Living in stable

social groups is associated with reduced brain size in woodpeckers (*Picidae*)

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Abstract

Group size predicts brain size in primates and some other mammal groups, but no such relationship has been found in birds. Instead, stable pair-bonding and bi-parental care have been identified as correlates of larger brains in birds. We investigated the relationship between brain size and social system within the family *Picidae*, using phylogenetically controlled regression analysis. We found no specific effect of duration or strength of pair bonds, but brain sizes were systematically smaller in species living in long-lasting social groups of larger sizes. Group living may only present a cognitive challenge in groups in which members have individually competitive relationships; we therefore propose that groups functioning for cooperative benefit may allow disinvestment in expensive brain tissue.

Keywords

Social intelligence theory; social complexity; group size; brain evolution

Background

The “social intelligence hypothesis” proposes that living in socially cohesive, semi-permanent groups of individuals with differentiated relationships presents a cognitive challenge, selecting for higher general intelligence (1, 2). This theory, also referred to as the “social brain hypothesis”, is strongly supported by positive correlations between brain and social group size within primates, and some other mammal groups (3-5). As expected, in taxa where groups consist of temporary aggregations, such as ungulates, there is no correlation (6). In birds, no effect of group size has been found; rather, brain enlargement is found to correlate with the stability of pair-bonding and bi-parental care (7-9). However, relatively few bird species live in long-lasting groups: most bird groupings larger than the bonded pair are often temporary and lack differentiated relationships . One previous attempt to examine the relationship between long-lasting groups and brain size in a taxonomically diverse range of birds found no increase beyond pair-bonding (10). The *Picidae* are unusual, presenting the benefit of being relatively taxonomically and ecologically homogenous, yet showing a range of social relationships, from solitary-living outside the breeding season, through extended pair-bonding, to various larger stable social organizations. We used this diversity to investigate whether potential social complexity - i.e. from long-term residence in a group of familiar, often related, conspecifics - might select for brain size increase in birds. We predicted that species with extended pair-bonds would have larger brains than more solitary species, as pair-bonding has been identified as a cause of brain expansion in birds (7, 10); and that species living long-term in larger groups would have larger brains than pair-bonded species, as has been found in primates and several other taxa of mammals (2-4).

Methods

Brain and body mass measurements

Brain volume measures for a total of 61 species were included in the analyses. Data for 39 species were already available (11); in addition, we measured brain size for 30 species at the London Natural History Museum, Tring, where possible averaging measurements of two different specimens for each (n=52). For the 9 species that overlapped between these two sources, measures correlated closely (r=0.995, n=9, p=0.01).

Categorization of social system

Information on woodpecker social organization (12) was categorized as follows. *Solitary* included species that were pair-bonded only when breeding and solitary otherwise (solitary for more than half of each year). *Pairliving* included species that showed long-term pair bonds and/or remained in family groups beyond the breeding season (more than half of each year with a partner or in a group).

Group-living included species that lived long-term in communal groups; in all cases, group members spent more than half of each year in association with conspecifics in addition to their mate and their last brood of young (see ESM for details of social systems).

Statistical methods

We analyzed the data using phylogenetic generalized least squares (PGLS) regression, which incorporates the phylogenetic relatedness of species into the model's error term (13). A maximum clade credibility (MCC) tree (i.e., the most probabilistic tree; see Figure 1) was identified using the software TreeAnnotator (14, 15) from a sample of 3000 phylogenies built using a family backbone by Hackett and colleagues (16, 17). All phylogenies were obtained from the website www.birdtree.org (17). Lambda (λ), a measure of phylogenetic signal that can vary between 0 (minimal) and 1 (maximal), was estimated from the model residuals using maximum likelihood, and used to control for statistical non-independence resulting from inter-species relatedness. Because analyses conducted using a single maximum clade credibility tree do not account for the possibility of phylogenetic uncertainty, we also conducted our analysis across the whole sample of 3000 phylogenies using Bayesian Markov chain Monte Carlo (MCMC) methods (results from the Bayesian MCMC analysis, which did not differ in pattern from those generated using the single MCC tree, can be found in ESM).

