

Brain Architecture and Social Complexity in Modern and Ancient Birds

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Key Words

Brain architecture · Cognitive · Social · Machiavellian intelligence · Multivariate · Birds · *Archaeopteryx*

Abstract

Vertebrate brains vary tremendously in size, but differences in form are more subtle. To bring out functional contrasts that are independent of absolute size, we have normalized brain component sizes to whole brain volume. The set of such volume fractions is the cerebrotypes of a species. Using this approach in mammals we previously identified specific associations between cerebrotypes and behavioral specializations. Among primates, cerebrotypes are linked principally to enlargement of the cerebral cortex and are associated with increases in the complexity of social structure. Here we extend this analysis to include a second major vertebrate group, the birds. In birds the telencephalic volume fraction is strongly correlated with social complexity. This correlation accounts for almost half of the observed variation in telencephalic size, more than any other behavioral specialization examined, including the ability to learn song. A prominent exception to this pattern is owls, which are not social but still have very large forebrains. Interpolating the overall correlation for *Archaeopteryx*, an ancient bird, suggests that its social complexity was likely to have been on a par

with modern domesticated chickens. Telencephalic volume fraction outperforms residuals-based measures of brain size at separating birds by social structure. Telencephalic volume fraction may be an anatomical substrate for social complexity, and perhaps cognitive ability, that can be generalized across a range of vertebrate brains, including dinosaurs.

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Introduction

How can the architectures of brains be compared to bring out functional contrasts independent of absolute size? For instance, among mammals, from the desman to the sperm whale, brain size varies by over five orders of magnitude. At the same time, across phylogeny mammalian brains also show broad similarities in structure, internal connectivity, and anatomical composition [Nieuwenhuys et al., 1998]. Thus, examining brain architecture to obtain functional principles presents a great challenge to comparative neuroanatomy.

One approach to this problem is to make quantitative comparisons [Jerison, 1973, 1991; Stephan et al., 1981; Armstrong, 1983; Finlay and Darlington, 1995; Barton and Dunbar, 1997]. Investigations have been directed at describing statistical trends and exceptions, and also find-

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ing explanations for these observations. The result has been a variety of approaches to comparing brains, each with its own strengths and weaknesses.

In one early approach, brain size was examined using body size as a reference measure [Jerison, 1973, 1991]. This approach revealed relationships that appear approximately to follow power laws of the form $Y = aX^b$; that is, a trend that can be fitted by a line in log-log coordinates. These are called allometric scaling relationships [Thompson, 1942] and have been found repeatedly throughout the animal kingdom for many anatomical components. Such scaling relationships, even though they do not yet have a definitive functional explanation, might be used as a baseline from which to compare individual species. Such comparison has been used to identify outliers – individual species that depart from the scaling trend. This approach succeeds in identifying general deviations, such as the extremes of human and dolphin brain size compared with other mammals of similar body mass. These deviations, also known as residuals, are usually expressed as an ‘encephalization quotient’ [Jerison, 1973].

Residuals analysis has also been attempted on individual parts of the brain. In this case residuals on the sizes of individual brain components have been calculated relative to body size [Armstrong, 1983; Harvey and Krebs, 1990; Deaner et al., 2000], whole brain [Douglas and Marcellus, 1975], or brain subdivisions [Barton et al., 1995; Barton and Harvey, 2000; Deaner et al., 2000] as reference measures using data for an entire set of animals, thus identifying specializations in brain components. In all cases, the residuals approach has several drawbacks. First, fit lines vary widely depending on how a data set is analyzed; both the slope and intercept depend on the taxonomic level at which the data are grouped [Gould, 1975; Martin and Harvey, 1985; Nealen and Ricklefs, 2001; Wang et al., 2002]. Therefore a linear fit to data pooled across taxonomic groups contains the intrinsic ambiguity that no species is associated with a single scaling trend. Scaling trends derived this way are thus unlikely to capture the overall statistical properties of the data set. Thus, residuals calculated relative to some fit may contain artifacts that are very difficult to interpret [Wang et al., 2002]. Second, individual brain components each have their own allometries [Fox and Wilczynski, 1986]; therefore, the combination of any two of them will hardly ever be expected to follow a strict power law [Zhang and Sejnowski, 2000]. Finally, even if taxonomic groups (clades) and brain components were subdivided to the point that basic size trends could be identified clearly, few functional rationales have yet been found to account for such rela-

tionships [although see Harvey and Krebs, 1990; Stevens, 2001, and the extensive work in circulatory systems by West et al., 1999].

In a second type of approach, the use of allometric relationships has been avoided by analyzing absolute brain component volumes [Finlay and Darlington, 1995; Finlay et al., 2001]. Such an approach has revealed that differences in component sizes across species tend to be correlated to each other, consistent with a developmental principle of concerted brain growth. In this model brain growth is regulated in part by a shared set of instructions that govern overall developmental rates. This work has since been extended to include multivariate analysis as a means of searching for patterns in growth spanning multiple brain regions [Finlay et al., 2001]. However, the results of such an analysis are dominated by the effects of absolute size differences among species. Also, most analyses of this type so far still begin by identifying common trends, an approach that once again depends on initial examination of the whole data set.

To overcome all of these problems, we recently constructed a simpler comparative measure and demonstrated that it corresponds with behavioral performance for several mammalian traits [Clark et al., 2001]. As a means of eliminating the effects of absolute size we normalized brain component data on a species-by-species basis by dividing a component’s volume by whole brain volume to obtain its volume fraction F [Jerison, 1991; Clark et al., 2001]. Although normalization is straightforward, it differs from prior analyses. Most importantly, this definition of relative component size does not depend on any cross-species fits. Volume fractions of all components of the brain for a given species can be defined as the ‘cerebrotype’ for that species, and it is possible to quantify the dissimilarity in brain structure between two species by simply calculating a distance between the two cerebrotypes in the component volume-fraction space. These distances can be analyzed easily using multivariate methods such as multidimensional scaling or principal component analysis (also known as singular value decomposition).

Of the possible reference standards for size normalization, we have chosen the whole brain as a baseline because generally, brain components connect principally with other brain components. Because larger targets are likely to require more neural projections, the combined size of all targets (i.e. the whole brain) is a natural size standard. Another method for normalization has been to divide the component size by brainstem size [Lefebvre et al., 1997; Deaner et al., 2000; de Winter and Oxnard, 2001]. However, that approach differs from ours because it tends to

emphasize extreme values of volume fraction and does not yield distance metrics with clear physical interpretations.

We have analyzed whole-brain cerebrotypes in search of size trade-offs and constancy within several types of vertebrate brain. Here we present our analysis of the avian forebrain (telencephalon). We will use previous work on mammals (especially primates) as a foundation for considering birds and an extinct group, the dinosaurs.

Mammals

Our previous examination of data from 19 mammalian taxa [Clark et al., 2001] showed a striking tendency for the volume fraction of cerebral cortex, F_{neo} , to vary strongly, from $16 \pm 6\%$ (mean \pm SD, Soricomorpha) to $74 \pm 5\%$ (Hominoidea); for the cerebellum, F_{cbl} , to remain almost constant at $13.5 \pm 2.4\%$; and for the remaining regions to be supplanted by increases in F_{neo} .

As a means of analyzing these variations, we used total-brain cerebrotypes to generate relational maps of mammalian brain architectures. We did this using multidimensional scaling, an algorithm that displays the variation of many volume fractions in a plane with maximum fidelity to the true distances between cerebrotypes. This method allows species to be compared without making a priori assumptions about allometric scaling relationships between components. Displaying the results of this analysis as points in a plane also avoids forcing the species to observe a tree structure, which can lead to misleading interpretations due to the fact that many species are either unavailable or extinct.

The resulting analysis provided a means of taxonomically grouping mammals by their brain structure. In the case of primates, cerebrotypes-based measures helped identify coordinated changes in brain architecture. According to the social intelligence hypothesis of primate brain evolution [Whiten and Byrne, 1988; Dunbar, 1995; Barton and Dunbar, 1997], a larger cerebral cortex may confer selection advantages by providing increased cognitive capacity for social dynamics. This social selection pressure would lead to progressive relative enlargement of the cerebral cortex over time.

Birds

Like mammals, birds are highly diverse and have spread to fill a variety of aerial, terrestrial, and marine niches throughout the planet. However, birds and mammals have diverged for more than 300 million years since their common tetrapod ancestor, yielding brain plans that differ in fundamental ways. Each lineage has distinctive

brain structural specializations [Nieuwenhuys et al., 1998], such as the retention of nuclear organization in birds and the appearance of a prominent laminated cerebral cortex in mammals.

Birds and mammals also share a number of convergent features. Both groups are warm-blooded and have a higher basal metabolic rate than most other vertebrates. Compared to other vertebrates, both groups have large brains relative to body weight; this relationship is nearly the same for these two groups but is significantly offset compared with reptiles and amphibians [Jerison, 1991]. Bird body sizes span most of the range for mammals (although mammals can be larger). Finally, certain bird and mammal lineages (songbirds and primates) have been suggested to have evolved with great rapidity [Wyles et al., 1983]. Given these similarities, birds present an attractive comparison group relative to mammals.

