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Caste, Sex, and Parasitism Influence Brain Plasticity in a Social Wasp

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Brain plasticity is widespread in nature, as it enables adaptive responses to sensory demands associated with novel stimuli, environmental changes and social conditions. Social Hymenoptera are particularly well-suited to study neuroplasticity, because the division of labor amongst females and the different life histories of males and females are associated with specific sensory needs. Here, we take advantage of the social wasp *Polistes dominula* to explore if brain plasticity is influenced by caste and sex, and the exploitation by the strepsipteran parasite *Xenos vesparum.* Within sexes, male wasps had proportionally larger optic lobes, while females had larger antennal lobes, which is consistent with the sensory needs of sex-specific life histories. Within castes, reproductive females had larger mushroom body calyces, as predicted by their sensory needs for extensive within-colony interactions and winter aggregations, than workers who frequently forage for nest material and prey. Parasites had different effects on female and male hosts. Contrary to our predictions, female workers were castrated and behaviorally manipulated by female or male parasites, but only showed moderate differences in brain tissue allocation compared to non-parasitized workers. Parasitized males maintained their reproductive apparatus and sexual behavior. However, they had smaller brains and larger sensory brain regions than non-parasitized males. Our findings confirm that caste and sex mediate brain plasticity in *P. dominula*, and that parasitic manipulation drives differential allocation of brain regions depending on host sex.

Keywords: brain plasticity, parasite, parasitic manipulation of host, *Polistes dominula*, sensory brain regions, social wasp, strepsiptera, *Xenos vesparum*

INTRODUCTION

Brain plasticity enables adaptive responses to different sensory demands such as novel stimuli, changing environments and social conditions (Taborsky and Oliveira, 2012; O'Donnell et al., 2013; Anderson and Finlay, 2014; Kamhi et al., 2017; Jernigan et al., 2021). For instance, neuroplasticity has evolved across many lineages as a result of variable selective pressures acting on the cognitive demands of sensory and perceptual systems (Barton et al., 1995; Barton and Harvey, 2000; Catania, 2005). Since brain tissue is energetically expensive, plasticity in specific brain structures may be linked to the sensory and processing needs of adaptive behaviors (Isler and Van Schaik, 2006;

Niven and Laughlin, 2008; Riveros and Gronenberg, 2010; Pyza, 2013; Montgomery et al., 2016; Dunbar and Shultz, 2017; Rozanski et al., 2021). Investment in neural tissue may be mediated by experience (Jones et al., 2009; Riveros and Gronenberg, 2010; Cabirol et al., 2018), diet (Murphy et al., 2014; DeCasien et al., 2017), environmental stimuli (Burns et al., 2009; Axelrod et al., 2018), tradeoffs with reproduction (Pitnick et al., 2006), and/or endocrine factors (Ball et al., 2002; Lendvai et al., 2013). Previous studies also provide compelling evidence for how neuroplasticity adaptively supports the division of labor in complex insect societies and matches sensory specialization (Groh and Meinertzhagen, 2010; Giraldo et al., 2013; Kamhi et al., 2017; Gordon et al., 2019; Arganda et al., 2020; Baudier et al., 2021).

Given that specialized behaviors are associated with a range of caste-specific sensory needs, corresponding investment in neural tissue is expected (Gronenberg et al., 1996; Ehmer et al., 2001; O′Donnell et al., 2007; Seid et al., 2011; Rehan et al., 2015; Arganda et al., 2020; Penick et al., 2021). Therefore, social insects provide the opportunity to compare differential investment in sensory brain regions between castes and sexes with different life histories (Gronenberg and Riveros, 2009; Beani et al., 2014), while controlling for genetic background. In insect brains, visual input travels from the eyes and is received and processed by the optic lobes, while olfactory input is received by the antennal lobes (Strausfeld, 1989; Anton and Homberg, 1999; Gronenberg and Hölldobler, 1999). From these lower-order sensory neuropils, projection neurons convey the computed information to the mushroom bodies (Akalal et al., 2006). In these higher-order brain centers, the chemical and visual information is further processed and integrated with internal information by intrinsic neurons and finally projected to premotor areas. The substructures of the mushroom body calyces, act as learning and memory centers that integrate sensory information and foraging experience. Specifically, olfactory information is processed in the lip, the visual information in the collar, and both sensory stimuli in the basal ring (Ehmer and Hoy, 2000; Akalal et al., 2006; Fahrbach, 2006). Finally, the central complex is implicated in spatial navigation (Pfeiffer and Homberg, 2014; Honkanen et al., 2019; Le Moël et al., 2019).

Here, we take advantage of the primitively eusocial paper wasp *Polistes dominula* to test how brain plasticity is associated with behavioral flexibility (Pardi, 1996; O'Donnell et al., 2014, 2018; O'Donnell and Bulova, 2017; Rozanski et al., 2021). In this temperate wasp species, the recognition of nestmates, caste, and sex relies on both chemical and visual cues (Dani et al., 2001; Cappa et al., 2016, 2020; Beani et al., 2019; Cini et al., 2019). Females are morphologically similar and organized in a flexible caste system, according to a dominance hierarchy (Pardi, 1948). The reproductive castes emerge in mid-summer and consist of males and gynes that will become foundresses the following spring. Gynes remain on the natal nest without performing any colony tasks and then mate, form winter aggregations, and enter diapause (Reeve, 1991). The following spring, foundresses initiate construction of nests and compete for the dominant position establish a dominance hierarchy. The dominant foundress monopolizes egg-laying, and the first offspring will become workers (Strassmann et al., 2004). Therefore, subordinate foundresses and workers are involved in nest building and defense, the rearing of larvae, and foraging (West-Eberhard, 1969). In the mid-summer, adult males and new gynes emerge. Males abandon the nest early after emergence and display lek-behavior at landmarks where they mate with gynes and die at the end of fall (Beani, 1996; Beani et al., 2014). Gynes store sperm for reproduction during the following spring (Cappa et al., 2013).