The regression model included social organization as a categorical independent variable on three levels (solitary, in species with pair bonds evident only while raising young; pair-living, in species where the pair and their young remain together for much or all of the year; group-living, in species living in larger and more permanent groupings of several different kinds), and log-transformed brain volume as the dependent variable. A log-transformed measure of body size was included as a covariate to adjust for allometric scaling effects on brain size. We tested for a main effect of social organization using ANOVA, and also made three planned contrasts between the categories of social organization (solitary versus pair-living, solitary versus group-living, and pair-living versus group-living) by changing which category was the reference level in the model. We conducted all analyses in R version 3.1.3 using the packages *APE*(18) and *caper*(19), and we viewed trees in FigTree(20).

Results

The full PGLS model provided a significantly better fit to the data than the null (intercept-only) model ($F_{(3,57)}$=63.54, p<.001, R^2=0.76, λ=0.79). Across 61 species of woodpecker, brain size was significantly associated with social organization ($F_{(2,57)}$=3.18, p<.05; see Figure 2). The results of pairwise comparisons between social organization categories were in the opposite direction to predictions. There was no significant difference in brain size between solitary and pair-living species (β=-0.01, t=-0.39, p=.70), nor was there a significant difference between pair-living and group-living species (β=-0.07, *t*=-1.68, *p*=.10; although there was 93% posterior support for a difference found in our Bayesian analysis, see ESM). However, comparison between solitary and group-living species revealed a significant reduction in brain size in species living in groups (β=-0.08, *t*=-2.52, *p*=.01). Moreover, the trend across all comparisons was that of a *negative* relationship between brain size and social complexity.

Discussion

The stable relationships within monogamous, pair-bonded species have been identified as the relevant dimension of cognitive challenge in birds (7, 8, 10); however, a separate study detected no obvious effect on brain size from extended pair-bonds in cooperatively breeding corvids (21). Our results similarly do not support a specific effect of extended pair-bonds in *Picidae*: we found that whether the pair-bond persists beyond the breeding season is unrelated to species' brain size. All woodpecker species are at least seasonally pair-bonded, since both adults work together to bring up the young; thus, whether pairs or extended families remain together throughout the year may be of less relevance than the relationship between breeding adults.

We found, for the first time in birds, a systematic reduction in brain size associated with larger stable social groupings. That woodpeckers living long-term in larger, potentially more complex, groups have relatively smaller brains was unexpected. Previous suggestions of no general relationship between sociality and brain size in birds (22) may result from the temporary or short-lived nature of groups formed in most bird species. While the previous finding of brain enlargement in species that forage in pairs or stable groups relative to those that are more solitary (10) might reflect different evolutionary pressures, or social categories that are only ostensibly like our own, in what was a more heterogeneous sample of bird species than ours. Also relevant, given that several of our group-living woodpeckers are also cooperative breeders, is the observation that cooperative breeding is associated with smaller brains in primates (23). However, this comparison warrants further investigation before firm conclusions can be drawn across taxa, given that cooperative breeding is limited to a single primate family, *Callitrichidae*, and previous investigations of the relationship between cooperative breeding and brain size in birds found no association (21). Because the *Picidae* family is ecologically relatively homogeneous, with most species sharing many aspects of life history, habitat and diet, it seems unlikely that an ecological effect drives our findings, although the possibility needs further investigation.

Our results support previous claims (10) that the evolutionary causes of long-term residence in stable group-living in birds are fundamentally different in nature to those of primates. Social groups in primates are believed to present a cognitive challenge to their members because of the inter-individual competition they promote, including coordination with cooperative allies that increases individual competitive power (1, 27). Most species of primate need to live in social groups because of predation pressure (28). Competition for resources such as mating and food is thereby created, which individuals can reduce by acquiring information: about group members’ ranks and affiliations, kinship and residence time, and any history of support or aggression. This amounts to a considerable cognitive challenge, increasing exponentially with group size: the result is selection for larger brains (29, 30). We suggest that, in contrast to primate groups, relationships in group-living birds are intrinsically cooperative, because these groups depend on cooperation among all members. Without the competitive element that serves as a challenge in primate societies, we propose that group-living allows disinvestment in expensive brain tissue.