Materials and Methods

We used brain and body weight measurements from 154 bird species [Portmann, 1947a; Boire and Baron, 1994]. Data came from 138 out of 140 species in Portmann and 28 species (including 16 species not measured by Portmann) from Boire and Baron. From these data sets we excluded the domesticated *Streptopelia risoria* (both data sets) and *Gallus domesticus* [Boire and Baron, 1994]; the lorikeet *Trichoglossus novae hollandiae* [Portmann, 1947a], for which behavioral data were lacking; and a *Caprimulgus* of unknown species [Boire and Baron, 1994]. *Pavo meleagris* [Boire and Baron, 1994] was inferred to be *Pavo cristatus* [Portmann, 1947a]. Measurements of brain parameters in theropod dinosaurs and *Archaeopteryx* came from reports using CT scanning of endocasts for three-dimensional reconstruction [Rogers, 1998; Larsson et al., 2000].

Telencephalic volume fractions (F_{tel}) were defined as the telencephalic volume divided by the total brain volume. However, Portmann [1947a] reported each species' brain components as indices normalized to the brain core ('tronc cérébral') of a member of the order Galliformes of comparable body size. Therefore F_{tel} was calculated from Tables 4–6 of Portmann [1947a] by dividing the index for the hemispheres by the sum of all the indices. In eleven cases of species common to both data sets, F_{tel} was the same on average (Portmann larger than Boire and Baron by $0.2 \pm 2.4\%$, mean \pm SD, $n = 11$) and the average of the two was used. For a twelfth species, the chicken, the wild value [*Gallus gallus*, $F_{tel} = 53.4\%$; from Portmann, 1947a] was larger than the domestic value [*Gallus domesticus*, $F_{tel} = 44.3\%$; from Boire and Baron, 1994], consistent with reports of telencephalic reduction in chickens [Rehkämper et al., 2003] and other vertebrates [Kruska and Rohrs, 1974] after domestication; therefore, the wild value was used. For *Corvus corax* the mean of male and female values was used. Raw telencephalic volumes were calculated from the Portmann data [1947a] as the basal brain core weight ('chiffre basal') multiplied by the hemispheric index.

Birds were sorted into categories of social structure using group size and the presence of social transactional interactions [del Hoyo et al., 1992; Cramp, 1994]. Group size was defined as the average num-

Table 1. Transactional birds. Social traits leading to the classification as transactional are listed in the order of their appearance in Portmann [1947a]

Family	Species	Social traits
Gruidae (Cranes)	<i>Balearica pavonina</i> <i>Grus virgo</i> <i>Grus antigone</i>	Complex and socially contagious dance seen in both adults and young, function unknown; related to pair bonding and nervousness ¹
Anatidae (Waterfowl)	<i>Mergus serrator</i> <i>Anas platyrhynchos</i> <i>Anser anser</i> <i>Cygnus olor</i>	Sociable communal gatherings ¹ Socially coordinated loafing and other activities ² Individual's whole behavior affected by family and pair bonds ¹ Socially coordinated loafing, flocking of value in facilitating social integration ¹
Falconidae (Falcons, caracaras)	<i>Falco tinnunculus</i>	Mock attack, spontaneous play ¹
Psittacidae (Parrots)	<i>Melopsittacus undulatus</i> <i>Agapornis fisheri</i> <i>Psittacula eupatria</i> <i>Amazona versicolor</i> <i>Cacatua sulphurea</i> <i>Psittacus erithacus</i> <i>Ara ararauna</i> <i>Ara chloropterus</i> <i>Pionus menstruus</i>	Fission-fusion social system ²
	<i>Nymphicus hollandicus</i>	Fission-fusion social system ² ; aerial play, 'social enjoyment' ¹
Picidae (Woodpeckers, wrynecks)	<i>Jynx torquilla</i> <i>Dendrocopos medius</i> <i>Dendrocopos major</i> <i>Picus canus</i> <i>Picus viridis</i> <i>Dryocopus martius</i>	Memory and cognitive tasks ¹
Hirundinidae (Swallows, martins)	<i>Delichon urbica</i> <i>Hirundo rustica</i>	Communal activities including nest-material collection and social flights in morning and evening ¹ Song-chorus, feather-play ¹
Muscicapidae (Old World flycatchers)	<i>Turdus merula</i>	Territory owner assemblies in aggressive displays ¹
Corvidae (Crows)	<i>Oriolus oriolus</i> <i>Garrulus glandarius</i> <i>Pica pica</i> <i>Pyrrhocorax pyrrhocorax</i> <i>Corvus monedula</i> <i>Corvus frugilegus</i> <i>Corvus corone</i> <i>Corvus corax</i>	Communal bathing/rain-bathing with mimicking by conspecifics ¹ Spring gatherings ¹ Ceremonial gatherings and funerals ¹ Skillful aerial acrobatics for no apparent reason ¹ Play; active food giving and sharing (de Kort et al., 2003) ¹ Weddings and parliaments; aerial tumbling displays within flock ¹ Cooperative alliances and foraging (Baglione et al., 2003) Play, individual recognition and communication ¹
Aegithalidae (Long-tailed tits)	<i>Aegithalos caudatus</i>	Communal roosting to avoid freezing, 'highly developed social behavior' ¹
Paridae (Tits and chickadees)	<i>Parus caeruleus</i> <i>Parus major</i>	Flock and integration behavior, learning of milk-bottle opening ¹ Problem-solving, learning of milk-bottle opening from conspecifics ¹
Fringillidae (Finches)	<i>Loxia curvirostra</i>	Ceremonial gatherings ¹
Passeridae (Old World sparrows)	<i>Montifringilla nivalis</i>	Long aerial evolutions; clubs for social drinking/bathing ¹
Spheniscidae (Penguins)	<i>Spheniscus magellanicus</i> <i>Spheniscus demersus</i>	Individual recognition of partners and chicks ²

The traits described are taken from many field observations as summarized in ¹ Cramp [1994] and ² del Hoyo et al. [1992].

ber of nonmigrating conspecifics typically found in close proximity to one another. Breeding-ground gatherings were excluded from this definition. Group size, which does not require direct observation of interactions, has previously been taken as a measure of social complexity [Dunbar, 1995]. Solitary birds (group size: 1 to 3 birds) are often territorial and interact mainly during the mating season. Covey birds (group size: 5 to 50 birds) commonly show dominance struc-

tures such as pecking orders and leks. Colonial birds (group size: hundreds to thousands of birds) show communal structures such as gregarious roosts and large foraging flocks.

Species were classified as being in a fourth category, transactional, if field observations included descriptions of between-individual social interactions or socially transferable cognitive tasks. Social interaction was defined as presumptively communicative behavior

observed only in the presence of conspecifics. Group communication such as alarm calls or flock movements were excluded from this definition. Cognitive acts included social interactions with no apparent direct impact on survival rate and problem-solving behavior. Classifications of the species unique to Portmann were made by a person blind to the knowledge of brain size or proportions.

Examples of transactional birds include magellanic penguins, which altruistically defend the nests of unrelated neighbors [Boersma, 1988; Capurro et al., 1988; del Hoyo et al., 1992]; cranes, which perform a socially contagious dance that is thought to reinforce individual pair bonds; mallards, which engage in socially coordinated loafing and other comfort activities [Desforges and Wood-Gush, 1975; Brodsky et al., 1988; Cramp, 1994]; and parrots, which form complex social hierarchies based on age, association, and experience reminiscent of primate fission-fusion social structures [Ingels, 1978; Lowry, 1991; del Hoyo et al., 1992]. An extreme example of transactionality is shown by crows, which display multiple transactional traits including 'ceremonial gatherings,' playfulness, problem-solving ability, and a capacity for social learning. A complete list of the transactional birds in the database analyzed here is given in table 1.

Regression tree analysis was performed to analyze the relationship between telencephalic volume fraction and behavioral categories. Regression tree analysis [Venables and Ripley, 1994] is a form of multivariate analysis in which a splitting of the group (in this case, by behavioral category) is found that minimizes the total deviance in the resulting subgroups, where deviance of a subgroup is defined as the sum of squared deviations from the subgroup's mean. Splitting was repeated as long as a split could be found that reduced deviance by at least 0.002 times the deviance of the whole group and that resulted in subgroups of at least 15 species each. Regression tree analysis was implemented using the R language (The R Project, <http://www.r-project.org/>).

Multivariate analysis of cerebrotypes was done either on a set of 138 species [Portmann, 1947a] using brain core, optic lobes, cerebellum, and telencephalon; or 28 species [Boire and Baron, 1994] using telencephalon, diencephalon, mesencephalic tegmentum, optic tectum, cerebellum, and myelencephalon. The two sets of measurements were analyzed separately. Euclidean cerebrototype distances were calculated and multidimensional scaling was performed as previously described [Clark et al., 2001].

As a way to compare the resolving power of the measures F_{tel} and residuals calculated in various ways, the degree to which the distributions of transactional and non-transactional birds overlap was expressed in units of the propagated standard deviation s calculated in quadrature. If for a measure x the mean and standard deviation are x_T and σ_T for transactional birds and x_{NT} and σ_{NT} for non-transactional birds, then the propagated standard deviation is $s = (\sigma_T^2 + \sigma_{NT}^2)^{1/2}$ and the difference (degree of non-overlap) between transactional and non-transactional distributions is $(x_T - x_{NT})/s$ standard deviations.

