christopher Helm.

Wright TF, Schirtzinger EE, Matsumoto T, Eberhard JR, Graves GR, Sanchez JJ, Capelli S, Muller H, Scharpegge J, Chambers GK, Fleischer RC (2008) A multilocus molecular phylogeny of the parrots (Psittaciformes): support for a Gondwanan origin during the Cretaceous. Mol Biol Evol 25:2141–2156.

Zeigler HP, Witkovsky P (1968) The main sensory trigeminal nucleus in the pigeon: a single-unit analysis. J Comp Neurol 134:255–264.

Zweers GA, Gerritsen AFC, Van Kranenburg-Vood PJ (1977) Mechanics of feeding of the Mallard (*Anas platyrhynchos L.*; Aves, Anseriformes). Contrib Vertebr Evol 3:1–109.

Zweers GA, Berkhoudt H, Vanden Berge JC (1994) Behavioral mechanisms of avian feeding. In: Biomechanics of feeding in vertebrates, advances in comparative environmental physiology (Bels VL, Chardon M, Vandewalle P, eds) 18:241–279.

Zweers GA, Gerritsen AFC (1997) Transition from pecking to probing mechanisms in waders. Neth J Zool 47:161–208.

Zweers GA, Vanden Berge JC (1996) Evolutionary transitions in the trophic system of the wader-waterfowl complex. Neth J Zool 47:255–287.

Zweers G, de Jong F, Berkhoudt H, Vanden Berge JC (1995) Filter feeding in flamingos (*Phoenicopterus ruber)*. Condor 97:297–324.