In addition, *P. dominula* is also parasitized by the strepsipteran insect *Xenos vesparum*, which provides a great opportunity to explore the effect of this parasite in allocation of brain tissue (Hughes and Libersat, 2018; Libersat et al., 2018). *X. vesparum* larvae enter worker wasp larvae in the early summer and develop inside their hosts (Manfredini et al., 2010). When the hosts emerge as adults, the parasites undergo pupation and behaviorally manipulate their hosts (Hughes et al., 2004b). After metamorphosis, adult female parasites remain as obligate endoparasites inside the host, while adult males emerge from the host, and mate with females. Parasite pupae decrease the size of corpora allata in female hosts and castrate them by irreversibly inhibiting ovary development (Strambi and Strambi, 1973; Strambi et al., 1982; Hughes et al., 2004b; Beani, 2006). Parasitized workers abandon the colony and aggregate on selected plants where parasite mating occurs (Hughes et al., 2004b; Beani et al., 2018). In contrast, male wasps are less-frequently parasitized, and instead maintain their reproductive apparatus and sexual behavior (Beani et al., 2011; Cappa et al., 2014). After mating, female parasites extend the lifespan of their worker host to overwinter like a gyne (Beani et al., 2021). Instead, female and male hosts parasitized by males die at the end of the summer (Beani et al., 2021).

While brain plasticity within and across social insects has been extensively studied (Godfrey and Gronenberg, 2019), no studies have explored plasticity within a species that has morphologically similar individuals, various colony tasks, and a parasite that potentially alters brain morphology. We predicted that the relative volume of selected brain regions reflects specific sensory needs for each caste and sex (reproductive females, female workers, and males) (Rozanski et al., 2021). We also predicted higher volume of visual regions in males to detect and identify potential mates or rival males in a lek, compared to females. On the contrary, we expected more olfactory processing by females compared to males due to social interactions in the colony. We also tested for the effect of parasitic manipulation in brain allometry. We predicted a stronger parasite effect in the brain of workers, because they are castrated and show strong behavioral manipulation, compared to parasitized males who reproduce and show no changes in behavior. Finally, little is known about the specific neuroendocrine effects of female and male parasites toward female and male hosts. Based on the strong behavioral alterations induced by the parasite on worker wasps (Strambi and Strambi, 1973; Beani et al., 2017), we expected a reduction of corpora allata regardless of parasite sex. Conversely, given the mild parasite impact on male hosts (Cappa et al., 2014; Beani et al., 2017), we predicted a small effect of *X. vesparum* on male corpora allata size.

MATERIALS AND METHODS

Field Collection

We collected reproductive females ($N = 10$ foundresses and $N = 9$ gynes), non-parasitized workers ($N = 10$), workers parasitized by one *X. vesparum* female ($N = 11$) or by one *X. vesparum* male ($N = 11$), non-parasitized males ($N = 10$), and males parasitized by one or two *X. vesparum* males ($N = 9$). All samples were collected during the first days of July of 2016 and 2018, in the plain of Sesto Fiorentino (Tuscany, Italy). Males parasitized by *X. vesparum* females and parasitized gynes are lacking in our data set, due to the protandrous emergence of *X. vesparum* (Hughes et al., 2004a), and to the scarcity of male and gyne reproductive larvae during the infection period in the early summer. Wasps from each caste emerge synchronously and at specific times throughout the summer, which controls for age (Molina and O'Donnell, 2008) and seasonality effects that can influence brain development. Non-parasitized and parasitized hosts are easily distinguished by inspecting for parasite extrusions between the abdominal tergites, and parasites can be identified as female or male because of the shape of their pupal sac (**Figure 1B**). Finally, to verify which individuals were parasitized, their abdomens were preserved and dissected in 70% ethanol. We confirmed the absence of pupal parasites in female workers and males without any visible signs of parasitism. In parasitized workers and males, we also confirmed sex of the parasites and gonad development predicted for each category (**Figure 1C**). Finally, we preserved each head capsule individually in a glyoxal fixative for subsequent histological sectioning (Prefer, Anatech Ltd., Battle Creek, United States).

Histology and Measurement of Brain Regions

We first dehydrated each head capsule with a series of increasing ethanol and acetone concentrations. We then used the established concentrations for the Embed 812 resin kit (Electron Microscopy Sciences, Hatfield, United States) to embed the head capsule while maintaining their brain dimensions, following the histology protocol for *Polistes* wasps (O'Donnell et al., 2015; Rozanski et al., 2021). The samples were moved repeatedly between an open-air rocking shaker (Thermo Fisher Scientific, Waltham, United States) and a vacuum to improve infiltration of the solvent.

Next, we placed each embedded head capsule in an individual plastic mold filled with the same concentration of resin in an oven at 60°C. After 72 h, the resin was polymerized. We sectioned each brain in consecutive coronal sections with a thickness of 17 μm and stained the tissue with toluidine blue, to visualize clearly defined boundaries for each brain region. We photographed the consecutive brain sections for each specimen using a Canon EOS 5D Mark III mounted on a Leica DM IL LED microscope at 4 x magnification, including a scale of 1,000 μm.