Results

We used brain measurements from 154 species [Portmann, 1947a; Boire and Baron, 1994]. The variation in volume fractions among species ranged from 0.9 to 8.3% (standard deviation) of total brain volume. The

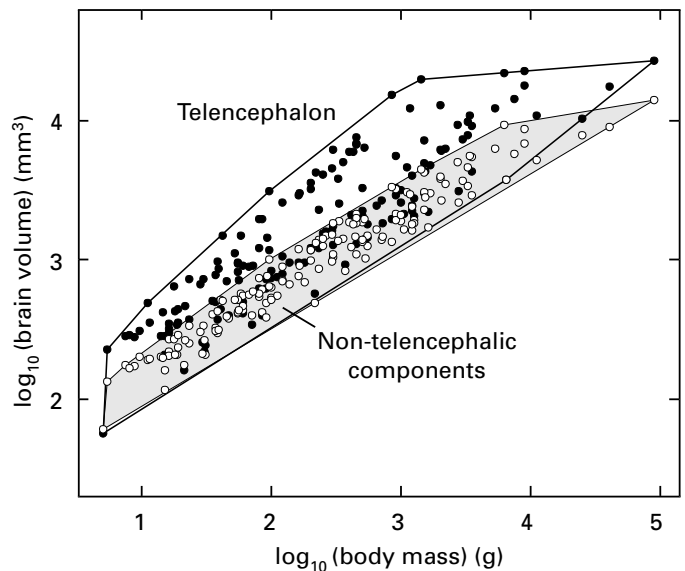


Fig. 1. Relative variation in brain components compared with body size. Volumes of telencephalon (filled symbols) and non-telencephalic brain components (open symbols) as a function of body size. Brain and body measurements came from published data [Portmann, 1947a; Boire and Baron, 1994]. The variation in telencephalon volume, visible as vertical spread of the data, is significantly more variable than non-telencephalic volume.

greatest variation occurred in the volume fraction of telencephalon (F_{tel}), $63.2 \pm 8.3\%$ (mean \pm s.d.; $n = 154$ species). The overall range for F_{tel} , 45–82%, is quite similar to the range found in mammals, 50–85% [Clark et al., 2001]. Likewise, for F_{cbl} , the overall range (4–22%; excluding *Lophochroa sulphurea*, the smallest is 6%) and variation ($12.4 \pm 3.2\%$, 154 species) are similar to mammals [range 6–23% by individual species, variation $13.5 \pm 2.4\%$ across 19 mammalian taxa; see figure 2 of Clark et al., 2001].

The variability in telencephalon and non-telencephalic brain components can also be quantified relative to body weight. Using a power law model (that is, a linear fit in log-log coordinates), the correlation of body size with brain size ($r^2 = 0.857$, $n = 154$) leaves 14.3% of the variance unexplained. The unexplained variance (fig. 1) is greater for telencephalic volume (20.0%) than for non-telencephalic volume (5.8%; $p < 0.0001$, one-tailed z test). The relative strictness of scaling of non-telencephalic volume is consistent with the idea that a given body size requires a certain amount of 'basal' brain [Portmann, 1947a, b; Boire and Baron, 1994]. Conversely, the variation in telencephalic volume suggests that this structure may fulfill additional functional roles.

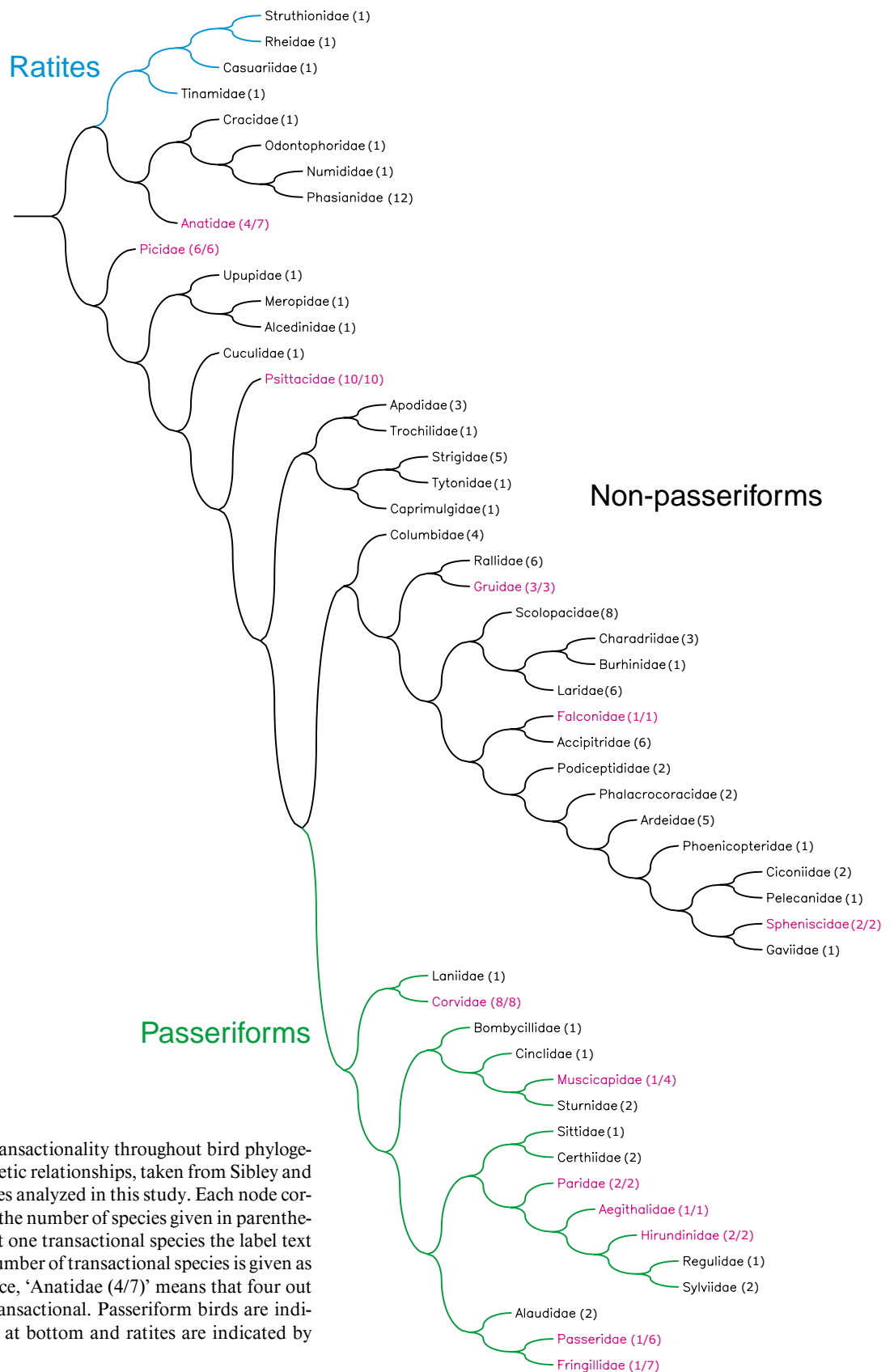


Fig. 2. The appearance of transactionality throughout bird phylogeny. This tree shows phylogenetic relationships, taken from Sibley and Ahlquist [1991] for the species analyzed in this study. Each node corresponds to one family, with the number of species given in parentheses. For families with at least one transactional species the label text is colored in magenta. The number of transactional species is given as a part of the total, for instance, ‘Anatidae (4/7)’ means that four out of the seven *Anatidae* are transactional. Passeriform birds are indicated by the green branches at bottom and ratites are indicated by blue branches at top.

Because telencephalic size co-varies with cognitive complexity in primates [Reader and Laland, 2002], we looked for quantifiable analogous parameters of bird behavior. As one measure, we assigned species to categories based on social interaction. We focused on the qualities of socially transferrable cognitive tasks, group size, and inter-individual interaction because they are relatively straightforward to observe. Other measures relating to cognitive complexity have previously been used, such as foraging and nesting innovations [Lefebvre et al., 1997, 1998; Nicolakakis and Lefebvre, 2000] and tool-making [Hunt et al., 2001; Weir et al., 2002]. These qualities are likely to share common neural substrates with social complexity. In primates, various measures of cognitive ability are strongly correlated with each other and with indices of cerebral cortical size [Reader and Laland, 2002]. Furthermore, group size has been used in primates as an indicator of social complexity [Dunbar, 1995]. We therefore considered social complexity as a rapid means of sorting species that does not require an exhaustive survey of known behaviors [Lefebvre et al., 1997, 1998, 2002; Nicolakakis and Lefebvre, 2000; Reader and Laland, 2002].

Transactional birds are found at locations throughout the bird phylogenetic tree (fig. 2), including both passeriforms (perching birds; green branches) and nonpasseriform birds (black branches). Transactionality can be a general family trait (for instance, Corvidae and Psittacidae) but often is not (for instance, Anatidae, Fringillidae, and Passeridae). Furthermore, transactionality is found in none of the ratites (blue branches, fig. 2), which are less derived and thus presumably more like ancestral birds. Taken together, these results suggest that transactional social complexity has arisen repeatedly and independently throughout bird evolution.

Social complexity corresponds strongly with F_{tel} . This relationship is apparent at the level of individual species (table 2). The largest values of F_{tel} are found in almost all transactional birds, including nine of the top ten. Of all the 42 transactional birds identified, 23 are in the top fifth of F_{tel} values. The exceptions are mostly owls. We therefore excluded owls from the data set as a case for separate consideration (see Discussion).

