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To cite this article: Francisca H. I. D. Segers, Christoph Grüter, Cristiano Menezes, Sidnei Mateus & Francis L. W. Ratnieks (2022) Correlated expression of phenotypic and extended phenotypic traits across stingless bee species: worker eye morphology, foraging behaviour, and nest entrance architecture, Journal of Apicultural Research, 61:5, 598-608, DOI: [10.1080/00218839.2022.2114711](https://doi.org/10.1080/00218839.2022.2114711)

To link to this article: <https://doi.org/10.1080/00218839.2022.2114711>



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ORIGINAL RESEARCH ARTICLE



Correlated expression of phenotypic and extended phenotypic traits across stingless bee species: worker eye morphology, foraging behaviour, and nest entrance architecture

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ABSTRACT

Stingless bees are the most species-rich group of eusocial bees and show great diversity in behaviour, ecology, nest architecture, colony size, and worker morphology. How this variation relates to varying selection pressures and constraints is not well understood. Variation can be caused by selection acting on behavioural or morphological traits, both alone and in correlation across traits. Here we tested whether behavioural and morphological traits important for foraging and defence are linked to nest-entrance architecture, an extended phenotype relevant to both foraging and nest defence. Using 23 species we investigated whether eye size, nest entrance size, landing behaviour and foraging method show cross-species correlations. A phylogenetically-controlled comparative analysis revealed that species with relatively smaller eyes build relatively larger entrances, which in turn are associated with faster landing approaches and fewer landing errors by foragers, both of which could reduce predation risk. Concerning foraging, mass-recruiting species have c. 10-times larger entrance holes than species with a solitary foraging strategy. Larger entrances could help species with mass recruitment to rapidly increase forager traffic or mount a strong defensive response when under attack. Our results show that studying correlations among different traits helps understand phenotypic diversity in species rich groups.

ARTICLE HISTORY

Received 1 September 2021

Accepted 2 August 2022

KEYWORDS

Stingless bees; nest entrance architecture; foraging; nest defense; species diversity; extended phenotype

Introduction

Organisms must simultaneously address many challenges in order to survive and reproduce. For example, an animal must obtain food for growth, mate, avoid diseases and predators, often all at the same time. The solutions to these challenges can conflict so that adaptive phenotypic traits often reflect compromises and trade-offs (e.g., Flatt & Heyland, 2011; Roff, 2001; Schluter et al., 1991; Shoval et al., 2012; Stearns, 1989). Countless and often subtle correlations among traits exist, beyond the well-studied major life-history trade-offs, all of which contribute to the diversity of the natural world. In foraging, for example, social insects face exploration-dominance trade-offs, where some species are better at dominating food sources, while others are better at discovering food sources, which in turn is thought to promote diversity in communities (Hubbell & Johnson, 1978; Lebrun & Feener, 2007; van Oudenhove et al., 2018).

With c. 550 described species in c. 60 genera, stingless bees (Meliponini) are the largest and most diverse group of eusocial bees (Grüter, 2020; Rasmussen & Cameron, 2009). They play important roles as pollinators in tropical and sub-tropical environments worldwide (Grüter, 2020; Heard, 1999; Ramalho, 2004; Roubik, 1989; Vit et al., 2018). Their diverse morphology and foraging styles mean that, as a group, stingless bees can exploit many different food sources (Grüter, 2020; Hrnčíř & Maia-Silva, 2013; Lichtenberg et al., 2017; Roubik, 1989). Stingless bees vary not only in their behaviour and morphology, but also in nest architecture, which is a key part of the extended phenotype of a colony. A particularly important, striking and variable architectural trait is the nest entrance, which is typically constructed by the colony from materials including wax, resin and mud (Figure 1) (Biesmeijer et al., 2007; Couvillon et al., 2008; Grüter, 2020; Roubik, 2006; Wille & Michener, 1973). Entrances vary from being

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Supplemental data for this article is available online at <https://doi.org/10.1080/00218839.2022.2114711>.

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Figure 1. Nest entrances of 19 of the 23 species studied (see [Figure S1](#) for two more species). (a) *Friesella schrottkyi*, (b) *Frieseomelitta silvestrii*, (c) *Frieseomelitta varia*, (d) *Lestrimelitta limao*, (e) *Leurotrigona muelleri*, (f) *Melipona flavolineata*, (g) *Melipona scutellaris*, (h) *Melipona rufiventris*, (i) *Nannotrigona testaceicornis*, (j) *Paratrigona lineata*, (k) *Plebeia droryana*, (l) *Partamona helleri*, (m) *Scaptotrigona bipunctata*, (n) *Scaptotrigona depilis*, (o) *Scaptotrigona polysticta*, (p) *Tetragona elongata*, (q) *Tetragonisca angustula*, (r) *Trigona braueri* and (s) *Trigona recurva* (photos by C. Grüter).

small and inconspicuous (e.g., in *Frieseomelitta* and some *Melipona*) to large and elaborate with ornate tubes of more than 50 cm length (e.g., in *Lestrimelitta*, *Geniotrigona* or *Scaptotrigona*) (see Wille & Michener, 1973). The size of the entrance has

implications for foraging and defence. Species with relatively small entrances have more restricted foraging traffic, but they also employ fewer guards to defend the nest (Biesmeijer et al., 2007; Couvillon et al., 2008). Having a large entrance and