Using the AxioVision SE64 (Zeiss, NY, United States), we outlined the area for each individual brain region (**Figure 1A**). We traced the antennal lobes and the three substructures of the optic lobes: medulla, lobula and lamina. We also traced the two calyx substructures process olfactory and visual stimuli: lip and collar, respectively, and the central complex. The remaining structures in the protocerebrum were grouped as the central brain (**Figure 1A**), following the established method for this species (Rozanski et al., 2021) and ants (Sheehan et al., 2019). Outlining of brain regions was done blind to the category for each sample. We quantified each brain region for every other section per brain, as this method shows high accuracy (i.e., $< 3.5\%$ error for 34 μm thick sections) (Ehmer and Hoy, 2000). We then determined the volume for each region by multiplying the area by the distance between sections (34 μm). We generated the 3-D brain reconstruction by using the software RECONSTRUCT (Fiala, 2005). To control for the effect of head size, we measured head width. Finally, we determined the cross-sectional area of the corpora allata by measuring the diameter of one of the two glands, following the method previously used for this species (Strambi and Strambi, 1973).

Statistical Analyses

We explored if differential volume in specific brain regions among phenotypes was the result of changes in allometric scaling (Ott and Rogers, 2010; Eberhard and Wcislo, 2011; Seid et al., 2011; O'Donnell et al., 2013; Stöckl et al., 2016; Sheehan et al., 2019). In *P. dominula*, the optic lobe represents on average 42% of the brain and may have an effect on relative neuropil scaling (Rozanski et al., 2021). Therefore, we compared investment in each sensory brain region to the central brain, instead of by the whole brain (Ott and Rogers, 2010; Stöckl et al., 2016; Sheehan et al., 2019).

We used the allometric equation $y = a^{*}x^{\beta}$ for the scaling relationship between brain regions x and y. We then logarithmically transformed the estimates β (slope) and α (intercept of a regression) by using the linear equation $\log(y) = \beta\log(x) + \log(a)$, where $\log(a) = \alpha$ (Dubois, 1897; Huxley and Teissier, 1936). Standardized Major (SMA) regression analyses were calculated by using the SMATR v.3 package for R (WartonI, Wright et al., 2006, Warton et al., 2012).

First, we tested for a common slope among non-parasitized phenotypes as a baseline comparison, consisting of males, reproductive females and workers ($H^0 = \beta_{males} = \beta_{reproductives} = \beta_{workers}$). We implemented log-likelihood tests followed by *post hoc* pairwise comparisons provided in the SMATR package. Since allometric scaling did not differ significantly between foundresses and gynes, we pooled them under a new category called "reproductives." Second, we tested for a common slope among non-parasitized workers, with one female parasite and with one male parasite, and between non-parasitized and parasitized males. The volume of brain regions did not differ between male wasp parasitized by one or two male *X. vesparum*, so we also pooled them. We compared allometric changes in the whole brain with head width, central brain with whole brain, and pooled sensory regions with changes in the central brain. Finally, we explored the allometric relationship between each sensory brain region and central brain, following our established method for this wasp species (Rozanski et al., 2021).

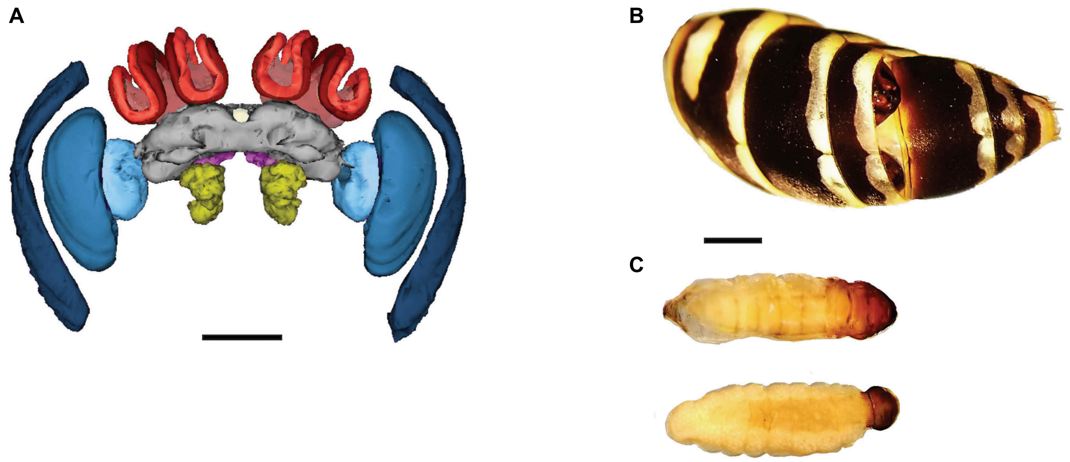

FIGURE 1 | Study system: a female brain, the abdomen of a parasitized female, and *Xenos vesparum* parasites. **(A)** Frontal view of a 3-D reconstructed brain of a female *Polistes dominula.* The sensory brain regions are color coded: substructures of the optic lobes (blue), antennal lobes (yellow), lip (bright red), collar (dark red) and the central complex (white). All sensory regions are normalized by the central brain (gray). For reference, the subesophageal zone is shown in bright pink and the mushroom body peduncles in light red. Scale bar = 500 μm. **(B)** A host abdomen shows a male *X. vesparum* pupa (top) and the cephalothorax of a neotenic female *X. vesparum* pupa (bottom) extruding from the tergites. **(C)** Same larvae of *X. vesparum* after being dissected from the host's abdomen: male parasite on top and female on the bottom. **(B,C)** Are scaled (scale bar = 2 mm).