Sorting the remaining birds into categories of social structure revealed a strong correspondence between F_{tel} and the level of social complexity (fig. 3a). Progressively increasing ranges of F_{tel} were seen for solitary ($58.9 \pm 6.3\%$; mean \pm s.d., $n = 29$) and covey ($58.1 \pm 6.2\%$, $n = 43$) birds, colonial birds ($61.5 \pm 5.7\%$, $n = 34$), and transactional birds ($71.0 \pm 6.5\%$, $n = 42$; ANOVA: $p < 0.001$). Pairwise comparison showed significant differences (two-

tailed t test, $p < 0.02$) between all groupings except for solitary vs. covey birds ($p = 0.3$) and solitary vs. colonial birds ($p = 0.09$). The F_{tel} for non-transactional birds ($59.4 \pm 6.2\%$) differs from transactional birds by 1.3 standard deviations. Thus, increased degrees of social complexity are accompanied by increased relative volumes of the telencephalon.

Instead of calculating F_{tel} , previous investigators have compared species by calculating residuals, defined as deviations from an overall trend in an entire data set, relative to an external measure, usually body weight. To examine the use of residuals more carefully, we plotted telencephalic volume against body weight in log-log coordinates (fig. 1). The data were fitted moderately well by a straight line. This line was subtracted from the data, giving residual telencephalic sizes ranging from -0.54 to $+0.64 \log_{10}$ unit. These residual values were higher for transactional birds ($+0.23 \pm 0.21 \log_{10}$ unit, mean \pm SD, 42 birds) compared with non-transactional birds ($-0.09 \pm 0.20 \log_{10}$ unit, 112 birds, a difference of 1.1 standard deviations).

However, closer inspection of the raw telencephalic volume data revealed that residuals fell into multiple groups that were well fitted by lines of similar slope but differing intercept, a phenomenon known as 'grade shifting' [Gould, 1975; Wang et al., 2002]. Because of grade shifting, residual calculations are strongly dependent on the taxonomic level at which species are grouped for analysis. Dividing the data according to Portmann's original three groupings of Alectoromorphae (40 species), Pelargomorphae (28 species), and Coraciomorphae (64 species, excluding owls) separated the grades: within each of the resulting groups the correlations between log (telencephalic volume) and log (body weight) had much less unexplained variance (8.0, 10.7, and 9.4%) than the data set taken as a whole (20.0%). Residuals calculated using these groupings showed essentially overlapping ranges of values for transactional ($+0.07 \pm 0.14 \log_{10}$ unit) and non-transactional ($-0.03 \pm 0.15 \log_{10}$ unit) birds (a difference of 0.5 standard deviation). An intermediate result was obtained when the birds were divided into the groupings passeriforms/nonpasseriforms/ratites (transactional $+0.17 \pm 0.23 \log_{10}$ unit, non-transactional $-0.09 \pm 0.15 \log_{10}$ unit, a difference of 1.0 standard deviation; r_{tel} values given for individual species in table 2). In summary, the choice of which residual to use is not obvious, but F_{tel} exceeds all of them at extracting the differences between transactional and non-transactional birds. It also has the fundamental advantage of being simple and unambiguously defined.

Table 2. Classification of birds by behavioral traits. Birds are arranged in descending order of telencephalic volume fraction (F_{tel}). Telencephalic residuals (r_{tel}) were calculated as described in the text within the subdivisions passeriforms/nonpasseriforms/ratites

Latin name (Family) Common name	F_{tel}	r_{tel}	Social structure	Migration	Mating habits	Diet	Flight	Vocalizations
<i>Ara ararauna</i> (Psittacidae)								
Blue-and-yellow Macaw	0.823	0.6424	trans.	sedentary	monog.	herbiv.	aerial	learned
<i>Ara chloropterus</i> (Psittacidae)								
Red-and-green Macaw	0.817	0.6106	trans.	sedentary	monog.	herbiv.	aerial	learned
<i>Corvus corax</i> (Corvidae)								
Common Raven	0.806	0.0306	trans.	sedentary	monog.	omniv.	aerial	learned
<i>Psittacus erithacus</i> (Psittacidae)								
Grey Parrot	0.792	0.5069	trans.	sedentary	monog.	herbiv.	aerial	learned
<i>Cacatua sulphurea</i> (Psittacidae)								
Yellow-crested Cockatoo	0.790	0.4679	trans.	sedentary	monog.	herbiv.	aerial	learned
<i>Pyrrhonorax pyrrhonorax</i> (Corvidae)								
Red-billed Chough	0.781	0.0562	trans.	sedentary	monog.	omniv.	aerial	learned
<i>Dryocopus martius</i> (Picidae)								
Black Woodpecker	0.771	0.5301	trans.	sedentary	monog.	carniv.	aerial	non-learned
<i>Corvus frugilegus</i> (Corvidae)								
Rook	0.771	0.0658	trans.	migratory	monog.	omniv.	aerial	learned
<i>Athene noctua</i> (Strigidae)								
Little Owl	0.770	0.3854	solitary	sedentary	monog.	carniv.	aerial	non-learned
<i>Corvus corone</i> (Corvidae)								
Carrion Crow	0.767	0.0296	trans.	sedentary	monog.	omniv.	aerial	learned
<i>Bubo bubo</i> (Strigidae)								
Eurasian Eagle-owl	0.765	0.3324	solitary	sedentary	monog.	carniv.	aerial	non-learned
<i>Pica pica</i> (Corvidae)								
Black-billed Magpie	0.765	0.1453	trans.	sedentary	monog.	omniv.	aerial	learned
<i>Amazona versicolor</i> (Psittacidae)								
St. Lucia Parrot	0.762	0.4371	trans.	sedentary	monog.	herbiv.	aerial	learned
<i>Nymphicus hollandicus</i> (Psittacidae)								
Cockatiel	0.761	0.3804	trans.	nomadic	monog.	herbiv.	aerial	learned
<i>Strix aluco</i> (Strigidae)								
Tawny Owl	0.759	0.4559	solitary	sedentary	monog.	carniv.	aerial	non-learned
<i>Psittacula eupatria</i> (Psittacidae)								
Alexandrine Parakeet	0.755	0.5439	trans.	nomadic	monog.	herbiv.	aerial	learned
<i>Corvus monedula</i> (Corvidae)								
Eurasian Jackdaw	0.755	0.1025	trans.	migratory	monog.	omniv.	aerial	learned
<i>Tyto alba</i> (Tytonidae)								
Barn-owl	0.749	0.4086	solitary	sedentary	monog.	carniv.	aerial	non-learned
<i>Agapornis fisheri</i> (Psittacidae)								
Fischer's Lovebird	0.747	0.4548	trans.	sedentary	monog.	herbiv.	aerial	learned
<i>Asio otus</i> (Strigidae)								
Long-eared Owl	0.745	0.4050	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Picus canus</i> (Picidae)								
Grey-faced Woodpecker	0.742	0.3982	trans.	sedentary	monog.	carniv.	aerial	non-learned
<i>Pionus menstruus</i>* (Psittacidae)								
Blue-headed parrot	0.740	0.3050	trans.	nomadic	monog.	herbiv.	aerial	learned
<i>Alauda arvensis</i> (Alaudidae)								
Eurasian Skylark	0.735	0.0421	covey	migratory	monog.	omniv.	aerial	learned
<i>Picus viridis</i> (Picidae)								
Eurasian Green Woodpecker	0.734	0.3603	trans.	sedentary	monog.	carniv.	aerial	non-learned
<i>Dendrocopos major</i> (Picidae)								
Great Spotted Woodpecker	0.726	0.3969	trans.	sedentary	monog.	omniv.	aerial	non-learned
<i>Pelecanus onocrotalus</i> (Pelecanidae)								
Great White Pelican	0.725	0.1657	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Dendrocopos medius</i> (Picidae)								
Middle Spotted Woodpecker	0.723	0.3653	trans.	sedentary	monog.	carniv.	aerial	non-learned
<i>Aegypius monachus</i> (Accipitridae)								
Cinereous Vulture	0.723	0.0617	solitary	sedentary	monog.	carniv.	aerial	non-learned
<i>Parus caeruleus</i> (Paridae)								
Blue Tit	0.720	0.2281	trans.	sedentary	monog.	omniv.	aerial	learned
<i>Garrulus glandarius</i> (Corvidae)								
Eurasian Jay	0.710	0.0877	trans.	sedentary	monog.	omniv.	aerial	learned
<i>Grus antigone</i> (Gruidae)								
Sarus Crane	0.710	0.0106	trans.	sedentary	monog.	omniv.	aerial	non-learned

Table 2 (continued)

