



Brain structure differences between solitary and social wasp species are independent of body size allometry

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Abstract

Evolutionary transitions in social behavior are often associated with changes in species' brain architecture. A recent comparative analysis showed that the structure of brains of wasps in the family Vespidae differed between solitary and social species: the mushroom bodies, a major integrative brain region, were larger relative to brain size in the solitary species. However, the earlier study did not account for body size effects, and species' relative mushroom body size increases with body size in social Vespidae. Here we extend the previous analysis by measuring the effects of body size variation on brain structure differences between social and solitary vespid wasps. We asked whether total brain volume was greater relative to body size in the solitary species, and whether relative mushroom body size was greater in solitary species, after accounting for body size effects. Both total brain volume and relative mushroom body volume were significantly greater in the solitary species after accounting for body size differences. Therefore, body size allometry did not explain the solitary versus social species differences in brain structure. The evolutionary transition from solitary to social behavior in Vespidae was accompanied by decreases in total brain size and in relative mushroom body size.

Keywords Eusociality · Mushroom bodies · Neuroecology · Paper wasps · Social brain hypothesis

Introduction

Neuroecology theory suggests shifts in species' behavior or ecology can select for evolutionary changes in brain structure and function. If cognitive capacity is correlated with the amount of neural tissue in a species' brains, brain tissue volume may serve as a proxy for physiologically costly investment in cognitive ability (Isler and Van Schaik 2006, 2009; Niven and Laughlin 2008; Kotrschal et al. 2013). Either total brain size (concerted brain evolution; Finlay et al. 2001) or the relative sizes of brain regions (mosaic brain evolution;

Hager et al. 2012) may evolve along with changes in species' ecology.

The social brain hypothesis posits that evolutionary transitions in social structure can drive adaptive changes in brain tissue investment (Reader and Laland 2002; Dunbar and Shultz 2007). Species comparisons among vertebrates often show positive associations of total brain size, or of the size of brain regions, with sociality (Burish et al. 2004; Perez-Barberia et al. 2007; Bshary et al. 2014; West 2014; but see DeCasien et al. 2017). Obligate group-living sociality arose independently in several orders of insects (Wilson and Hölldobler 2005), raising the question of whether the typical vertebrate social brain effects hold for social insects (Gronenberg and Riveros 2009; Lihoreau et al. 2012; Farris 2016). A comparative analysis of solitary and social insects (paper wasps: Vespidae) documented brain structure differences between solitary and social species that were distinct from the vertebrate pattern: solitary vespid wasps had relatively larger mushroom bodies, an integrative brain region involved in learning and memory (Zars 2000; Fahrbach 2006; Farris and Van Dyke 2015), than their social relatives (O'Donnell et al. 2015). Mushroom body neuron development (i.e., dendritic size and complexity) was positively

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associated with mushroom body volume and with complex task performance in paper wasps and in other social Hymenoptera (Farris et al. 2001; Jones et al. 2009), suggesting greater mushroom body volume is associated with cognitive ability. Greater mushroom body size in the solitary species than in their social relatives was therefore interpreted as supporting the distributed cognition hypothesis (O'Donnell et al. 2015): cooperative communication and division of tasks among colony mates in social species can reduce the cognitive demands on individuals, permitting evolutionary reductions in individual brain tissue investment (Kverková et al. 2018).

However, body size-related brain allometry is an important consideration in comparative analyses of adaptive brain evolution (O'Donnell and Bulova 2017), and a recent comparative analysis showed that the relative size of the mushroom body neuropil decreased at smaller body sizes in swarm-founding wasps (O'Donnell et al. 2018). This finding raised questions about the validity of the solitary social species comparison in Vespidae (O'Donnell et al. 2015): the relatively greater mushroom body sizes of large-bodied solitary potter wasps could be driven by body size-associated allometry, rather than by cognitive differences due to solitary versus social behavior.

The goal of this study was to re-assess the solitary versus social species comparison in the Vespidae by accounting for body-size effects on brain allometry. We measured head capsule volumes of the subject species used by O'Donnell et al. (2015). We used head capsule volumes as an index of body size because head size is likely to be directly relevant to brain volume. We also measured body weights of the subject species, and head capsule weights of a subset of the species, to assess whether head capsule volume measures reflected overall body size variation. We extended the analysis of brain evolution by comparing total brain volume relative to body size in solitary versus social species, and we asked whether social and solitary species differed in relative mushroom body volume after accounting for body size effects. If distributed cognition effects are important in vespid wasp brain evolution, then solitary potter wasps should have greater total brain volume (the concerted brain evolution prediction), and/or greater relative mushroom body volume (a mosaic brain evolution prediction), than the social species after accounting for the effects of body size.

