A test of neuroecological predictions using paperwasp caste differences in brain structure (Hymenoptera: Vespidae)

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Abstract Adaptive brain architecture hypotheses predict brain region investment matches the cognitive and sensory demands an individual confronts. Social hymenopteran queen and worker castes differ categorically in behavior and physiology leading to divergent sensory experiences. Queens in mature colonies are largely nest-bound while workers depart nests to forage. We predicted social paperwasp castes would differ in tissue allocation among brain regions. We expected workers to invest relatively more than queens in neural tissues that process visual input. As predicted, we found workers invested more in visual relative to antennal processing than queens both in peripheral sensory lobes and in central processing brain regions (mushroom bodies). Although we did not measure individual brain development changes, our comparative data provide a preliminary test of mechanisms of caste differences. Paperwasp species differ in the degree of caste differentiation (monomorphic versus polymorphic castes) and in colony structure (independent- versus swarm-founding); these differences could correspond to the magnitude of caste brain divergence. If caste differences resulted from divergent developmental programs (experience-expectant brain growth), we predicted species with morphologically distinct queens, and/or swarm-founders, would show greater caste divergence of brain architecture. Alternatively, if adult experience affected brain plasticity (experience-dependent brain growth), we predicted independent-founding species would show greater caste divergence of brain architecture. Caste polymorphism was not related to the magnitude of queen-worker brain differences, and independent-founder caste brain differences were greater than swarm-founder caste differences. Greater caste separation in independent-founder brain structure suggests a role for adult experience in the development of caste-specific brain anatomy.

Keywords Antennal lobe · Brain evolution · Mushroom body · Neural plasticity · Optic lobe

Introduction

Brain tissues are compartmentalized into anatomically discrete regions that perform distinct cognitive processes (Tanaka et al. 2012; Arrenberg and Driever 2013; Brown and Piscopo 2013; Mantini et al. 2013). Brain tissue is metabolically and developmentally expensive (Laughlin 2001; Niven and Laughlin 2008; Navarrete et al. 2011). Natural selection should act on brain architecture such that the relative investment in each brain region matches the animal’s cognitive demands (Chittka and Niven 2009; Gronenberg and Riveros 2009; Shultz and Dunbar 2010). Investment in functionally distinct brain regions should reflect behavior and ecology at the individual and species levels (Cooper et al. 1993; Catania 2005; Linsey et al. 2007).

Social insect castes present an excellent opportunity to test adaptive brain architecture hypotheses. Queens and workers play distinct social roles, and neuroecological theory predicts their different behaviors and sensory experience will be reflected in distinct brain architectures (Gronenberg and Riveros 2009). In most social insects, reproductive castes are categorically distinct phenotypes that result from developmental plasticity (West-Eberhard 1981). In female eusocial Hymenoptera, reproductive queens and sterile workers can...
develop from similar genotypes depending on the environment early in larval development (Hunt et al. 2007; Martins et al. 2010). We asked whether brain investment differed between reproductive castes—egg-laying queens and sterile workers—in eusocial paperwasps (Vespidae, Polistinae). Paperwas queen and workers differ strongly in behavior and ecology. Queens are generally nest-bound, rarely flying from mature colonies, while workers perform diverse tasks including leaving the nest to forage (Herman et al. 2000; Bruyndonckx et al. 2006; Chavarria-Pizarro and West-Eberhard 2010; De Souza and Prezoto 2012). However, paperwasps vary widely in colony size and social complexity. Independent-founding species have relatively small colonies, and adult females are relatively plastic in their reproductive roles. Dominance interactions among females affect social status and opportunities for reproduction (Molina and O’Donnell 2008). Swarm-founding wasps have larger colonies with less plasticity in reproductive roles (Jeanne 2003). Paperwasp species further differ in the degree of female caste differentiation. Paperwasps range from species with no detectable caste categories (independent-founders and some swarm-founders) to swarm-founding species with discrete queen/worker body size and shape differences (O’Donnell 1998a; Noll et al. 2004).

