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Is there a relationship between forebrain size and group size in birds?

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ABSTRACT

The social complexity hypothesis of brain size evolution posits that demands from group living can favour an enlargement in brain size to allow individuals to process the greater amount of social information generated by group members more efficiently. We tested the hypothesis in birds using estimates of forebrain size from three different data sets. Phylogenetically corrected analyses indicated a lack of relationship between forebrain size and two indices of social complexity, namely mean or maximum flock size in the non-breeding season. Forebrain size was also unrelated to the propensity to flock. In contrast to primates, where the social complexity hypothesis was first proposed, it is conceivable that in birds social demands in the non-breeding season may be insufficient to drive brain size evolution. Future research could focus on the possibility that more specific areas of the avian brain are associated with group size and could be extended to cooperative breeding species that forage in more complex groups over much of the year.

Keywords: birds, flock size, forebrain size, phylogenetic analysis, social complexity hypothesis.

INTRODUCTION

Living in groups has been suggested to be cognitively demanding (Kummer *et al.*, 1997). Interacting successfully with other group members requires information about various factors, including identity, age, sex, dominance rank, position and competitive ability. This information needs to be processed efficiently by individuals to increase the fitness benefits of group living. Consequently, animals with such degrees of social interactions are expected to show increases in cognitive abilities and underlying neural structures; the so-called social complexity hypothesis of brain size evolution (Barton, 1996).

The extent to which cognitive skills differ between species has been tested primarily in mammals. For instance, primates living in long-lasting social groups show more developed cognitive abilities (namely, ordinal positioning and transitive inference) in relation to species that live in aggregations with little social structure (e.g. D'Amato and Columbo, 1990;

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Harris and McGonigle, 1994; Chen *et al.*, 1997). Moreover, enlarged brain size in some mammalian species has been associated with increases in group size (Dunbar, 1998; Barton, 2000), on the basis that relatively larger brains allow individuals to operate more successfully in larger groups by facilitating the ease with which increased social information is processed. Nevertheless, it is not clear to what extent the relationship between brain size and group size is empirically robust. For instance, in primates, the relationship appears stronger in some tribes than others (Dunbar, 1998). In addition, it remains to be seen how the relationship will hold when more data on brain size in mostly solitary species, such as the orangutan (*Pongo pygmaeus*), become available. Different scaling methods for comparative tests of the social complexity hypothesis in primates have also produced different results (Deaner *et al.*, 2000). More tests are therefore needed to provide empirical support for the hypothesis.

The social complexity hypothesis need not be limited to mammalian taxa. Indeed, if living in groups is cognitively demanding, enhanced cognitive abilities and more developed neural structures should be found in other social vertebrate taxa (Holekamp *et al.*, 1990; Balda *et al.*, 1997). For instance, the pinyon jay (*Gymnorhinus cyanocephalus*), a highly social bird species, learned to track dyadic relationships more rapidly and showed a more accurate mechanism of transitive inference than the closely related, less social western scrub jay (*Aphelocoma californica*) (Bond *et al.*, 2003). As in mammals, the avian brain possesses areas devoted to multimodal integration capacities (Rehkämper and Zilles, 1991; Emery and Clayton, 2004). In fact, certain avian brain structures, including the forebrain, which is the avian equivalent of the mammalian neocortex, have been shown to be associated with complex foraging behaviours. For instance, the use of innovative foraging strategies was correlated to forebrain size (Lefebvre *et al.*, 1997) and more specifically to multimodal integration areas in the avian brain (Timmermans *et al.*, 2000). Birds also show an impressive degree of enhanced cognitive skills, such as tool use (Lefebvre *et al.*, 2002; Weir *et al.*, 2002), relative comparison and object permanence (Pepperberg, 2002).

Therefore, we believe that birds are interesting models to test the social complexity hypothesis. A thorough test of this hypothesis requires: (a) estimates of forebrain size from different sources; (b) objective indices of social complexity; (c) an extensive literature search to assess the value of these indices; and (d) a control for phylogenetic effects that could bias the relationships. Here, we meet all these requirements and present a test of the social complexity hypothesis during the non-breeding season, when most social birds form flocks (Beauchamp, 2002a), evaluating how three different objective indices of social complexity – namely, mean flock size, maximum flock size and the occurrence of flocking – could have affected changes in the size of the avian forebrain.