For categories that shared a common slope, we used log-likelihood tests to calculate the slope index (SI) for the brain region comparisons described above. The SI determined if a brain region is allometric ($\beta \neq 1$), meaning that sensory brain region (y)/central brain (x) would change with size. We also used a Wald Test to calculate the common shift (H^0 = equal axis among phenotypes), for any shift along the x axis. Finally, we calculated how much larger a sensory region (y) is compared to the central brain (y), by using a grade shift index (GSI) to compare phenotypes (i.e., $H^0 = \alpha_{males} = \alpha_{reproductives} = \alpha_{workers}$). The GSI reflected changes in intercept α (elevation) with no changes in the slope β. This method facilitates pairwise volumetric comparisons between phenotypes (i.e., $e^{\alpha\ males - \alpha\ reproductives}$), by implementing a Wald test. For example, if GSI > 1, males had larger volume of a brain region compared to reproductives, and if GSI < 1 the relationship would be inverse. We specify the direction of change for each of the analyzed categories in "Results" section and **Supplementary Tables 1**, **2**. Lastly, we also ran a Kruskal-Wallis test with subsequent pairwise comparisons to determine corpora allata growth across castes and to test the effect of both parasite and host sex.

RESULTS

Investment in Sensory Regions by Caste and Sex

All brain regions, except for the central complex showed a common slope, but had differences in the GSI, common shift and/or SI depending on the specific region (**Figure 2** and **Supplementary Table 1**). Males and reproductive females had proportionally larger pooled sensory regions compared to workers (GSI = 1.056, P = 0.01 and GSI = 1.036, P = 0.006, respectively, **Figure 2C**). Males had proportionally smaller antennal lobes when compared to reproductive females (GSI = 0.87, $P < 0.001$), as an effect of both changes in elevation and a common shift (**Figure 2D** and **Supplementary Table 1**). Males also had smaller antennal lobe volume than workers (GSI = 0.926, P = 0.002, **Figure 2D**). Males had larger optic lobes than reproductive females (GSI = 1.064, P = 0.001) and workers (GSI = 1.103, $P < 0.001$, **Figure 2E** and **Supplementary Table 1**). Within females, reproductives had larger antennal lobes (GSI = 1.057, P = 0.002, **Figure 2D**) and calyces compared to workers (GSI = 1.042, P = 0.003, **Figure 2F**). Reproductives had increased optic lobe volume compared to workers (GSI = 1.037, P = 0.02, **Figure 2E**). Finally, workers showed an isometric increase in the central complex (P = 0.052), in contrast to a hypoallometric reduction of this navigational brain region in reproductive females and males (**Figure 2I**).

Investment in Sensory Regions by Parasitized and Non-parasitized Wasps

Workers parasitized by one female or one male *X. vesparum* showed no differences in allocation of most sensory brain regions, compared to non-parasitized workers (**Figures 3A, C, G**). Indeed, non-parasitized workers shared a common slope with workers with a female or a male *X. vesparum*, and no volumetric differences in the antennal lobes (**Figure 3D**) or the optic lobes (**Figure 3E** and **Supplementary Table 1**). However, we did find a change in the slope index of the whole brain in workers parasitized by a female, compared to non-parasitized workers or those parasitized by a male ($P < 0.001$, **Figure 3B** and **Supplementary Table 1**). Workers parasitized by one female had an isometric pattern, resulting in larger calyces (P = 0.031, **Figure 3F**) and collars (P = 0.045, **Figure 3H**), than non-parasitized workers and those parasitized by one male. Lastly,