Materials and methods

Taxon sampling

Most of the subject species were the same ones we sampled in the previous study of social and solitary vespid brain structure (O'Donnell et al. 2015). To increase representation

of large-bodied social paper wasps we added one additional species of *Polistes* (*P. gigas*). The social paper wasps we sampled came from all four tribes of the subfamily Polistinae (Piekarski et al. 2018): two independent-founding Ropalidiini, one independent-founding Mischocyttarini, two independent-founding Polistini, and 19 swarm-founding Epiponini. We also sampled five species of solitary-nesting potter wasps (Eumeninae), for a total of $n=29$ subject species. We measured head capsule volumes, head capsule dry weights, and body dry weights (thorax and abdomen) to test for possible body size allometry effects on total brain size and brain structure (O'Donnell and Bulova 2017; O'Donnell et al. 2018).

Subject species, collection dates and locations were: solitary potter wasps, Eumeninae: *Coeleumenes burmanicus*, *Delta esuriens*, *Delta pyriforme*, *Phimenes flavopictus*, *Rhynchium quinquecinctum*, May 2014, May 2014, Taiwan: 21°57.8'N, 120°49.5'E. Social Mischocyttarini: *Mischocyttarus mastigophorus*, August 2006, Costa Rica, 10°18.1'N, 84°47.9'W. Social Polistini: *Polistes instabilis*: July 2005, Costa Rica, 10°27.2'N, 85°7.5'W; *Polistes gigas*, May 2014, Taiwan: 21°57.8'N, 120°49.5'E. Social Ropalidiini: *Parapolybia varia*, *Ropalidia fasciata*: May 2014, Taiwan: 21°57.8'N, 120°49.5'E. Social Epiponini: *Polybia jurinei*: November 1994, Ecuador, 0°40.5'S, 76°25.8'W; *Agelaisia xanthopus*, *Polybia emaciata*: August 2006, Costa Rica, 10°18.1'N, 84°47.9'W; *Nectarinella championi*, *Polybia raii*: August 2006, Costa Rica, 10°14.4'N, 84°54.3'W; *Apoica pallens*, *Angiopolybia zischkai*, *Charterginus fulvus*, *Leipomeles dorsata*, *Parachartergus smithii*, *Polybia dimidiata*, *Polybia richardsi*, *Protopolybia exigua*, *Synoeca septentrionalis*: June 2007, Ecuador, 0°40.3'S, 76°24.0'W; *Polybia flavitincta*: March 2012, Costa Rica: 10°25.6'N, 84°1.2'W; *Brachygastra smithii*, *Polybia aequatorialis*, *Polybia plebeja*, *Polybia rejecta*: July 2012, Costa Rica 10°16.3'N, 84°49.4'W.

Body size measurements: head capsule volume estimates

Whenever possible we photographed the subjects we used for neuroanatomical analyses prior to histological processing and we measured head capsule sizes on these individuals; for most of the species we measured the head capsules and body weights on conspecifics collected from the same colonies as the neuroanatomy subjects, or from nearby colonies (with 1 km) collected in the same field season. To measure head size, we dissected the wasps' head capsules from the body at the foramen or "neck" (the narrow attachment-point to the alitrunk). We photographed each head using a digital camera mounted on a dissecting scope and used the ruler tool in ImageJ and photographs of a stage micrometer to convert linear pixel counts to mm. Heads were photographed

in frontal view with the foramen area facing away from the camera and resting against a horizontal glass surface. We measured head width at the widest point, head height from the ventral center edge of the clypeus along the midline to the vertex, and we used half head width as an approximation of head depth. We then estimated head capsule volume for each individual using the formula for an ellipsoid:

$$\frac{4}{3} \times \pi \times \frac{1}{2} \text{ head width (mm)} \times \frac{1}{2} \text{ head height (mm)} \times \frac{1}{2} \text{ head depth (mm)}.$$

We used species' mean estimated head volumes as an index of species-typical body size in statistical analyses.

Body size measurements: head capsule and body weights

We measured dry weights of body parts to validate the head capsule volume estimates, and to provide alternative body size predictor variables for analyzing the allometric relationships of brain architecture. We dissected wasps' head capsules from the remainder of the body (thorax and abdomen) by cutting at the foramen (neck). Head capsules and bodies were dried to constant weight in a convection oven at 50 °C. We weighed the body parts separately on a digital balance to the nearest 0.0001 g. We measured body weights for all subject species, and head capsule weights for $n = 23$ of the subject species. Whenever possible we weighed five heads and five bodies simultaneously and divided by the number of subjects to obtain species mean dry weight.