METHODS

Forebrain size estimates

We used three different data sets involving independent measurements of forebrain size. Some species occurred in more than one data set. The largest (Appendix A)* contained data on forebrain size and consisted of 140 European species, including some exotic captive species (Portmann, 1947). The second (Appendix B) contained data on forebrain size and

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* The appendices to this paper can be accessed online at www.evolutionary-ecology.com

hippocampus size and consisted of 55 mostly American species, including nine that overlapped with the first data set. The third (Appendix C) contained data on forebrain size and other brain structures and consisted of 32 species, half of which overlapped with the first data set (Timmermans *et al.*, 2000). Body mass of the measured birds was taken from cited references or obtained by request from the authors.

Flock size estimates

We thoroughly searched different literature sources for evidence of flocking in each species. Flocking behaviour was assessed during the non-breeding season to avoid potential conflicts with parental duties. We used three different estimates of flocking behaviour: mean flock size, maximum flock size and flocking propensity. Mean and maximum flock size represented quantitative estimates of sociality that should complement each other, as several references only provided one or the other but not always both. Flocks could include individuals from only one species or from several different species. For some species, mean and/or maximum flock size was available for the two types of flocks. In these cases, we used estimates of sociality from the most typical flock arrangement.

Flocking propensity represented a qualitative assessment of social complexity, since quantitative estimates were not always available. Each species was classified as solitary or gregarious based on the most common flocking arrangement. Gregarious species foraged most commonly in flocks including more than two birds.

Data analysis

Estimates of forebrain size, body mass, mean and maximum flock size were $\log_{10}$-transformed before analysis. To test the predicted relationship between forebrain size and mean or maximum flock size, we first used non-phylogenetically corrected regression models based on the raw data. In these models, we regressed residual values of forebrain size, which we obtained from a log–log linear regression of forebrain size on body mass, on our estimates of mean or maximum flock size.

For the phylogenetically corrected analysis, we used regression models passing through the origin with body mass as a cofactor. The phylogenetically corrected regressions proceeded with independent contrasts of the above variables to partial out the potential effect of common ancestry (Harvey and Pagel, 1991). We used the CAIC program to calculate independent contrasts, ignoring branch lengths throughout (Purvis and Rambaut, 1995). For each data set, the program calculated differences between our different measurements at each node of a phylogenetic tree derived mostly from molecular sources:

- Tree for data set A: Sibley and Ahlquist (1990), Griffiths (1994), Badyaev (1997), Livezey (1997, 1998), Arnaiz-Villena *et al.* (1998, 2001), Groth (1998), McCraken and Sheldon (1998), Miyaki *et al.* (1998), Cibois and Pasquet (1999), Johnson and Sorenson (1999), Kimball *et al.* (1999), Voelker (1999), Wink and Heidrich (1999), Crochet *et al.* (2000), Kryukov and Odati (2000), van Tuinen *et al.* (2000, 2001), Allende *et al.* (2001), Johnson (2001), Johnson *et al.* (2001), Barker *et al.* (2002), Yuri and Mindell (2002).
- Tree for data set B: Sibley and Ahlquist (1990), Kvist *et al.* (1996), Slikas *et al.* (1996), de los Monteros and Cracraft (1997), Groth (1998), Patten and Fugate (1998), Cibois and

Pasquet (1999), Lanyon and Omland (1999), Lovette and Bermingham (1999), Klicka *et al.* (2000), Kryukov and Odati (2000), Barker *et al.* (2002), Yuri and Mindell (2002).

- Tree for data set C: Kimball *et al.* (1999), Armstrong *et al.* (2001), van Tuinen *et al.* (2001), Barker *et al.* (2002).

Inspection of residuals from the above phylogenetically corrected regressions revealed the presence of extreme outliers in data set B. The outliers all originated from one study (Healy and Krebs, 1992). We therefore excluded results from this study in the analysis.

We repeated the phylogenetically corrected analysis with contrasts of forebrain size, based this time on residual values obtained from a log–log linear regression of forebrain size on body mass, regressed against contrasts of mean or maximum flock size, and found no differences in the results. An alternative approach to scale forebrain size would be to divide forebrain size by whole brain size in each species (Clark *et al.*, 2001; Burish *et al.*, 2004). However, we found that this relative index was closely correlated to our forebrain size–body mass residuals ($r = 0.90$). Because the results did not vary between indices, we present those calculated from our first approach.

The CAIC program can also deal with discrete characters by calculating contrasts only over branches with a transition in the discrete variable (Nunn and Barton, 2001). If forebrain size is related to sociality, transitions from solitary to gregarious foraging should be accompanied by consistent changes in the contrasts for forebrain size. We used the Wilcoxon signed ranks test to determine whether the resulting contrasts differed from zero. In this analysis, the contrasts for brain structures were calculated from the residuals of a linear regression of forebrain size on body mass.