We used the relative volumes of brain regions that process two distinct sensory inputs—the compound eyes (vision) and the antennae (chemosensation and tactile)—to test whether caste differences correspond to environmental context. Distinct brain regions process visual information from the compound eyes and chemosensory input from the antennae in social Hymenoptera, including paperwasps (Gronenberg 1999; Ehmer and Hoy 2000; O’Donnell et al. 2011). Anatomically distinct peripheral lobes process visual and chemosensory inputs (optic and antennal lobes, respectively; Gronenberg 1999; Hansson and Stensmyr 2011), and these lobes innervate distinct regions of central processing neuropils called mushroom bodies (Strausfeld et al. 1998; Fahrbach 2006). The optic lobes innervate the collar region of the mushroom body calyx, and the antennal lobes innervate the lip region of the mushroom body calyx (Gronenberg 1999). Both the antennal and optic lobes show structural plasticity following changes in sensory input and experience (Barth et al. 1997; Eickhoff et al. 2012; Arenas et al. 2012). Differences in mushroom body calyx volume are related to caste and task performance in many social Hymenoptera including paperwasps (Gronenberg et al. 1996; Farris et al. 2001; O’Donnell et al. 2004, 2007; Muscedere and Traniello 2012).

Because queens and workers occupy different sensory environments, and paperwasp brain regions vary in size with experience, we predicted there would be caste differences in relative investment in visual versus antennal processing brain regions. We used the ratio of visual processing to antennal processing tissue volume as an index of the degree of reliance on visual versus antennal inputs, both in the peripheral lobes and in the mushroom bodies. Paperwas queen are largely nest-bound and experience less complex visual environments and lower light levels than their foraging workers. Behavioral activity under lower light conditions is associated with decreases in visual processing tissue (Catania 2005; Barton et al. 1995; Fujun et al. 2012). We predicted paperwasp workers would invest relatively more than their queens in visual processing brain regions (the optic lobes and the collar regions of the mushroom body calyx; Gronenberg 1999; O’Donnell et al. 2011).

Different developmental programs could lead to caste-specific brain architecture (experience-expectant brain growth). Alternatively, brain structure could respond to individuals’ caste-specific environments (experience-dependent brain growth; Fahrbach et al. 1998; Farris et al. 2001). We used comparisons of paperwasp species with different social structures as an indirect means of assessing the relative importance of experience-expectant and experience-dependent brain development. We categorized our subject species as independent-founders (primitively eusocial) and swarm-founders (advanced eusocial), and we identified species with morphologically distinct queens (highly eusocial) (O’Donnell 1998a; Jeanne 2003; Noll et al. 2004). We tested whether the magnitude of queen-worker differences in brain architecture differed between the three social structure categories (independent-founders, caste monomorphic swarm-founders, and caste dimorphic swarm-founders). The degree of specialization of reproductive castes on different social roles increases as larger, more complex societies evolve from independent-founding ancestors with smaller colonies (Bourke 1999; Anderson and McShea 2001; Jeanne 2003). If experience-expectant growth predominates, we expected caste differences to be greater in species with morphologically distinct queen/worker castes and/or greater in swarm-founders relative to independent-founders. In contrast, reproductive caste status in independent-founders is relatively plastic and influenced by dominance interactions (Molina and O’Donnell 2008). If experience-dependent brain growth predominates, queen-worker differences could be stronger in independent-founders.