Data accessibility

The dataset supporting this article have been uploaded as part of the supplementary material.

Ethical statement

No ethical approval was required.

Competing Interests

We have no competing interests.

Author contributions

All authors contributed equally. RB designed the study and constructed the paper; CLE planned and reported the statistical analyses, and helped to critically revise the paper; NF measured specimens, assembled the data and helped to draft the paper. All authors agree to be held accountable for the content herein and gave final approval for publication.

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Figure 1. Evolutionary relationships among woodpeckers

Maximum clade credibility tree with mean node heights, produced using TreeAnnotator (14).

Species are coloured by social organization: blue: solitary; red: pair-living; yellow: group-living.

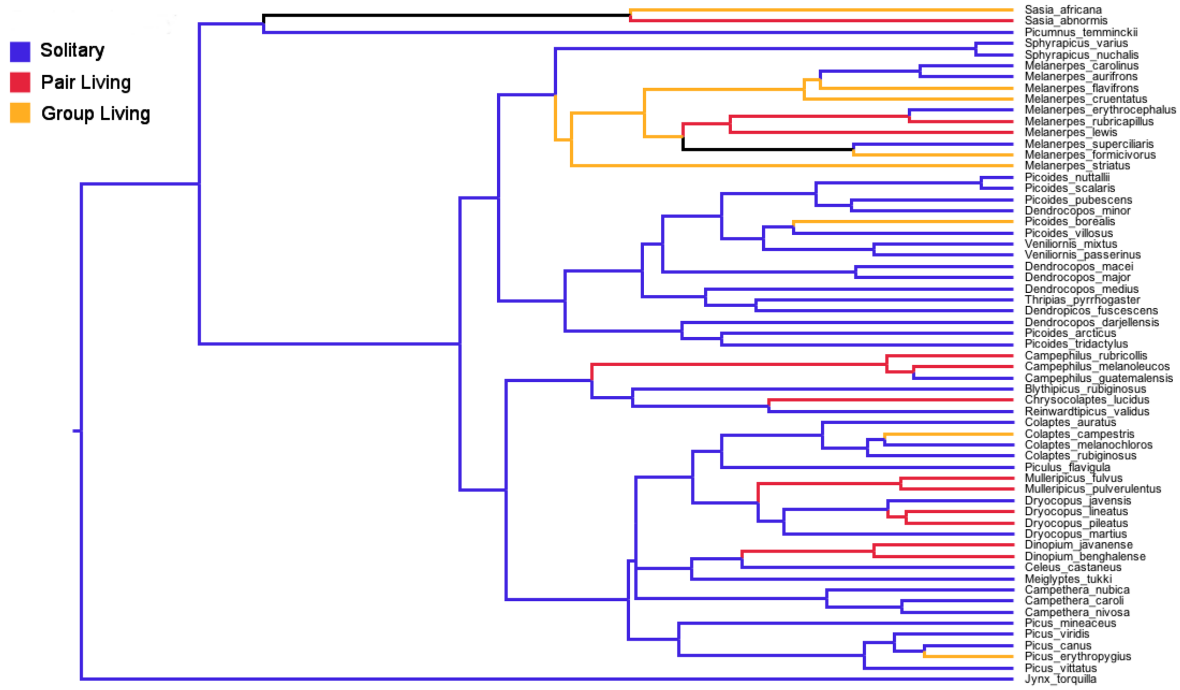

Figure 2. Relationship between body size and brain size of woodpecker species at different levels of social organization

Dots represent log-transformed body weight and log-transformed brain volume for species that live in solitary (blue), pair-living (red) and group-living (yellow) social organizations. Lines represent the slopes and intercepts estimated by the PGLS regression for all three groups.