RESULTS

In data set A, there was no relationship between residuals from a log–log regression of forebrain size on body mass and either mean flock size ($F = 1.3$, $P = 0.25$) or maximum flock size ($F = 0.49$, $P = 0.45$). In addition, there was no relationship between the contrasts for forebrain size and the contrasts for mean ($F = 1.1$, $P = 0.30$; Fig. 1A) or maximum flock size ($F = 0.04$, $P = 0.84$) once the significant effect of body mass contrasts ($P < 0.0001$) was taken into account. There was no consistent increase in forebrain size contrasts along the 16 transitions from solitary to flock-feeding ($S = 12$, $P = 0.28$).

In data set B, there was no relationship between residuals from a log–log regression of forebrain size on body mass and either mean flock size ($F = 1.6$, $P = 0.20$) or maximum flock size ($F = 1.9$, $P = 0.18$). In addition, there was no relationship between the contrasts for forebrain size and the contrasts for mean ($F = 1.0$, $P = 0.32$; Fig. 1B) or maximum flock size ($F = 1.3$, $P = 0.26$) after controlling for the significant effect of body mass contrasts ($P < 0.0001$). There was also no consistent increase in forebrain size contrasts along the eight transitions from solitary to flock-feeding ($S = 1$, $P = 0.48$).

In data set C, there was no relationship between residuals from a log–log regression of forebrain size on body mass and either mean flock size ($F = 0.49$, $P = 0.49$) or maximum flock size ($F = 0.02$, $P = 0.89$). In addition, there was no relationship between the contrasts for forebrain size and the contrasts for mean ($F = 0.2$, $P = 0.69$; Fig. 1C) or maximum flock size ($F = 0.0$, $P = 0.99$) once the significant effect of body mass contrasts ($P < 0.0001$) was removed. The small number of transitions from solitary to flock-feeding ($n = 4$) precluded the analysis of flocking propensity.

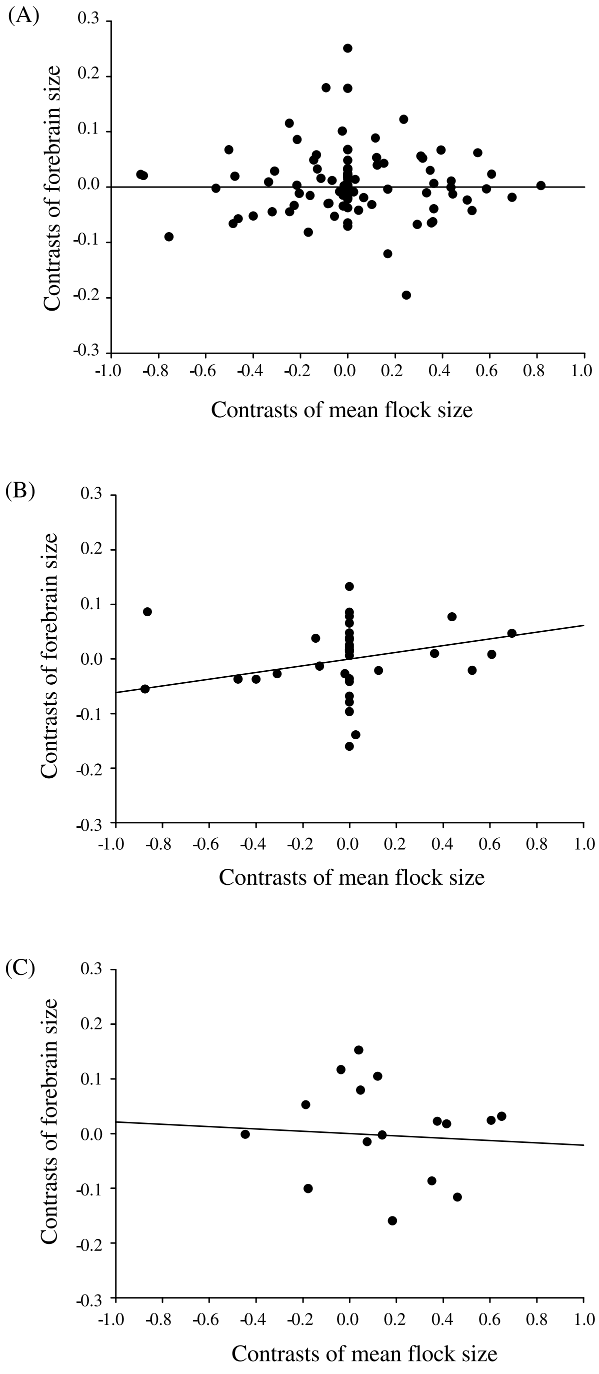

Fig. 1. Relationship between forebrain size and mean flock size in birds in three different data sets (A, B and C). Residuals from the regression of forebrain size contrasts on body mass contrasts are plotted against the contrasts of mean flock size.