Materials and methods

Subject species

We analyzed the brain architecture of one species from each of 12 genera of Neotropical eusocial paperwasps (Polistinae). Our subjects spanned the 19 currently recognized Neotropical paperwasp genera, including the 2 relatively basal independent-founding genera (Polistes, Mischocyttarus) and 10 derived swarm-founding genera (Fig. 1; Wenzel and.
Wasp colonies were collected into and stored in a buffered aldehyde-based fixative (Prefer fixative, Anatech, Ltd.) for 1–5 years until histological processing. Subject species, collection dates, and locations were as follows: *Polistes instabilis*; July 2005, Costa Rica, 10°27.2’N, 85°7.5’W; *Mischocyttarus mastigophorus* and *Agelaia xanthopus*; August 2006, Costa Rica, 10°18.1’N, 84°47.9’W; *Nectarinella championi*; August 2006, Costa Rica, 10°14.4’N, 84°54.3’W; *Apoica pallens*, *Angiopolybia zischkai*, *Charterginus fulvus*, *Leipomeles dorsata*, *Parachartergus smithii*, *Polybia dimidiata*, and *Protopolybia exigua*; June 2007, Ecuador, 0°40.3’S, 76°24.0’W; *Brachygaster smithii*; July 2012, Costa Rica, 10°16.3’N, 84°49.4’W. All wasps were collected from nests in the field except *B. smithii* which were collected from a swarm. We categorized three species as having morphologically distinct reproductive castes based on published morphometric analyses and our observations (Shima et al. 1994, 1996; Hunt et al. 2001; Noll et al. 2004).

Determining subjects’ caste

All subjects were mature wasps with fully hardened, deeply colored cuticles. We did not know the individual histories of the subjects and we assume our haphazardly chosen samples are representative of each caste. To determine the subjects’ caste, we dissected their gasters (the terminal body region in aculeate Hymenoptera) in the fixative. We exposed the ovaries and examined them at ×10 magnification under a binocular dissecting scope. Workers had filamentous ovarioles with no visible opaque oocyte swellings. Queens had robust, well-developed ovaries with at least one fully opaque, oblong oocyte per ovariole. Individuals with intermediate ovaries were observed, but we only used the two extreme phenotypes as subjects for this study.

Histology and neuroanatomy

Histological processing was conducted in several bouts from September 2007 to September 2013. We collected neuroanatomical data on *n*=82 paperwasp subjects. We sampled four to nine wasps per species, with two to six individuals sampled from each caste (Table 1). We cut the fixed wasps’ head capsules from the thorax at the narrow neck-like juncture behind the gena and removed the antennae and mandibles. Head capsules were dehydrated through a series of increasing ethanol concentrations, acetone, and then increasing concentrations of plastic resin (resin composition: 5.5 g of EMbed 812 (a mixture of bisphenol A/epichlorohydrin epoxy resin (CAS #25068–38-6) and epoxy modifier (CAS #2425–79-8)), 5.7 g of dodecyl succinic anhydride, 0.65 g of dibutyl phthalate, and 0.31 g of 2,4,6-tri(dimethylaminoethyl)phenol). We incubated individual wasp heads in 0.1-ml resin in pyramid molds at 60 °C for 72 h, then glued the resin to 0.5-ml acrylic cylinders with cyanoacrylate adhesive, and cut each head along the frontal plane into 12- to 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 a transparent mounting medium.

We used a microscope-mounted digital camera to photograph the tissue sections at 2,560×1,920 pixel resolution, using ×2.5 or ×5 microscope objectives (depending on species). For each wasp, we began photographing every other section at 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 we 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 distance between sections to yield volume. We estimated the volumes of the following brain subregions: parts of the optic lobes (the medulla and the lobula), the glomeruli of the antennal lobes, and the mushroom body (MB) calyx lip and collar. Other brain regions were pooled into a volume referred to as brain remainder as an index of brain size: brain remainder volume=∑ of estimated volumes of MB peduncle and lobes, central complex, and any protocerebrum, deutocerebrum, and tritocerebrum not included in the brain regions named above. We measured only brain neuropils (regions of dendritic arborization and axonal connections); we did not measure adjacent regions containing the cell bodies (somata) of the brain’s intrinsic neurons. For analyses of caste
Analysis of caste differences

We used general linear models to analyze the data (SPSS v. 20, IBM Corp., 2011). We developed multivariate models to test relationships of response variables (brain region volume ratios or brain size-corrected volumes) with predictor variables. We report type II sums of squares: the magnitude and significance of the effect of each variable in the order the variable was entered into the statistical model. In the statistical models, we first corrected for species differences by entering species as a factor. We tested for differences between queens and workers by entering caste as a factor. Finally, we tested whether species with and without morphological castes (O’Donnell 1998a; Noll et al. 2004) and independent- versus swarm-founders differed in the magnitude of queen-worker differences by using interaction terms: (caste by yes/no morphological differences) and (caste by independent/swarm-founding).