Latin name (Family) Common name	F_{tel}	r_{tel}	Social structure	Migration	Mating habits	Diet	Flight	Vocalizations
<i>Parus major</i> (Paridae) Great Tit	0.707	0.1864	trans.	sedentary	monog.	omniv.	aerial	learned
<i>Melopsittacus undulatus</i> ** (Psittacidae) Budgerigar	0.705	0.2075	trans.	nomadic	monog.	herbiv.	aerial	learned
<i>Leptoptilos crumeniferus</i> (Ciconiidae) Marabou Stork	0.704	0.2530	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Anser anser</i> (Anatidae) Greylag Goose	0.699	-0.0150	trans.	migratory	monog.	herbiv.	aerial	non-learned
<i>Loxia curvirostra</i> (Fringillidae) Red Crossbill	0.695	0.0988	trans.	sedentary	monog.	herbiv.	aerial	learned
<i>Somateria mollissima</i> (Anatidae) Common Eider	0.692	-0.0056	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Melanocorypha calandra</i> (Alaudidae) Calandra Lark	0.691	-0.0389	colonial	migratory	monog.	omniv.	aerial	learned
<i>Anas platyrhynchos</i> ** (Anatidae) Mallard	0.691	-0.0373	trans.	migratory	monog.	omniv.	aerial	non-learned
<i>Passer domesticus</i> (Passeridae) House sparrow	0.686	0.0402	colonial	sedentary	monog.	omniv.	aerial	learned
<i>Coccothraustes coccothraustes</i> (Fringillidae) Hawfinch	0.686	0.0539	covey	migratory	monog.	omniv.	aerial	learned
<i>Sitta europaea</i> (Sittidae) Wood Nuthatch	0.685	0.1460	solitary	sedentary	monog.	omniv.	aerial	learned
<i>Lanius collurio</i> (Laniidae) Red-backed Shrike	0.683	0.0548	solitary	migratory	monog.	carniv.	aerial	learned
<i>Sturnus vulgaris</i> (Sturnidae) Common Starling	0.683	-0.0529	colonial	migratory	polyg.	omniv.	aerial	learned
<i>Carduelis carduelis</i> (Fringillidae) European Goldfinch	0.680	0.0668	colonial	migratory	monog.	herbiv.	aerial	learned
<i>Balearica pavonina</i> (Gruidae) Black Crowned-crane	0.678	0.0770	trans.	sedentary	monog.	omniv.	aerial	non-learned
<i>Cygnus olor</i> (Anatidae) Mute Swan	0.677	-0.2123	trans.	migratory	monog.	omniv.	aerial	non-learned
<i>Carduelis cannabina</i> (Fringillidae) Eurasian Linnet	0.674	0.0010	colonial	migratory	monog.	herbiv.	aerial	learned
<i>Phoenicopterus ruber</i> (Phoenicopteridae) Greater Flamingo	0.667	-0.0229	colonial	migratory	monog.	omniv.	aerial	non-learned
<i>Upupa epops</i> (Upupidae) Eurasian Hoopoe	0.666	0.1219	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Spheniscus magellanicus</i> * (Spheniscidae) Magellanic Penguin	0.663	0.1145	trans.	migratory	monog.	carniv.	flightless	non-learned
<i>Aquila chrysaetos</i> (Accipitridae) Golden Eagle	0.661	0.0450	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Struthio camelus</i> (Struthionidae) Ostrich	0.659	0.0315	covey	nomadic	polyg.	herbiv.	flightless	non-learned
<i>Dromaius novaehollandiae</i> (Casuariidae) Emu	0.658	0.0330	covey	nomadic	polyg.	omniv.	flightless	non-learned
<i>Otus scops</i> (Strigidae) Eurasian Scops-owl	0.654	0.2253	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Anas penelope</i> (Anatidae) Eurasian Wigeon	0.654	-0.0685	covey	migratory	monog.	herbiv.	aerial	non-learned
<i>Limnodromus griseus</i> * (Scolopacidae) Short-billed dowitcher	0.654	-0.0684	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Spheniscus demersus</i> (Spheniscidae) Jackass Penguin	0.651	0.1112	trans.	sedentary	monog.	carniv.	flightless	non-learned
<i>Sturnus roseus</i> (Sturnidae) Rosy Starling	0.650	-0.0315	colonial	migratory	monog.	omniv.	aerial	learned
<i>Carduelis spinus</i> (Fringillidae) Eurasian Siskin	0.648	0.0704	colonial	migratory	monog.	herbiv.	aerial	learned
<i>Montifringilla nivalis</i> (Passeridae) White-winged Snowfinch	0.645	-0.0956	trans.	sedentary	monog.	omniv.	aerial	learned
<i>Turdus merula</i> (Muscicapidae) Eurasian Blackbird	0.642	-0.1338	trans.	migratory	monog.	omniv.	aerial	learned

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Table 2 (continued)

Latin name (Family) Common name	F_{rel}	r_{rel}	Social structure	Migration	Mating habits	Diet	Flight	Vocalizations
<i>Phalacrocorax carbo</i> (Phalacrocoracidae) Great Cormorant	0.642	-0.0036	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Taeniopygia guttata</i> * (Passeridae) Zebra finch	0.641	-0.2510	colonial	sedentary	monog.	herbiv.	aerial	learned
<i>Delichon urbica</i> (Hirundinidae) Northern House-martin	0.639	-0.1180	trans.	migratory	monog.	carniv.	aerial	learned
<i>Fringilla coelebs</i> (Fringillidae) Chaffinch	0.638	-0.0240	covey	migratory	monog.	omniv.	aerial	learned
<i>Porphyrio porphyrio</i> (Rallidae) Purple Swamphen	0.637	0.1158	covey	sedentary	monog.	omniv.	flightless	non-learned
<i>Serinus canaria</i> (Fringillidae) Island Canary	0.633	0.1014	colonial	sedentary	monog.	omniv.	aerial	learned
<i>Botaurus stellaris</i> (Ardeidae) Great Bittern	0.633	-0.0424	solitary	migratory	polyg.	carniv.	aerial	non-learned
<i>Buteo buteo</i> (Accipitridae) Common Buzzard	0.632	0.1826	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Regulus regulus</i> (Regulidae) Common Goldcrest	0.630	0.1317	covey	migratory	monog.	carniv.	aerial	learned
<i>Pandion haliaetus</i> (Accipitridae) Osprey	0.630	0.1554	covey	migratory	monog.	herbiv.	aerial	non-learned
<i>Haematopus ostralegus</i> (Charadriidae) Eurasian Oystercatcher	0.629	-0.0442	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Scolopax rusticola</i> (Scolopacidae) Eurasian Woodcock	0.628	-0.0374	solitary	migratory	polyg.	carniv.	aerial	non-learned
<i>Fulica atra</i> (Rallidae) Common Coot	0.628	-0.0248	colonial	migratory	monog.	omniv.	flightless	non-learned
<i>Ciconia ciconia</i> (Ciconiidae) White Stork	0.625	0.0298	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Cinclus cinclus</i> (Cinclidae) White-Throated Dipper	0.622	-0.0858	solitary	migratory	monog.	carniv.	aerial	learned
<i>Bombycilla garrulus</i> (Bombycillidae) Bohemian Waxwing	0.622	-0.1640	colonial	migratory	monog.	omniv.	aerial	learned
<i>Hirundo rustica</i> (Hirundinidae) Barn Swallow	0.621	-0.1064	trans.	migratory	monog.	carniv.	aerial	learned
<i>Ardea cinerea</i> ** (Ardeidae) Grey Heron	0.620	-0.0046	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Aegithalos caudatus</i> (Aegithalidae) Long-tailed Tit	0.620	0.1194	trans.	sedentary	monog.	carniv.	aerial	learned
<i>Falco tinnunculus</i> (Falconidae) Common Kestrel	0.620	0.1708	trans.	migratory	monog.	carniv.	aerial	non-learned
<i>Grus virgo</i> (Gruidae) Demoiselle Crane	0.619	0.0134	trans.	migratory	monog.	omniv.	aerial	non-learned
<i>Certhia familiaris</i> (Certhiidae) Eurasian Tree-creeper	0.618	0.0584	solitary	migratory	monog.	omniv.	aerial	learned
<i>Larus marinus</i> (Laridae) Great Black-backed Gull	0.616	-0.0504	covey	migratory	monog.	omniv.	aerial	non-learned
<i>Jynx torquilla</i> (Picidae) Eurasian Wryneck	0.615	0.0096	trans.	migratory	monog.	carniv.	aerial	non-learned
<i>Anas crecca</i> (Anatidae) Common Teal	0.614	-0.0189	covey	migratory	monog.	omniv.	aerial	non-learned
<i>Turdus philomelos</i> (Muscicapidae) Song Thrush	0.614	-0.1274	covey	migratory	monog.	omniv.	aerial	learned
<i>Phalacrocorax auritus</i> * (Phalacrocoracidae) Double-crested cormorant	0.608	-0.0683	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Prunella modularis</i> (Passeridae) Hedge Accentor	0.606	-0.0045	solitary	migratory	monog.	omniv.	aerial	learned
<i>Troglodytes troglodytes</i> (Certhiidae/Troglodytidae) Winter Wren	0.605	0.0715	solitary	migratory	monog.	carniv.	aerial	learned
<i>Oriolus oriolus</i> (Corvidae) Eurasian Golden Oriole	0.605	-0.1468	trans.	migratory	monog.	omniv.	aerial	learned
<i>Egretta alba</i> (Ardeidae) Great White Egret	0.602	-0.0854	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Sylvia borin</i> (Sylviidae) Garden Warbler	0.602	-0.1029	covey	migratory	monog.	omniv.	aerial	learned

Table 2 (continued)