Histology and neuroanatomy methods

We dehydrated head capsules through a series of increasing ethanol concentrations to 100%, followed by acetone, then through increasing concentrations of plastic resin in acetone (O'Donnell et al. 2015). We incubated individual wasp heads in 0.1 ml resin in pyramid molds at 60 °C for 72 h, then glued the cured resin to 0.5 ml acrylic cylinders with cyanoacrylate adhesive. We cut each head along the frontal plane into 12–16 μm thick sections (depending on species) using a rotary microtome with disposable steel histology blades. Sections were mounted on gelatin-coated microscope slides and the tissue was stained with Toluidine blue. We cleared the stained sections in a series of increasing ethanol concentrations and cover-slipped under transparent mounting medium.

We used a microscope-mounted digital camera to photograph the tissue sections at 2560 \times 1920 pixel resolution, using 2.5 \times or 5 \times microscope objectives (depending on the size of the species being imaged). For each wasp, we began photographing every other section starting with the section where brain tissue first became visible. ImageJ version 1.46

digital imaging analysis software (<http://rsbweb.nih.gov/ij/>) was used to quantify the volumes of brain structures. We outlined the target brain regions and quantified the number of image pixels in the structure using ImageJ, and then converted the pixel counts to area using a photograph of a stage micrometer taken at the same resolution and magnification as a size reference. We multiplied the areas by section thickness to yield volume.

We measured the volumes of the brain neuropils (regions of dendritic arborization and axonal connections) and did not include the layers of neuronal cell bodies that surround the brain. The mushroom body calyx lip, collar and basal ring, and the mushroom body axonal bundles (peduncles and lobes) were pooled to yield total mushroom body volume. Two regions of the optic lobes (medulla and lobula) were pooled to yield optic lobe volume, and the total volume of the olfactory glomeruli yielded antennal lobe volume. We used total volume of all other neuropils in the head capsule as an index of brain size, henceforth referred to as central brain volume. Total brain volume was the sum of all brain regions measured (optic and antennal lobes, mushroom bodies and central brain volume).

Statistical analyses

Analyses were performed in SPSS software (version 24) and Sigmaplot (version 12.5) on species mean values of all variables. Brain volumes, head capsule volumes, and body weights were \log_{10} transformed for all analyses. Ratios of volumes or weights were not transformed. We used *t*-tests for independent samples to test for overall mean body size differences (head volume and body weight) between solitary and social species. We tested for differences in brain structure between social and solitary species using general linear models (GLM), with sociality (social versus solitary) as a fixed-effect predictor variable. We entered head capsule volume or body weight (thorax and abdomen) as a covariate in the analyses to account for body size effects. To ensure that comparing the relatively large-bodied potter wasps to the smallest-bodied social species did not bias the results of the analyses, we performed separate analyses comparing the five potter wasp species with only the five largest social species.

To account for phylogenetic effects on the relationships of brain structure with body size, we first calculated the residuals of linear regressions of the mushroom body/brain size ratio, and of $\log(\text{total brain volume})$, against $\log(\text{head capsule volume})$. We then used Phylocom version 4.2 software (Webb et al. 2008) to account for phylogenetic effects in the analysis of the relationship of species sociality (social versus solitary as a binary variable) with both sets of brain structure residuals. We calculated independent contrasts with all branch lengths set to one (default setting) in the vespid phylogeny. Phylogenetic relationships

were obtained from Piekarski et al. (2018). We tested for significance of the independent contrasts trait correlation by consulting a significance table for Pearson correlation coefficients.

Results

Body size measurements

Head capsule volume estimates were strongly linearly related with head capsule weight (Supp. Fig. 1; $r^2=0.95$, $p<0.0001$) and with body weight (Supp. Fig. 1; $r^2=0.96$, $p<0.001$). The solitary potter wasps were larger on average than the social species (for head capsule volumes, t test, $t=3.47$, $df=26$, $p<0.005$; for body weights, $t=4.06$, $df=26$, $p<0.001$), but there was overlap in size distributions among the larger social species and the potter wasps. The five largest social species did not differ significantly in head capsule volume ($t=0.47$, $df=8$, $p=0.65$) nor in body weight ($t=1.02$, $df=8$, $p=0.34$) from the five potter wasp species, and the largest species we sampled (*Polistes gigas*) was social (Fig. 1).