DISCUSSION

We found no evidence for an association between forebrain size and three different indices of social complexity during the non-breeding season in birds, using both raw species data and phylogenetically corrected data. Nevertheless, a recent study documented a positive relationship between forebrain size and social complexity in birds (Burish *et al.*, 2004). However, their index of social complexity was not clearly defined. For instance, woodpeckers (Picidae), which have a large relative forebrain, were classified as socially complex despite the fact that most species in this clade are solitary (Winkler *et al.*, 1995). Other species at the lower end of the spectra in terms of relative forebrain size, such as gulls (Laridae), pigeons (Columbidae) and sandpipers (Scolopacidae), have not been considered socially complex despite living in groups very similar in size and complexity to those of other species higher in the spectra such as parrots (Psittacidae) and ducks (Anatidae) (see Beauchamp, 2002a, and references therein). Evidence for social learning was used to classify some species as socially complex despite the fact that social learning bears little relationship with sociality (Reader and Lefebvre, 2001). We believe that our test of the social complexity hypothesis, which is based on more objective indices of social complexity and on a larger data set, is more comprehensive and that the relationship between forebrain size and social complexity in birds cannot be supported with the information available so far.

The reasons why brain size has been associated with group size in primates and other mammalian taxa, but not in birds, are not immediately obvious. According to the social complexity hypothesis, relative enlargement of brain structures involved in the processing of visual information represents one potential mechanism underlying the relationship (Joffe and Dunbar, 1997; Barton, 1998). Socio-visual information may be highly diverse (e.g. individual recognition, gaze direction, neighbour distance, number of conspecifics, movements of conspecifics), and may require the development of perceptual and primary, secondary and tertiary visual areas in the brain capable of dealing with such information load (Barton, 2000). Although interesting, the link between social life and visual perception and processing in birds is far from understood (Fernández-Juricic *et al.*, 2004). Birds have highly developed visual systems that could allow them to monitor conspecifics when foraging (Martin, 1993). However, the evidence for behavioural monitoring remains controversial in birds. Some studies suggest that birds pay little attention to the vigilance of conspecifics (Lima, 1995; Lima and Zollner, 1996; Beauchamp, 2002b), whereas others indicate that birds can scan the behaviour of companions when information about food location (Templeton and Giraldeau, 1995; Bekoff, 1996; Coolen *et al.*, 2001) or neighbour location (Fernández-Juricic and Kacelnik, 2004) is involved. More information on how visual information from conspecifics is handled at the neural level is needed to address this issue further.

The lack of relationship between forebrain size and flock size may also stem from specific patterns in brain evolution. We have assumed a correlated evolutionary pattern by which the enlargement of one brain structure, due to certain ecological or social factors, elicits an expansion in adjacent structures, which would thus increase overall brain size (Finlay *et al.*, 2001). However, neural responses to the increasing demands of social life could be mediated by changes within specific regions that fail to modify overall forebrain size (Barton and Harvey, 2000). Social life could affect other neurological aspects, such as neural differentiation, neural connectivity and neural rearrangement that may facilitate processing capacity (Finlay *et al.*, 2001, p. 3552). For instance, neurogenesis in the neostriatum caudale, high vocal centre and Area X, all involved in vocal communication, increased when zebra finches (*Taeniopygia guttata*) were housed in large heterosexual groups but not when kept singly or in male–female pairs (Lipkind *et al.*, 2002). Thus, the social complexity hypothesis in birds could be further tested when specific areas of the avian forebrain involved in the processing of social information are uncovered.

We examined the relationship between forebrain size and group size in the non-breeding season. The possibility that sociality during the breeding season could account for interspecific variation in forebrain size may be another future direction. Cooperative breeding, a breeding system in which more than a pair of birds share parental duties (Cockburn, 1998), was not reported often in our three data sets. In many cooperative breeding species, individuals forage together for most of the year in tightly knit groups. Cooperative breeding has a phylogenetic component (Edwards and Naeem, 1993) that offers the possibility to assess the link between brain structures and sociality in a different evolutionary context.

When more data on the size and structural complexity of other brain areas in birds become available, it will be possible to determine the level of complexity in both brain architecture and social life that is needed to drive brain evolution. We conclude that variation in forebrain size among avian species is not related to flock size during the non-breeding season.

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