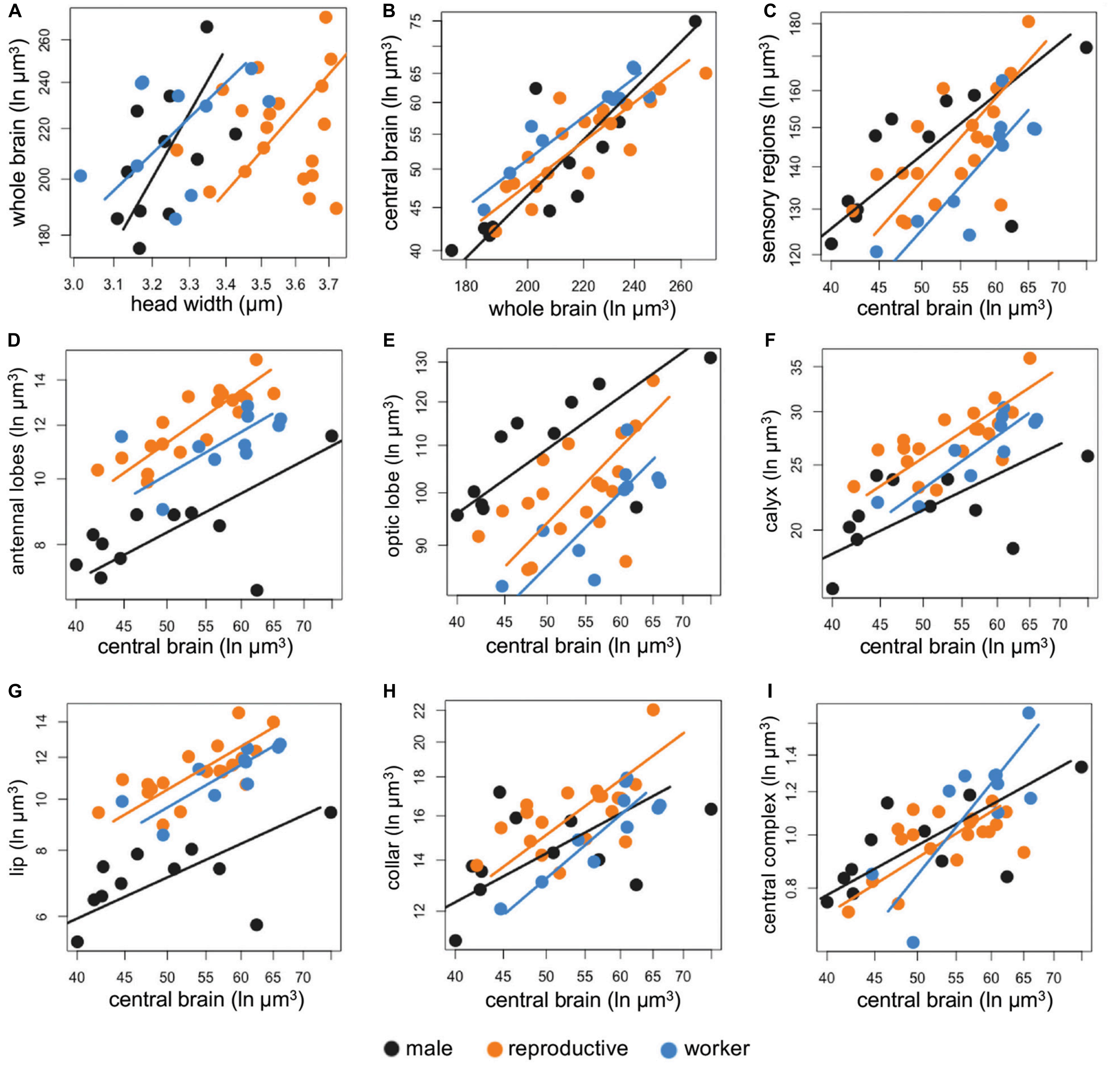

FIGURE 2 | (A–I) Comparison of the investment in sensory regions by sex and caste. The volume of each brain region was log-transformed, and each dot represents one individual. The males are depicted in black, reproductives (gynes and foundresses) in dark orange and workers in blue. The corresponding colored lines represent the slope for each category, and each dot represents an individual. Given that most comparisons shared a common slope, see **Supplementary Table 1** for full Standardized major axis (SMA) results.

workers with one male parasite had a hypoallometric reduction of the central complex in comparison to non-parasitized workers and those parasitized by a female ($P = 0.027$, **Figure 3I**).

In contrast, parasitized and non-parasitized males showed differential allocation toward specific brain regions. They shared a common slope and differences in grade shifts for the following brain regions: whole brain, antennal brain, lip, and central complex (**Supplementary Table 2**). Parasitized males had a proportionally smaller whole brains than non-parasitized males (GSI = 1.15, $P < 0.001$, **Supplementary Table 2** and **Figure 4A**). However, due to a common shift along the main slope axis, parasitized males had proportionally large antennal lobes ($P = 0.01$, **Figure 4D**), lip ($P = 0.001$, **Figure 4G**) and central complex ($P < 0.001$, **Figure 4I**) compared to non-parasitized males (**Supplementary Table 1**). In contrast, parasitized males showed a disproportionately reduced volume of the central brain ($P = 0.02$, **Figure 4B**), but disproportionately large volume of pooled sensory regions ($P = 0.03$ **Figure 4C**), optic lobes ($P = 0.03$,