Table 1  Mean estimated volumes (mm³) of brain regions for queen and worker castes from 12 species of social paperwasps

<table>
<thead>
<tr>
<th>Species</th>
<th>Caste</th>
<th>Caste sample size</th>
<th>Mean MB collar</th>
<th>Mean MB lip</th>
<th>Mean OL</th>
<th>Mean AL</th>
<th>Mean remainder</th>
<th>Mean total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agelaia xanthopus</td>
<td>Queens</td>
<td>4</td>
<td>0.047</td>
<td>0.030</td>
<td>0.043</td>
<td>0.024</td>
<td>0.111</td>
<td>0.255</td>
</tr>
<tr>
<td>Agelaia xanthopus</td>
<td>Workers</td>
<td>3</td>
<td>0.061</td>
<td>0.035</td>
<td>0.064</td>
<td>0.030</td>
<td>0.152</td>
<td>0.343</td>
</tr>
<tr>
<td>Angiospolibia pallens</td>
<td>Queens</td>
<td>2</td>
<td>0.016</td>
<td>0.008</td>
<td>0.041</td>
<td>0.011</td>
<td>0.074</td>
<td>0.149</td>
</tr>
<tr>
<td>Angiospolibia pallens</td>
<td>Workers</td>
<td>3</td>
<td>0.015</td>
<td>0.005</td>
<td>0.033</td>
<td>0.009</td>
<td>0.070</td>
<td>0.133</td>
</tr>
<tr>
<td>Apoica pallens</td>
<td>Queens</td>
<td>5</td>
<td>0.055</td>
<td>0.025</td>
<td>0.032</td>
<td>0.023</td>
<td>0.097</td>
<td>0.232</td>
</tr>
<tr>
<td>Apoica pallens</td>
<td>Workers</td>
<td>4</td>
<td>0.060</td>
<td>0.028</td>
<td>0.042</td>
<td>0.026</td>
<td>0.123</td>
<td>0.278</td>
</tr>
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<td>0.020</td>
<td>0.012</td>
<td>0.076</td>
<td>0.016</td>
<td>0.111</td>
<td>0.235</td>
</tr>
<tr>
<td>Brachygastra smithii</td>
<td>Workers</td>
<td>5</td>
<td>0.019</td>
<td>0.012</td>
<td>0.065</td>
<td>0.016</td>
<td>0.109</td>
<td>0.221</td>
</tr>
<tr>
<td>Chartergirinus fulvus</td>
<td>Queens</td>
<td>3</td>
<td>0.018</td>
<td>0.010</td>
<td>0.050</td>
<td>0.011</td>
<td>0.078</td>
<td>0.166</td>
</tr>
<tr>
<td>Chartergirinus fulvus</td>
<td>Workers</td>
<td>5</td>
<td>0.011</td>
<td>0.006</td>
<td>0.049</td>
<td>0.010</td>
<td>0.074</td>
<td>0.150</td>
</tr>
<tr>
<td>Leipomeles dorsata</td>
<td>Queens</td>
<td>3</td>
<td>0.007</td>
<td>0.004</td>
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<td>0.005</td>
<td>0.040</td>
<td>0.082</td>
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<td>Leipomeles dorsata</td>
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<td>0.005</td>
<td>0.041</td>
<td>0.085</td>
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<td>Queens</td>
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<td>0.046</td>
<td>0.022</td>
<td>0.026</td>
<td>0.010</td>
<td>0.147</td>
<td>0.250</td>
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<td>Mischocyttarus mastigophorus</td>
<td>Workers</td>
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<td>0.039</td>
<td>0.015</td>
<td>0.031</td>
<td>0.008</td>
<td>0.159</td>
<td>0.252</td>
</tr>
<tr>
<td>Nectarinella championi</td>
<td>Queens</td>
<td>2</td>
<td>0.017</td>
<td>0.011</td>
<td>0.031</td>
<td>0.014</td>
<td>0.040</td>
<td>0.114</td>
</tr>
<tr>
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<td>Workers</td>
<td>3</td>
<td>0.012</td>
<td>0.008</td>
<td>0.034</td>
<td>0.016</td>
<td>0.042</td>
<td>0.112</td>
</tr>
<tr>
<td>Parachartergus smithii</td>
<td>Queens</td>
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<td>0.018</td>
<td>0.011</td>
<td>0.051</td>
<td>0.013</td>
<td>0.091</td>
<td>0.184</td>
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<tr>
<td>Parachartergus smithii</td>
<td>Workers</td>
<td>5</td>
<td>0.013</td>
<td>0.009</td>
<td>0.056</td>
<td>0.015</td>
<td>0.093</td>
<td>0.185</td>
</tr>
<tr>
<td>Polistes instabilis</td>
<td>Queens</td>
<td>2</td>
<td>0.038</td>
<td>0.027</td>
<td>0.142</td>
<td>0.028</td>
<td>0.225</td>
<td>0.459</td>
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<tr>
<td>Polistes instabilis</td>
<td>Workers</td>
<td>6</td>
<td>0.048</td>
<td>0.023</td>
<td>0.199</td>
<td>0.032</td>
<td>0.222</td>
<td>0.525</td>
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<td>Queens</td>
<td>2</td>
<td>0.025</td>
<td>0.015</td>
<td>0.029</td>
<td>0.016</td>
<td>0.124</td>
<td>0.209</td>
</tr>
<tr>
<td>Polybia dimidiata</td>
<td>Workers</td>
<td>2</td>
<td>0.037</td>
<td>0.016</td>
<td>0.054</td>
<td>0.017</td>
<td>0.152</td>
<td>0.275</td>
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<td>Queens</td>
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<td>0.015</td>
<td>0.006</td>
<td>0.043</td>
<td>0.008</td>
<td>0.049</td>
<td>0.121</td>
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<td>Protopolybia exigua</td>
<td>Workers</td>
<td>3</td>
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<td>0.006</td>
<td>0.050</td>
<td>0.008</td>
<td>0.050</td>
<td>0.127</td>
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</tbody>
</table>