Latin name (Family) Common name	F_{tel}	r_{tel}	Social structure	Migration	Mating habits	Diet	Flight	Vocalizations
<i>Accipiter gentilis</i> (Accipitridae) Northern Goshawk	0.602	0.0487	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Rallus aquaticus</i> (Rallidae) Water Rail	0.601	0.0176	solitary	migratory	monog.	omniv.	aerial	non-learned
<i>Pavo cristatus</i> ** (Phasianidae) Indian peafowl	0.599	-0.2962	covey	sedentary	polyg.	omniv.	flightless	non-learned
<i>Motacilla alba</i> (Passeridae) White Wagtail	0.598	-0.1420	covey	migratory	monog.	carniv.	aerial	learned
<i>Numenius arquata</i> (Scolopacidae) Eurasian Curlew	0.597	-0.0832	colonial	migratory	monog.	omniv.	aerial	non-learned
<i>Egretta garzetta</i> (Ardeidae) Little Egret	0.597	-0.0832	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Rhynchotus rufescens</i> * (Tinamidae) Red-winged tinamou	0.594	0.0166	covey	sedentary	polyg.	omniv.	flightless	non-learned
<i>Anthus pratensis</i> (Passeridae) Meadow Pipit	0.593	-0.0910	colonial	migratory	monog.	carniv.	aerial	learned
<i>Muscicapa striata</i> (Muscicapidae) Spotted Flycatcher	0.593	-0.1210	solitary	migratory	monog.	omniv.	aerial	learned
<i>Burhinus oedicephalus</i> (Burhinidae) Eurasian Thick-knee	0.588	-0.0458	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Ixobrychus minutus</i> (Ardeidae) Little Bittern	0.588	-0.0651	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Lophura nycthemera</i> (Phasianidae) Silver Pheasant	0.587	-0.2127	covey	sedentary	polyg.	omniv.	flightless	non-learned
<i>Gallinula chloropus</i> (Rallidae) Common Moorhen	0.585	-0.1052	covey	migratory	monog.	omniv.	aerial	non-learned
<i>Acrocephalus scirpaceus</i> (Sylviidae) Eurasian Reed-warbler	0.585	-0.0944	solitary	migratory	monog.	carniv.	aerial	learned
<i>Phasianus colchicus</i> ** (Phasianidae) Common pheasant	0.584	-0.2853	covey	sedentary	polyg.	omniv.	flightless	non-learned
<i>Philomachus pugnax</i> (Scolopacidae) Ruff	0.581	-0.1376	colonial	migratory	polyg.	omniv.	aerial	non-learned
<i>Alectoris chukar</i> * (Phasianidae) Chukar	0.578	-0.2683	covey	sedentary	polyg.	omniv.	flightless	non-learned
<i>Mergus serrator</i> (Anatidae) Red-breasted Merganser	0.578	-0.0964	trans.	migratory	monog.	carniv.	aerial	non-learned
<i>Gallinago gallinago</i> (Scolopacidae) Common Snipe	0.578	-0.0934	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Larus argentatus</i> (Laridae) Herring Gull	0.577	-0.1784	colonial	migratory	monog.	omniv.	aerial	non-learned
<i>Crex crex</i> (Rallidae) Corn Crane	0.575	-0.1084	solitary	migratory	polyg.	omniv.	aerial	non-learned
<i>Fratercula arctica</i> (Laridae) Atlantic Puffin	0.572	0.1186	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Rhea americana</i> * (Rheidae) Greater Rhea	0.568	-0.0811	covey	sedentary	polyg.	omniv.	flightless	non-learned
<i>Goura cristata</i> (Columbidae) Western crowned-pigeon	0.566	-0.2246	covey	sedentary	monog.	omniv.	aerial	non-learned
<i>Podiceps cristatus</i> (Podicipedidae) Great Crested Grebe	0.564	-0.2757	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Cuculus canorus</i> (Cuculidae) Common Cuckoo	0.564	-0.0404	solitary	migratory	polyg.	carniv.	aerial	non-learned
<i>Numida meleagris</i> * (Numididae) Helmeted guineafowl	0.564	-0.3758	covey	sedentary	monog.	omniv.	flightless	non-learned
<i>Erithacus rubecula</i> (Muscicapidae) European Robin	0.564	-0.0567	solitary	migratory	monog.	omniv.	aerial	learned
<i>Tachymarptis melba</i> (Apodidae) Alpine Swift	0.560	-0.1354	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Apus apus</i> (Apodidae) Common Swift	0.557	-0.1230	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Alcedo atthis</i> (Alcedinidae) Common Kingfisher	0.556	0.0347	solitary	migratory	monog.	carniv.	aerial	non-learned

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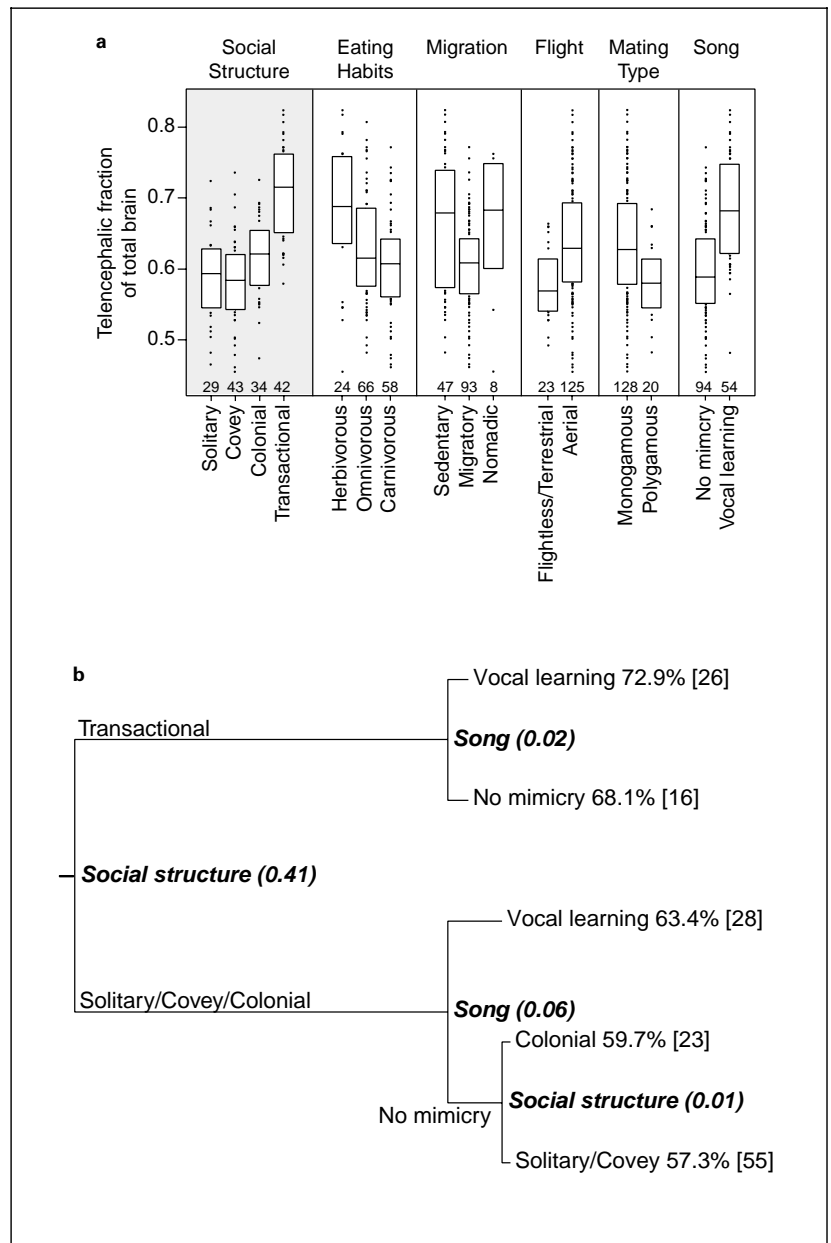
Table 2 (continued)