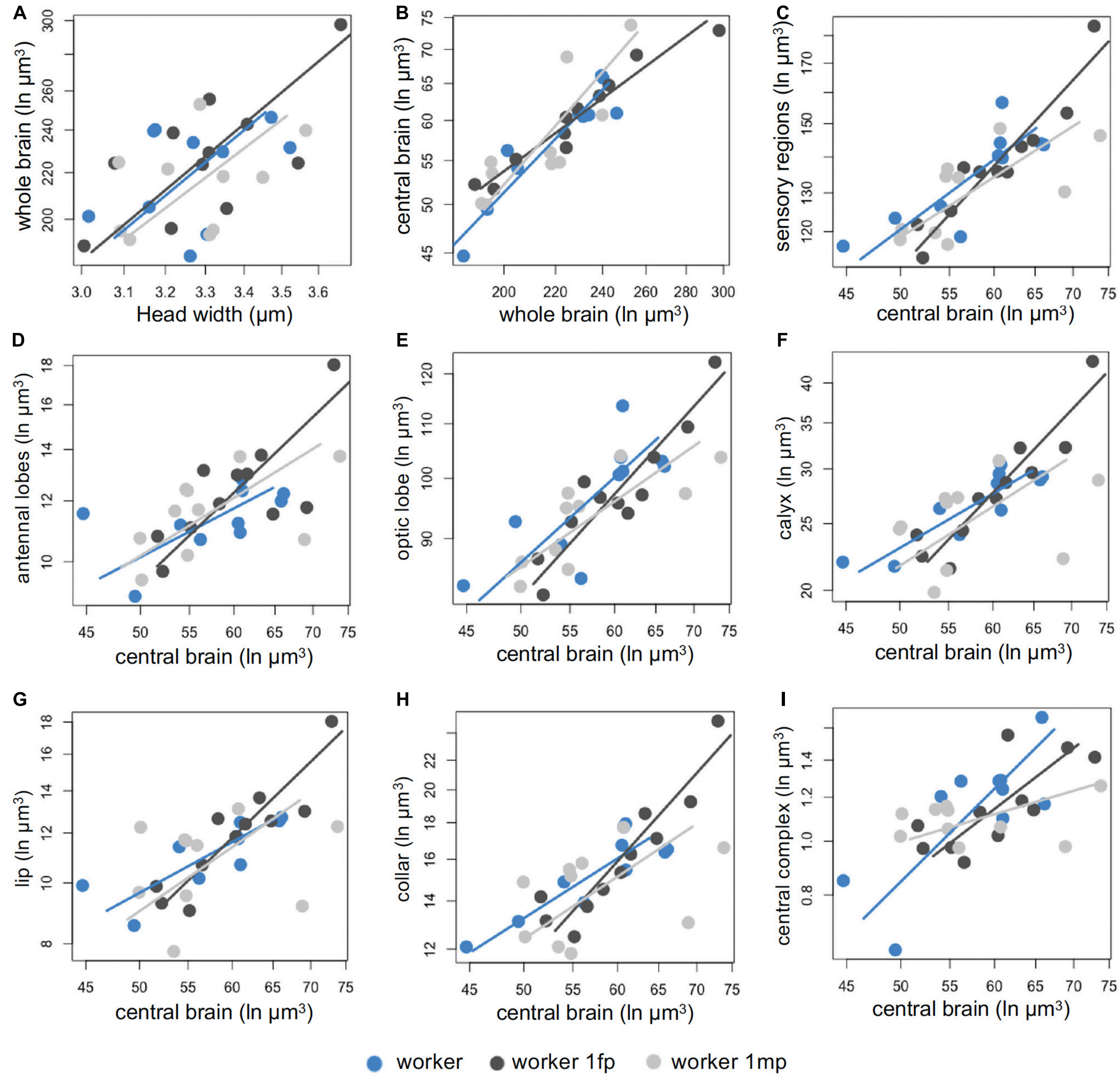

FIGURE 3 | (A–I) Comparison of the investment in sensory regions by parasitized and non-parasitized workers. Categories are depicted as non-parasitized workers (blue), workers parasitized by one female *X. vesparum* (dark gray) and workers parasitized by one male *X. vesparum* (light gray). The corresponding color-coded line represents the slope for each category and each dot represents an individual. Some comparisons shared a common slope, see **Supplementary Table 1** for full statistical results.

Figure 4D), calyces ($P = 0.04$, **Figure 4F**), and collar ($P = 0.02$, **Figure 4H**) compared to non-parasitized males (**Figure 4** and **Supplementary Table 2**).

Corpora Allata Development According to Sex, Caste, and Parasitism

The corpora allata were significantly smaller in all males compared to females ($\chi^2 = 46.86$, df = 6, $P < 0.001$, **Figure 5**). Although not significant, foundresses showed the expected trend toward large corpora allata compared to gynes ($Z = 2.02$, $P = 0.07$) and workers ($Z = 0.79$, $P = 0.06$). *Post hoc* pairwise tests showed no significant differences in workers parasitized by one female ($Z = 1.62$, $P = 0.1$) and by one male ($Z = 4.41$, $P = 0.5$) compared to non-parasitized workers. Gland size also did not differ according to parasite sex ($Z = -0.84$, $P = 0.39$), or between parasitized and non-parasitized males ($Z = -0.02$, $P = 0.98$).

DISCUSSION

We provide several lines of evidence supporting the focal hypothesis that brain plasticity facilitates differential sensory needs and life histories within the same species. First,