Body-size allometry of total brain volume and sociality

After accounting for head capsule volume effects, solitary potter wasps' total brain volumes were significantly larger than social wasp brain volumes (Fig. 1; $F_{1,25}=45.00$,

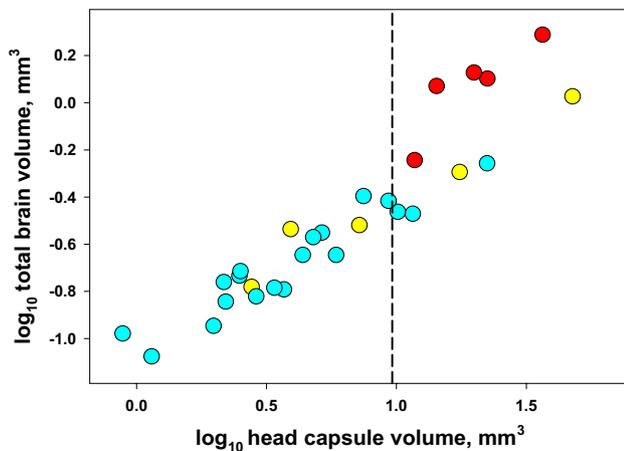


Fig. 1 Species-mean total brain volume plotted against head capsule volume for five species of solitary potter wasps and 24 species of social Vespidae (all data \log_{10} transformed). Symbol colors indicate level of sociality for each species. Red: solitary species. Yellow: independent-founding social species. Light blue: swarm-founding social species. Vertical dashed line indicates the head size-cutoff for the five largest species of social Vespidae

$p<0.001$); this relationship also held when using body weight as the index of size ($F_{1,25}=22.11$, $p<0.001$). After accounting for head volume effects, solitary potter wasp total brain volumes were also significantly higher than the brain volumes of the five largest social wasps we sampled ($F_{1,7}=40.43$, $p<0.001$).

The ratio of total brain volume to head volume decreased with body size for the social species (Fig. 2), but the brain volume/head volume ratio was significantly greater for solitary potter wasps compared to all social species after accounting for head capsule volume effects ($F_{1,25}=23.37$, $p<0.001$) and body weight effects ($F_{1,25}=19.65$, $p<0.001$). The brain volume/head capsule volume ratio was also significantly higher for solitary potter wasps when comparing them to only the five largest social species ($F_{1,7}=24.32$, $p<0.005$).

Sociality and body-size allometry of relative mushroom body volumes

The brain size-relative volume of the mushroom body neuropils (mushroom body/central brain ratio) was significantly higher for the solitary potter wasp species than for social species after accounting for head capsule volume effects (Fig. 3; $F_{1,25}=32.59$, $p<0.001$) and body weight effects ($F_{1,25}=25.36$, $p<0.001$). The brain size-relative volume of the mushroom bodies was also significantly higher for the solitary potter wasp species than for the five largest social paper wasps after accounting for head capsule volume effects ($F_{1,7}=23.87$, $p=0.002$).

After accounting for phylogenetic effects (Independent Contrasts), the residuals of brain structure versus body size

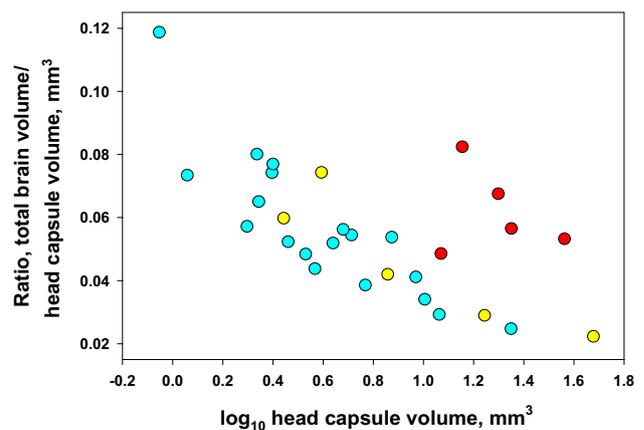


Fig. 2 Ratio of brain volume to head capsule volume, plotted against \log_{10} head capsule volume, for five species of solitary potter wasps and 24 species of social Vespidae (all data \log_{10} transformed). Symbol colors indicate level of sociality for each species. Red: solitary species. Yellow: independent-founding social species. Light blue: swarm-founding social species

did not differ significantly between solitary and social species (for relative mushroom body size: $r=0.12$, $p>0.50$; for brain volume: $r=0.21$, $p>0.30$).