Latin name (Family) Common name	F_{tel}	r_{tel}	Social structure	Migration	Mating habits	Diet	Flight	Vocalizations
<i>Ortalis canicollis</i> * (Cracidae) Chaco chachalaca	0.555	-0.2370	covey	sedentary	monog.	omniv.	flightless	non-learned
<i>Tachybaptus ruficollis</i> (Podicipedidae) Little Grebe	0.554	-0.1084	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Columba livia</i> ** (Columbidae) Rock Pigeon	0.552	-0.1549	colonial	sedentary	monog.	herbiv.	aerial	non-learned
<i>Larus ridibundus</i> (Laridae) Common Black-headed Gull	0.551	-0.0190	covey	migratory	monog.	omniv.	aerial	non-learned
<i>Vanellus vanellus</i> (Charadriidae) Northern Lapwing	0.551	-0.0627	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Calidris minutilla</i> * (Scolopacidae) Least sandpiper	0.549	-0.2104	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Columba palumbus</i> (Columbidae) Common Woodpigeon	0.545	-0.2531	colonial	migratory	monog.	herbiv.	aerial	non-learned
<i>Chrysolophus pictus</i> ** (Phasianidae) Golden pheasant	0.545	-0.1721	solitary	sedentary	polyg.	omniv.	flightless	non-learned
<i>Tetrao urogallus</i> (Phasianidae) Western Capercaillie	0.544	-0.3749	covey	sedentary	polyg.	herbiv.	flightless	non-learned
<i>Coturnix chinensis</i> (Phasianidae) Blue-breasted Quail	0.541	-0.2498	covey	nomadic	monog.	omniv.	flightless	non-learned
<i>Colinus virginianus</i> * (Odontophoridae) Northern bobwhite	0.538	-0.4100	covey	sedentary	monog.	omniv.	flightless	non-learned
<i>Lymnocyptes minimus</i> (Scolopacidae) Jack Snipe	0.537	-0.1181	solitary	migratory	monog.	omniv.	aerial	non-learned
<i>Gallus gallus</i> ** (Phasianidae) Red Junglefowl	0.534	-0.2701	covey	sedentary	polyg.	omniv.	flightless	non-learned
<i>Porzana porzana</i> (Rallidae) Spotted Crane	0.533	-0.1061	solitary	migratory	monog.	omniv.	aerial	non-learned
<i>Perdix perdix</i> (Phasianidae) Grey partridge	0.527	-0.3524	covey	sedentary	monog.	omniv.	flightless	non-learned
<i>Tetrao tetrix</i> (Phasianidae) Black Grouse	0.527	-0.3387	covey	migratory	polyg.	herbiv.	flightless	non-learned
<i>Sterna hirundo</i> ** (Laridae) Common tern	0.523	-0.1134	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Accipiter nisus</i> (Accipitridae) Eurasian Sparrowhawk	0.517	-0.0177	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Tringa hypoleucos</i> (Scolopacidae) Common Sandpiper	0.511	-0.1542	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Charadrius vociferus</i> * (Charadriidae) Killdeer	0.503	-0.2384	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Meleagris gallopavo</i> * (Phasianidae) Wild turkey	0.502	-0.5253	covey	sedentary	polyg.	omniv.	flightless	non-learned
<i>Gavia stellata</i> (Gaviidae) Red-throated Loon	0.501	-0.2533	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Coturnix coturnix</i> ** (Phasianidae) Common quail	0.491	-0.3096	covey	migratory	monog.	omniv.	flightless	non-learned
<i>Chlorostilbon mellisugus</i> * (Trochilidae) Blue-tailed emerald	0.481	-0.3852	solitary	sedentary	polyg.	omniv.	aerial	learned
<i>Chaetura pelagica</i> * (Apodidae) Chimney swift	0.478	-0.3250	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Merops apiaster</i> (Meropidae) European Bee-eater	0.473	-0.1991	colonial	migratory	monog.	carniv.	aerial	non-learned
<i>Caprimulgus europaeus</i> (Caprimulgidae) Eurasian Nightjar	0.464	-0.3245	solitary	migratory	monog.	carniv.	aerial	non-learned
<i>Sterna albifrons</i> (Laridae) Little Tern	0.460	-0.0639	covey	migratory	monog.	carniv.	aerial	non-learned
<i>Geopelia cuneata</i> (Columbidae) Diamond Dove	0.454	-0.2859	covey	nomadic	monog.	herbiv.	aerial	non-learned

All species are taken from Portmann [1947a] alone except for those from * Boire and Baron [1994] or ** appearing in both references.

Social structures: transactional (trans.), colonial, covey and solitary. Migration: sedentary, migratory or nomadic. Mating habits: monogamous (monog.) or polygamous (polyg.). Diet: herbivorous (herbiv.), omnivorous (omniv.) or carnivorous (carniv.). Flight: aerial or flightless. Vocalizations: learned or non-learned.

Fig. 3. Analysis of telencephalic volume fraction and social complexity in birds. **(a)** Relationships between avian behavioral characteristics and telencephalic volume fraction (F_{tel}). Boxplots of F_{tel} values indicate median (midline), 25% and 75% quartiles (box edges), and values outside the middle two quartiles (dots). The numbers below the boxes indicate the number of species in each category. **(b)** Regression tree showing optimal separation of F_{tel} . For partitioning, all six behavioral characteristics from **(a)** were used. The regression tree gave a major split by social structure accounting for the predominant component of the variation in F_{tel} . **Bold** labels indicate the trait by which a group was split and the value of the fraction of total deviance in F_{tel} accounted for by the node; the branch length is also proportional to this fraction. For each subgroup the labels indicate the last category of subdivision, the mean F_{tel} and the number of species in that subgroup. The minimum deviance reduction [Venables and Ripley, 1994] was set at 0.002 of total deviance and the minimum subgroup size was set at 15 species.



To test for possible links between F_{tel} and behavioral traits not explicitly cognitive in nature, we also divided the species in five other ways (fig. 3a): (1) Eating habits; into herbivores (diet over 90% plants and seeds), carnivores (diet over 90% meat, including mammals, birds, fish, marine invertebrates, and insects), and omnivores (all remaining species). (2) Migration pattern; into sedentary (permanent residents), migratory (seasonal residents), and nomadic (long-distance travelers that establish new home territories) [Faaborg, 1988]. (3) Flight

capacity; into flightless/terrestrial (no flight, or heavy flight for less than 200 meters) and aerial. (4) Mating type; into monogamous (including long-term pair bonding, serial monogamy, and pair bonding with promiscuity) or polygamous [including polygyny, polyandry, polygynandry, and leks; Faaborg, 1988; del Hoyo et al., 1992]. (5) Learned vocalization; no mimicry (no known capacity for learned vocalizations) or vocal learning (capable of intraspecies or interspecies learned vocalizations). The vocal learners were Psittacidae (parrots), Trochilidae

(hummingbirds), and oscine songbirds [all the passeriforms in the data set; Kroodsma et al., 1982].

One difficulty in quantitatively determining the contributions of these traits to F_{tel} is the possibility that memberships in different categories may co-vary with one another. This problem can be addressed with regression tree analysis [Venables and Ripley, 1994], a form of multivariate analysis that is particularly appropriate for small data sets.

For this data set, the largest contributions to variation in F_{tel} came from social structure (fig. 3b). The first branch point separated transactional birds into a group with higher F_{tel} (average difference, 12%) than colonial, covey and solitary birds. This split accounted for 0.41 of the total deviance in F_{tel} . Smaller amounts of variation could be accounted for by splitting each of these groups by the ability to learn vocalizations (0.06 deviance reduction from splitting transactional birds, 0.02 deviance reduction from splitting non-transactional birds). In both cases vocal learners had F_{tel} values approximately 5% larger than their non-learning counterparts, consistent with the observation that the song system occupies less than a tenth of the telencephalic volume [DeVoogd et al., 1993]. Finally, non-transactional, non-vocal learning birds could be split into groups of solitary/covey and colonial birds for a final reduction of 0.01 of deviance. Therefore, a considerable fraction (0.42) of the variation in F_{tel} can be accounted for by the single general factor of social complexity as defined by our groupings.

We searched for correlates of behavioral categories in other patterns of brain architecture. Within the telencephalon, the neostriatum/hyperstriatum ventrale complex has been observed to be a good predictor of feeding innovation, a measure of cognitive complexity [Timmermans et al., 2000]. Examination of detailed volumetric data of the species listed in Boire and Baron [Boire, 1989] showed that these components occupied nearly constant fractions of telencephalon (neostriatum $41.1 \pm 0.8\%$, hyperstriatum ventrale $16.5 \pm 1.7\%$; mean \pm SD, 28 species). Thus for available data the internal cerebrotype of the telencephalon varies little, and examination of its components did not add additional information. We also examined the rest of the brain. Analysis of non-telencephalic volume fractions revealed no significant correlation between behavioral groupings and any single brain component (ANOVA and t test; data not shown). In search of more subtle relationships we also performed multidimensional scaling on the cerebrotypes; the resulting relational maps did not show strong clustering by phylogenetic grouping or behavioral traits (not shown). Thus in our analysis the

most prominent structural correlate of behavioral traits is the telencephalic volume fraction F_{tel} , and subdividing this structure does not provide additional information.

F_{tel} might vary not only according to behavioral needs but also by random drift during evolution. To test this idea species were arranged according to a published phylogeny [Sibley and Ahlquist, 1991]. At each node the absolute value of the difference in DNA hybridization temperature [Sibley and Ahlquist, 1991] was calculated as a measure of evolutionary distance. This quantity and the absolute values of differences in F_{tel} were only weakly correlated (rank correlation $r_S = +0.27$; $p = 0.06$). Thus variation in DNA hybridization can account for just $0.27^2 = 0.07$ of the variation in F_{tel} , showing that variations in telencephalic size cannot be explained by random evolutionary divergence alone [Harvey and Pagel, 1991].

Discussion

The proposal that intelligence and social complexity are linked dates back to the writings of Charles Darwin [Darwin, 1871]. Since then, anatomical analysis has suggested a central role for the cerebral cortex in the rise of social or 'Machiavellian' intelligence in primates [Whiten and Byrne, 1988; Dunbar, 1995; Barton and Dunbar, 1997]. Our recent results show that in birds as well, the degree of social complexity correlates strongly with relative telencephalic size. The telencephalon therefore plays a central role in guiding social interactions in two highly divergent vertebrate taxa.

Variation in the architecture of bird brains has been considered previously by Portmann [1946, 1947a, b]. He found that taxa with relatively large adult brains (scaled to body size) tend at hatching to be altricial, reaching physical independence late and thus requiring intensive parental care. The adult brains of altricial birds are also those with large hemispheres; that is, with a large F_{tel} . Conversely, precocial birds tend to have smaller adult brains and smaller values of F_{tel} . In conjunction with our results, this suggests that in birds accelerated telencephalic growth, altriciality, and social complexity are closely linked traits.