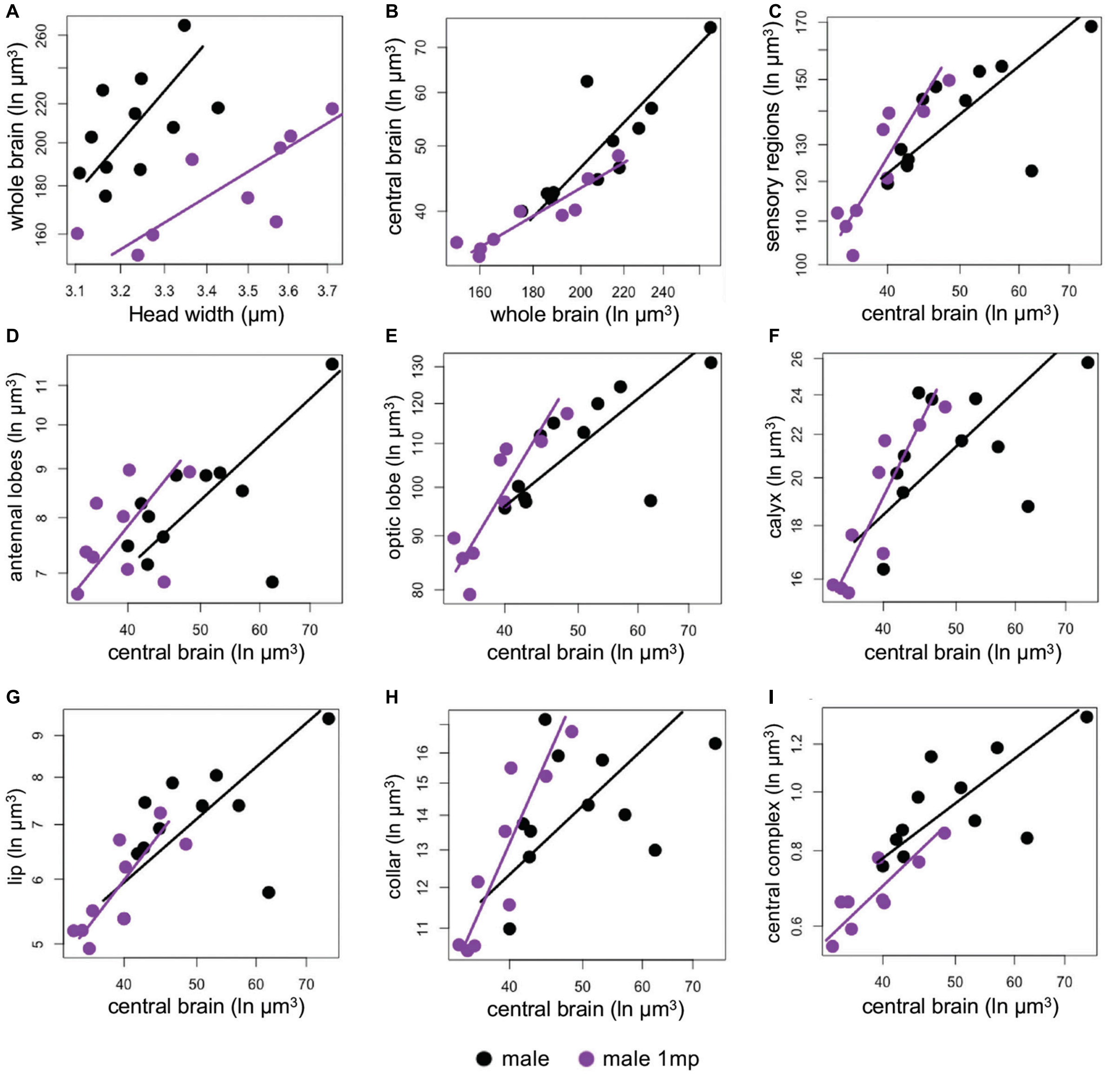

FIGURE 4 | (A–I) Comparison of the investment in sensory regions by parasitized (purple) and non-parasitized males (black). SMA fits are log-transformed per categories with the lines based on intercepts and slopes (purple for parasitized and black for non-parasitized males). Most volumetric comparisons did not share a common slope, see **Supplementary Table 2** for full SMA tests.

reproductive females also had larger calyces compared to worker females, reflecting sensory needs associated with division of labor. Second, males and females showed a consistent and significant differential investment in volume of the optic and antennal lobes. This pattern implies a life history-based plasticity of otherwise genetically shared backgrounds in *Polistes dominula*. Furthermore, we provide novel evidence for the effect of the *Xenos vesparum* parasite in neural investment by female and male hosts. Contrary to our prediction, non-parasitized and parasitized workers show moderate volumetric differences in brain sensory regions, while parasitized males showed a more drastic effect in allocation of neural tissue compared to non-parasitized males. Overall, our results are consistent with differential investment in brain regions being advantageous across social wasp species (O′Donnell et al., 2011).

The observed differential investment in sensory brain regions reflect the distinct life cycles of *P. dominula* males and females, similarly to previous studies in bees and ants (Van Praagh et al., 1980; Arnold et al., 1985; Menzel et al., 1991; Gronenberg, 2008; Mysore et al., 2009). Together, these findings suggest that in social Hymenoptera, male sexual behavior is a fundamental driver of neural organization (Beani et al., 2014). Male *P. dominula* leave their nest within a few days after emergence and gather at distinct leks to increase their mating opportunities (Beani, 1996). When attempting to mate, males can visually distinguish between females and competing males, and between workers and gynes

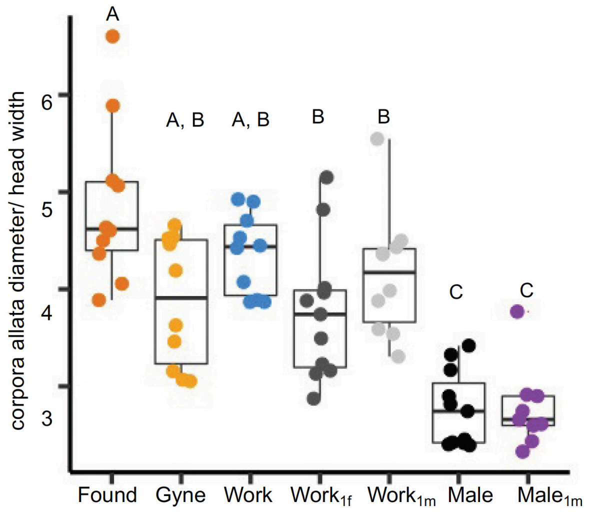

FIGURE 5 | Corpora allata size in reproductive females, workers, males, parasitized workers, and parasitized males. The cross-sectional area of the corpora allata was calculated by measuring its diameter in microns and normalized with head size. Wasp categories are color coded: found (foundresses), gynes, work (workers), work$_{1fm}$ (workers with 1 female parasite), work$_{1m}$ (worker with 1 male parasite), males and male$_{1m}$ (male with 1 male parasite). Each boxplot shows the median, 25th and 75th percentiles. The whiskers show the 5th and 95th percentiles.

(Cappa et al., 2013; de Souza et al., 2017; da Silva et al., 2021). Therefore, larger optic lobes may facilitate detection and discrimination between potential mates or male intruders in their defended territories (Beani et al., 2014). Males have smaller antennal lobes, which is likely due to experiencing less complex olfactory stimuli, as they do not engage in frequent chemically-based social interactions in the colony. In contrast, reproductive females have proportionally larger antennal lobes, lips and collars, which is consistent with other studies that show sensory needs associated with division of labor, interactions among nestmates, learning and memory (Gronenberg et al., 1996; Ehmer and Hoy, 2000; O′Donnell et al., 2011; Mora-Kepfer, 2014; Jernigan et al., 2021; Mertes et al., 2021; Rozanski et al., 2021; Uy et al., 2021). Thus, the social environment of female wasps has a wider range of chemical and sensory processing cues compared to males (Beani et al., 2014).