Discussion

Size allometry and solitary versus social species brain structure

Brain architecture had significant allometric relationships with body size in wasps of the family Vespidae. Body size allometry was evident in both total brain volume (concerted brain evolution) and in the relative size of a key central processing brain region, the mushroom bodies (mosaic brain evolution): body size-relative brain size decreased, and relative mushroom body size increased, with body size in the Vespidae. However, the significant brain architecture differences between solitary species (potter wasps) and social paper wasps were independent of body size allometry. Solitary-nesting Eumeninae showed both larger total brain volumes, and relatively larger mushroom bodies, than social Vespidae after accounting for the effects of body size. These patterns held both when using head capsule volume as an index of body size, and when using body weight (thorax plus abdomen) as an index of body size.

Implications for social brain evolution

The brain structure differences between solitary and social wasp species are consistent with predictions of the distributed cognition hypothesis for brain evolution. Distributed

cognition models posit that cognitive demands on individuals in solitary-nesting species are greater than those faced by their social relatives. In vespid wasps, females of solitary-living species must successfully forage, and construct and defend nests, alone (West-Eberhard 2005). Individuals' cognitive demands could be reduced in the social species (Farris 2016; Keating-Godfrey and Wulfila Gronenberg 2019), due to the specialization that accompanies division of labor, or due to the fact that social information sharing among colony mates can reduce the pressure for individual cognitive competence (Lihoreau et al. 2012; Bergman and Beehner 2015).

There was no evidence for lineage-specific differences in brain-body size relationships among the social species we examined: the brain structure/body size data values for the independent-founding clades were generally within the range of variation seen among the swarm-founding species of Epiponini. However, this finding should be considered preliminary because species sample sizes were small for the Ropalidiini ($n=2$), Mischocyttarini ($n=1$) and Polistini ($n=2$). In a previous study, several measures of social complexity including independent-founding versus swarm-founding, colony size and degree of queen/worker differentiation all failed to predict species differences in relative mushroom body size among social species (O'Donnell et al. 2015). Together with our finding that body size evolution does not explain the solitary/social species differences, these patterns suggest the evolutionary transition from solitary nesting to social behavior (i.e., obligate group living with reproductive division of labor) was accompanied by a shift in brain architecture.

Opportunities for future comparative research

Because all the solitary potter wasps we sampled belong to the subfamily Eumeninae (Piekarski et al. 2018), which is the sister clade to the social taxa, phylogenetic effects on brain architecture in the Vespidae cannot be ruled out (O'Donnell et al. 2015). Additional comparative tests for changes in brain architecture (e.g., relative mushroom body size) with the evolution of sociality in other clades are needed to test the generality of the patterns we documented.

We suggest the following taxa are good targets for future study. Our sample did not include any species in the Zethinae, which were recently elevated to subfamily status and are the sister clade to all social Vespidae (Piekarski et al. 2018). Sampling brain architecture in the zethines, which include at least one communal nesting species (*Zethus miniatus*: West-Eberhard 2005), could further inform evolutionary transitions in brain architecture within the Vespidae. Another key comparison would take advantage of the evolutionary origin of sociality in the Southeast Asian hover wasps (Stenogastrinae), where sociality arose independently from the vespids we sampled (Hines et al. 2007; Piekarski et al. 2018). Some

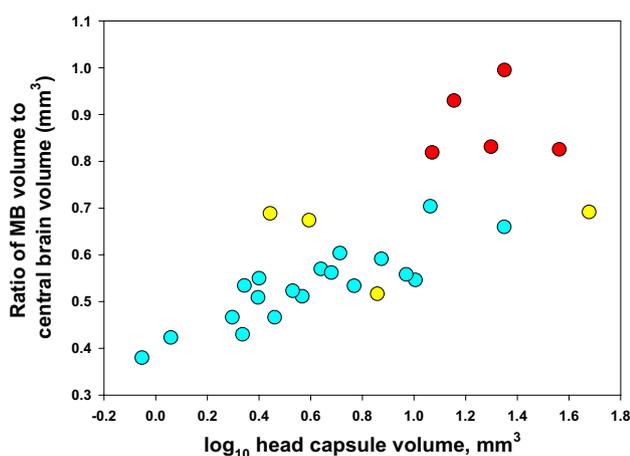


Fig. 3 Species-mean relative mushroom body volume plotted against log head capsule volume for five species of solitary potter wasps and 23 species of social Vespidae. Symbol colors indicate level of sociality for each species. Red: solitary species. Yellow: independent-founding social species. Light blue: swarm-founding social species

species of stenogastrines share features of social behavior with social Polistinae, including overlap of adult generations on nests and reproductive division of labor (Turillazzi 2012). Distributed cognition models predict smaller size-relative brain volume and mushroom body volume in the stenogastrines relative to solitary-nesting Vespidae. Finally, multiple evolutionary transitions among social and solitary nesting in bees (Danforth 2002) make them prime candidates for additional comparative tests of the patterns we documented.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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