MB mushroom body, OL optic lobe, AL antennal lobe, Remainder brain remainder, sum of other brain structures, Total total volume of all brain structures measured

Results

Paperwasp castes differed significantly in brain architecture. Caste mean volumes for all brain structures we quantified are given in Table 1. Workers invested more than queens in visual processing brain tissues relative to antennal processing brain tissues. This caste difference was seen in both peripheral and central brain regions. In the peripheral sensory lobes, worker optic lobe/antennal lobe ratios were greater than queen ratios (Fig. 2; species differences: \( F_{1,68}=12.14, p<0.001 \); caste differences: \( F_{1,68}=4.75, p=0.033 \)). The peripheral visual/antennal ratio differences were mainly due to significantly smaller optic lobes in queens (Fig. 3; \( F_{1,68}=5.19, p=0.03 \)); the castes did not differ significantly in antennal lobe volume (Fig. 3; \( F_{1,68}=0.425, p=0.52 \)). Polymorphic species did not differ from monomorphic species in the magnitude of peripheral visual/antennal ratio caste differences (Fig. 2; \( F_{1,68}=0.17, p=0.69 \)). Independent- and swarm-founding species did not differ significantly in the magnitude of peripheral visual/antennal ratio caste differences (\( F_{1,68}=2.47, p=0.12 \), but independent-founders were among the most extremely caste-divergent species (Fig. 2).
Workers also had higher relative visual investment than queens in the brain’s central processing regions (mushroom bodies). Worker mushroom body calyx collar (visual)/lip (antennal) volume ratios were higher than queen ratios (Fig. 2; $F_{1,68}=7.47, p=0.008$). Queens had both significantly larger mushroom body lip regions (Fig. 3; $F_{1,69}=9.55, p=0.003$) and significantly larger mushroom body collar regions (Fig. 3; $F_{1,69}=4.19, p=0.04$) than workers. The magnitude of mushroom body calyx caste differences was similar for caste dimorphic and monomorphic species (Fig. 2; $F_{1,68}=0.078, p=0.78$). Independent-founding species had stronger queen-worker differences than swarm-founders (Fig. 2; $F_{1,68}=13.47, p<0.001$).