Our findings support the view that a major functional role of the vertebrate telencephalon is the regulation of social interaction. They also suggest that a layered cerebral cortex is not necessary for such telencephalic functions. This may be true for other cognitive skills besides social intelligence: a number of the birds described in our study as 'transactional' are known to have reasoning abilities as demonstrated by tool use or advanced communica-

tion. For instance, crows can modify objects into tools without prior experience [Weir et al., 2002] and can manufacture functionally lateralized (“handed”) tools using skilled, multiple-step crafting procedures [Hunt, 2000; Hunt et al., 2001]. Proto-tool use, defined as the use of a fixed object to assist in performing a task, has also been observed in a number of birds [Lefebvre et al., 2002] including woodpeckers. Parrots are capable of impressive feats of communication and reasoning and can master concepts such as number, relative comparison, and object permanence [Pepperberg and Brezinsky, 1991; Pepperberg, 2002]. These birds have large relative telencephalic volume, and their cognitive capabilities include planning, reasoning, and prediction functions generally considered the province of the mammalian cerebral cortex. These functions may thus be a general property of the vertebrate telencephalon.

Although the relationship between social complexity and telencephalic size is strong, two exceptions exist: woodpeckers and owls. Not all woodpeckers are reported to be transactional, despite their large telencephalons. Acorn woodpeckers communally create, defend, and maintain massive granaries consisting of tens of thousands of food storage sites. The great spotted woodpecker ($F_{tel} = 0.726$) has been observed in the wild to peck on a public-address system to amplify its sounds specifically in the direction of a conspecific, and in the laboratory is capable of cognitive tasks of a complexity matching that found in crows and parrots [del Hoyo et al., 1992]. On the other hand, many woodpeckers are thought to be aggressive and solitary. These varied observations indicate either that not all woodpeckers are transactional or that these birds present special difficulties for behavioral observation.

The one unequivocal exception to the rule associating a high F_{tel} with social complexity is owls. Owls ($F_{tel} = 65\text{--}77\%$) are solitary, and the behavioral literature on them is notably lacking in reports of social cooperation, tool use, or other evidence of cognitive complexity. Understanding the functional role of the owl’s forebrain in behavioral complexity must await improved observations. One topic of particular interest is the internal cerebrotypes of the owl telencephalon, which could differ from other birds, especially considering the specialized sound-localizing abilities of owls. Generally, it remains to be seen whether the advanced cognitive function imputed to owls by folklore has any observable ethological correlate.

Dinosaurs

Our findings for mammals [Clark et al., 2001] and birds indicate that the telencephalon’s role in guiding social

interactions has either evolved independently multiple times or, more likely, has persisted throughout hundreds of millions of years of evolution. In either case, because we found such a strong relationship between forebrain size and sociality in birds, we became motivated to examine their predecessors, the dinosaurs. This case is of particular interest because behavioral data for these animals is speculative, based on fossil footprints or physical features [Hopson, 1977]. Thus brain structure may provide a major source of indirect information [Edinger, 1961].

We applied our findings in living birds to an extinct bird, *Archaeopteryx*. Extrapolation from living birds is a putative source of limits on the degree of social complexity of their extinct predecessors. Although until now published descriptions of fossil braincases [Molnar, 1985; Wittmer, 1990; Chatterjee, 1991; Elzanowski, 1991; Elzanowski and Galton, 1991; Currie and Zhao, 1993] have only rarely included volume estimates of divisions of the brain, our work indicates that such measurements may be of interest.

Dinosaurs (Saurischia and Ornithischia) arose in the late Triassic era approximately 230 million years ago. Until their extinction approximately 65 million years ago, along with other reptiles (Pterosauria and Crocodylia) they were the dominant terrestrial vertebrates [Hopson, 1977; Sereno, 1999]. They spanned a large range of body sizes, from 45 kg to nearly 100,000 kg; the lower end of this range overlaps with the upper ranges of living reptiles and birds [Hopson, 1977]. Approximately 150 million years ago, during the Late Jurassic, they gave rise to an ancient bird, *Archaeopteryx*.

Some dinosaur skulls have been preserved with sufficient integrity that endocasts reveal the size and external form of the brain [Edinger, 1961, 1964]. The general form of dinosaur brains is reptilian [Jerison, 1969; Hopson, 1977; Larsson et al., 2000]. For instance, the features of *Allosaurus* brains are very similar to those of modern crocodylians [Rogers, 1998]. The sizes of dinosaur brains are also consistent with predictions made by extrapolating values from modern reptiles along allometric straight-line fits [Jerison, 1969; Hopson, 1977]. However, an exception to these patterns in shape and size is found in the case of *Archaeopteryx* [Edinger, 1926; Hopson, 1977], whose brain is more like a modern bird’s in having more prominent hemispheres and following the external contours of the skull. *Archaeopteryx*’s body was an estimated 300–500 g [Jerison, 1969; Hopson, 1977] and its brain was approximately 1.1 cm³ [Larsson et al., 2000], placing it much closer to the brain-body allometric relationship for living birds than for living reptiles.

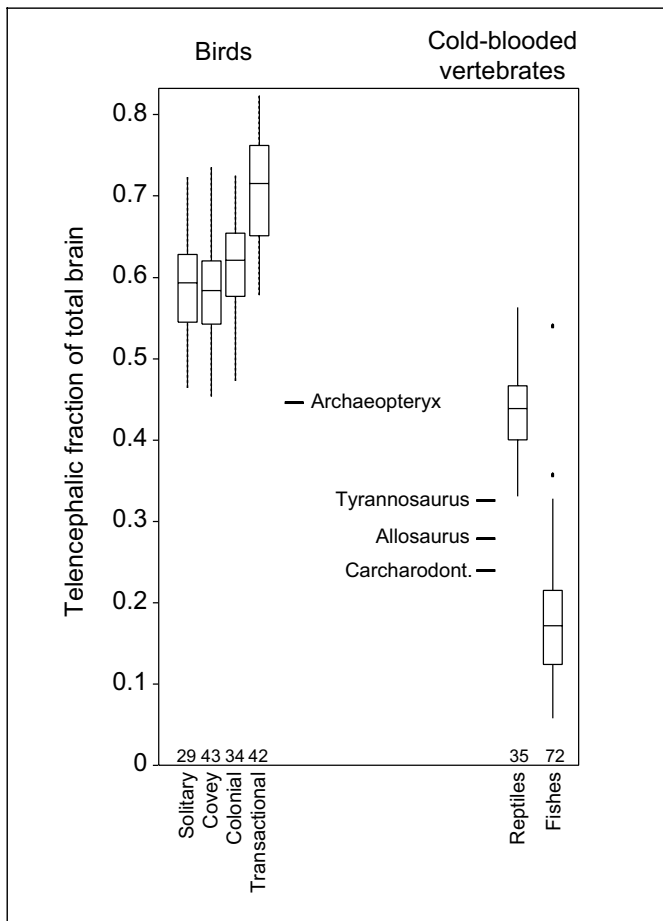


Fig. 4. Comparison of dinosaur telencephalic volume fractions with living forms. Dinosaur telencephalic volume fractions F_{tel} were estimated from CT scan reconstructions of endocasts of four dinosaurs [Larsson et al., 2000]. Boxplots are calculated from bird data as cited in the text, from 35 reptile species in Platel [1976], and from 70 fish species in Ridet and Bauchot [1990]. The outlier points for the fishes indicate values more than 1.5 box length above the 75% quartile.

Because impressions found in endocasts can reveal surface features such as the boundaries between brain components, gross aspects of dinosaur brain architecture can be compared with living forms (fig. 4). One feature that can be distinguished is the telencephalon [Rogers, 1998; Larsson et al., 2000]. This allows estimation of F_{tel} . The telencephalons of theropods have been measured using three-dimensional reconstruction by CT scanning of endocasts [Rogers, 1998; Larsson et al., 2000]. This method has found F_{tel} values of 24% (*Carcharodontosaurus*), 28% (*Allosaurus*), and 33% [*Tyrannosaurus*; Larsson et al., 2000]. These values are at or below the range of living reptiles [33–56%; Platel, 1976] and considerably

smaller than any bird. In contrast, an *Archaeopteryx* endocast shows a value for F_{tel} of 45%. This value is within the range of solitary and covey birds. In particular, the brain proportions of *Archaeopteryx* are similar to diamond doves and domesticated chickens, two covey birds which have the smallest F_{tel} (45 and 44%, respectively) of all birds considered here. Extrapolation from the known behavior and brain structure of living forms suggests that brains of dinosaurs (and thus their social complexity and perhaps other cognitive traits) were comparable to those of reptiles or fishes living today, and that *Archaeopteryx* is likely to have had a social complexity comparable to that of modern barnyard chickens.

Future Directions

Quantitative approaches to neuroanatomy and behavior can be improved in a number of ways. From an ethological standpoint, it would be useful to arrive at a measure of behavioral complexity that can be applied across species [Bullock, 1993]. An ideal solution to this problem would allow comparisons not only within large clades (e.g. birds, mammals) but also across all animals. However, even though problem-solving ability and social complexity have been observed in animals as divergent as crows, octopuses, dolphins, and humans, comparing them with each other is at present quite difficult.

Another unresolved issue is the detailed functional interpretation of volume fraction. In other words, what is the relationship between a structure's relative or absolute size and its functional role in the entire nervous system? Underlying the simple measures of macroscopic volume is a wide array of changes that also vary systematically across species [Harrison et al., 2002]. For instance, the cellular components of cerebral cortex change in number [Changizi, 2001; Elston et al., 2001], size [Elston et al., 2001] and connectivity [Braitenberg, 2001]; the relationship between these parameters to function is unknown. With sufficient understanding of the underlying cellular and network processes, it may be possible to rationalize size in terms of neural processing.

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