Within females, reproductives had proportionally larger calyces than workers, which coincides with division of labor in these social wasps (O′Donnell et al., 2007). Foundresses consistently engage in social interactions both within the colony and as gynes during winter aggregations, utilizing visual and chemical cues toward recognition (Dani et al., 2001; Cini et al., 2019). In contrast, most workers spend less time interacting with foundresses and brood on the nest, and allocate more time performing tasks such as foraging for prey and building material (Gamboa et al., 1978). Our results are similar to studies in *P. dominula* (Ehmer et al., 2001), *P. instabilis* (Molina and O'Donnell, 2007), and *Mischocyttarus mastigophorus* (O′Donnell et al., 2007) that correlate large calyces with social dominance. Contrastingly, in ants, honey bees, and *Polybia* paper wasps, subordinate forager workers have large calyces (Withers et al., 1993; Gronenberg et al., 1996; O′Donnell et al., 2004). However, these social insects form large colonies, and show specialized division of labor and age polyethism. Specifically, workers transition from tasks inside the nest to more sensory-demanding tasks outside the nest such as navigation and learning landmarks, which supports the pattern of large calyces (Gronenberg and Riveros, 2009; O′Donnell et al., 2011; Cabirol et al., 2018). Finally, differences in nutrition may also influence allocation of brain tissue between workers and foragers. In *P. metricus*, lower nutrition is associated with higher foraging and brain gene expression in workers (Toth et al., 2009; Daugherty et al., 2011). Similarly, in the primitively-eusocial bee *Augochlorella aurata*, queens have larger mushroom bodies than workers, due to increased nutrition as larvae (Pahlke et al., 2019).

Contrary to our expectations, parasites have small effects on the brain architecture of workers and did not elicit a significant reduction in the corpora allata. Male parasites induced a reduction of the central complex, compared to non-parasitized workers or workers parasitized by one female. This difference in the central complex, which is mainly implicated in spatial navigation, is not consistent with the lack of differences in behavior between workers infected by the two sexes. Noticeably, workers parasitized by one *X. vesparum* female showed larger calyces than non-parasitized workers and those parasitized by one male. Interestingly, workers parasitized by one female enter diapause and resemble the behavioral and physiological phenotype of overwintering gynes, while workers parasitized by a male die at the end of summer like non-parasitized ones (Beani et al., 2021). Thus, it is likely that the female parasite should minimize cognitive impairment of its worker host.

In contrast, male parasites had a more drastic effect in the brain architecture of *P. dominula* males, which are parasitized less frequently than females. Parasitized males had significantly smaller whole brains and central brains than non-parasitized males. They also showed a significant increase in the volume of several sensory brain regions, including the antennal and optic lobes, and two substructures of the calyx: lip and collar. Remarkably, neuroendocrine manipulation does not seem to occur in parasitized males, as they develop their corpora allata, testes, seminal vesicles and accessory glands and attempt to mate (Cappa et al., 2014; Beani et al., 2017). The inability to castrate the male may likely result in brain manipulation instead. Given that the brain is an expensive tissue to produce (Niven and Laughlin, 2008; Keesey et al., 2020), the parasite may reallocate energy and resources to develop inside the host, resulting in the observed small brains.

Notably, only a few studies have tested for neuroanatomical changes induced by parasites that do not directly infect in the brain, but instead lodge inside insect body cavities. The parasitic fungus *Ophiocordyceps* manipulates the behavior of their ant host, but does not induce structural changes in the brain (Hughes et al., 2011). Instead, the fungal hyphae surround muscle fibers (Hughes et al., 2011; Fredericksen et al., 2017). The hairworm *Paragordius tricuspidatus* induces neurogenesis in the mushroom bodies of its cricket host, before manipulating it to jump into the water to continue the parasite's lifecycle

(Thomas et al., 2003). Infected crickets also showed differential expression of proteins in the head (Biron et al., 2006). Together with our findings, these results suggest that different parasites likely hijack distinct neural mechanisms to control the behavior of their insect hosts (Hughes and Libersat, 2018).

Overall, our results demonstrate that brain plasticity is associated with sensory needs in males and within female castes of *P. dominula*, but that parasitic manipulation can also drive differential investment of brain regions depending on both host and parasite sex. Intriguingly, workers infected with a female parasite show a strong manipulation effect of the parasite on caste determination, lipid storage, and prolonged lifespan in parasitized females that act as their main host (Beani et al., 2021), but more dampened effects on allocation of brain tissue. In turn, the reproductive apparatus and behavior of parasitized males are essentially unaffected, but they experience stronger volumetric changes in brain regions. Previous work has shown that *X. vesparum* drives gene expression changes of workers toward a gyne-like pattern; thus, the parasite is manipulating the transcriptomic plasticity of the caste system (Geffre et al., 2017). Parasitized females also show low levels of haemolymphatic protein and juvenile hormone compared to non-parasitized females, but with no difference between non- parasitized and parasitized males (Strambi and Strambi, 1973; Strambi et al., 1982). Our study shows that strepsipteran do not drive evident neuroanatomical changes in their females hosts, suggesting that this parasite may be relying on other manipulation mechanisms (Libersat et al., 2018).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

LB and FC collected the wasp and parasite field samples. KG performed histological preparation of specimens and collected volumetric data. FU analyzed the data. KG, LB, FC, and FU contributed to the first draft of the manuscript. All authors provided input to concept and design of this project, data interpretation, along with reviewing and editing the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.803437/full#supplementary-material

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