**Discussion**

**Caste environments**

Brain architecture differed significantly between queen and worker paperwasps. Queens tended to invest less in visual relative to antennal processing tissues, both in the peripheral sensory lobes and in the central processing brain regions (mushroom body calyces). In the peripheral lobes, the queen-worker caste difference was driven mainly by lower optic lobe volumes in queens; in the mushroom body calyx, queens had both larger antennal processing lip regions and larger visual processing collar regions (O’Donnell et al. 2011).

Species and caste differences in sensory ecology are likely to be important predictors of brain investment diversity among social insects (Muscedere and Traniello 2012). Paperwasp queen and worker behavioral profiles are consistently different. Once colonies are established, the lives of queens converge on a largely nest-bound existence. Queens in mature colonies perform few tasks other than egg laying and brood care (West-Eberhard 1978; Herman et al. 2000; Noll and Zucchi 2000; Bruyndonckx et al. 2006; Chavarria-Pizarro and West-Eberhard 2010). In contrast to queens, paperwasp workers perform diverse tasks including nest defense and leaving the nest to forage (O’Donnell 1998b, 2006; Molina and O’Donnell 2008; De Souza and Prezoto 2012). Foraging and other tasks expose flying workers to elevated light levels and complex visual stimuli relative to the nest environment. Our data suggest paperwasp caste differences in behavior and sensory environment are reflected in brain anatomy, such that the cognitive requirements of each caste typically match their patterns of investment in functionally distinct brain regions.

**Implications of species differences for brain development**

Although we found comparative evidence for significant caste differences in sensory brain investment, species differed in the magnitude and direction of queen-worker differences. In both
founders. In independent-founders, a female We found stronger caste differences in independent-founders. Swarm-founder colonies are larger and have stron-
gressive challenges (Gronenberg et al. 1996; Kuhn-Buhlmann
fessional processes and for plastic, experience-
dependent processes in adult social insect brain growth
(Fahrbach et al. 1998; Farris et al. 2001). Adult queen-
worker brain differences could result from caste-specific neural proliferation or caste-specific gene expression prior
to adult emergence (Toth et al. 2009; Farris et al. 2011;
Chen et al. 2012; Shi et al. 2013). Developmentally pro-
grammed caste differences in brain structure are seen in
Apis mellifera honey bees (Fahrbach et al. 1998; Groh and
Roessler 2008; Roat and da Cruz-Landim 2011). A non-
exclusive alternative is that queen-worker differences in paperwasp brain architecture are responses to caste-
specific environments that affect neuron growth (Durst
et al. 1994; Fahrbach et al. 1998; Farris et al. 2001).
Brain regions increase in size in response to novel cogni-
tive challenges (Gronenberg et al. 1996; Kuhn-Buhlmann
and Wehner 2006). In both bees and ants, changes in
female behavior are followed by changes in brain archi-
tecture, and volume plasticity has been documented in
each of the brain regions we studied (Barth et al. 1997;
Jones et al. 2009; Arenas et al. 2012). Brain region
volumes can also regress following reductions in cognitive
demand (Gronenberg and Liebig 1999; Julian and
Gronenberg 2002; Groh et al. 2006).

We suggest that if experience-expectant caste differences predominate, then caste differences would be more extreme in polymorphic species and/or in swarm-
versus independent-founders. Swarm-founder colonies are larger and have stronger patterns of reproductive division of labor (Jeanne 2003).
We found stronger caste differences in independent-
founders. In independent-founders, a female’s social envi-
ronment after adult emergence, including access to nutri-
tion and dominance interactions, plays an important role in
reproductive caste differences (O’Donnell 1998b; Molina

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Polistinae), and a new key to the genera of paper wasps of the new
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