Table 1. An overview of the species used in the study, with the species averages of head width, eye length (both in mm), head surface (mm²), landing speed (cm/sec), forager weight (mg) and landing errors (as proportion of arrivals). Location refers to where colonies were located during data collection (RP: Ribeirão Preto, São Paulo; SS: São Simão, São Paulo; B: Belém, Pará). The *T. nataliae* and *F. silvestrii* colonies came originally from Nova Xavantina, Mato Grosso. References provide information about the recruitment style.

| Species | Location | Colonies | Head width | Head surface | Eye length | Rel. eye length | Speed | Total traffic/s | Error rate | Weight | Rel. inner entrance | Rel. outer entrance | Mass-recruitment | Reference |
|------------------------------------|----------|----------|------------|--------------|------------|-----------------|-------|-----------------|------------|--------|---------------------|---------------------|------------------|--|
| <i>Friesella schrottkyi</i> | RP | 2 | 1.42 | 1.42 | 0.92 | 0.64 | 5.09 | 0.63 | 0.17 | 2.92 | 9.83 | 15.98 | | |
| <i>Friesomelitta silvestrii</i> | RP | 3 | 1.86 | 2.27 | 1.11 | 0.58 | 5.63 | 0.04 | 0.00 | 7.05 | 2.22 | 209.81 | No | Nieh (2004) |
| <i>Friesomelitta varia</i> | RP | 3 | 2.26 | 3.18 | 1.39 | 0.64 | 6.58 | 0.20 | 0.03 | 10.45 | 4.18 | 165.96 | No | Esch et al. (1965) |
| <i>Geotrigona mombuca</i> | RP | 2 | 2.43 | 3.77 | 1.62 | 0.70 | | 0.10 | 0.13 | 12.41 | 9.00 | 12.31 | Yes | Aguilar et al. (2005) |
| <i>Lestrimelitta limao</i> | RP | 2 | 1.99 | 3.21 | 1.23 | 0.54 | 32.07 | 1.49 | 0.06 | 11.76 | 237.06 | 416.38 | Yes | Aguilar (2004) |
| <i>Leurotrigona muelleri</i> | RP | 2 | 1.06 | 0.83 | 0.66 | 0.51 | 8.34 | 0.13 | 0.14 | 2.19 | 15.92 | 56.97 | No | Nieh (2004) |
| <i>Melipona flavolineata</i> | B | 3 | 3.55 | 8.17 | 2.18 | 0.55 | 14.39 | 0.08 | 0.09 | 61.73 | 5.53 | 39.79 | | |
| <i>Melipona quadrifasciata</i> | RP | 3 | 3.93 | 9.84 | 2.15 | 0.52 | 16.64 | 0.07 | 0.03 | 69.14 | 5.44 | 144.36 | No | Jarau et al. (2003), Jarau and Hrnčíř (2009) |
| <i>Melipona rufiventris</i> | SS | 2 | 3.86 | 9.28 | 2.24 | 0.58 | 22.96 | 0.12 | 0.00 | 57.42 | 5.42 | 38.03 | No | Jarau et al. (2003), Jarau and Hrnčíř (2009) |
| <i>Melipona scutellaris</i> | RP | 3 | 4.19 | 11.00 | 2.51 | 0.58 | 23.74 | 0.09 | 0.00 | 80.33 | 8.61 | 138.09 | No | Jarau et al. (2003), Jarau and Hrnčíř (2009) |
| <i>Melipona seminigra</i> | B | 3 | 3.96 | 10.38 | 2.36 | 0.55 | 48.93 | 0.11 | 0.05 | 79.07 | 13.78 | 140.74 | No | Jarau et al. (2003), Jarau and Hrnčíř (2009) |
| <i>Nannotrigona testaceicornis</i> | RP | 3 | 1.67 | 2.28 | 1.18 | 0.62 | 33.75 | 0.85 | 0.10 | 6.89 | 57.45 | 80.72 | No | Nieh (2004) |
| <i>Paratrigona lineata</i> | RP | 2 | 1.73 | 2.19 | 1.31 | 0.74 | | 0.22 | 0.10 | 5.65 | 10.67 | 19.57 | | |
| <i>Paratrigona helleri</i> | RP | 2 | 2.52 | 4.29 | 1.62 | 0.64 | | 0.19 | 0.03 | 15.97 | 420.82 | 1126.40 | Yes | Nieh (2004); Aguilar (2004) |
| <i>Plebeia droryana</i> | RP | 3 | 1.60 | 1.71 | 1.04 | 0.63 | 11.78 | 0.22 | 0.03 | 4.36 | 14.69 | 35.78 | No | Nieh (2004) |
| <i>Scaptotrigona bipunctata</i> | RP | 3 | 2.72 | 4.02 | 1.34 | 0.50 | | 0.47 | 0.04 | 19.35 | 162.19 | 331.33 | Yes | Aguilar (2004) |
| <i>Scaptotrigona depilis</i> | RP | 4 | 2.82 | 5.34 | 1.47 | 0.57 | 39.83 | 1.16 | 0.03 | 16.94 | 45.80 | 93.51 | Yes | Jarau et al. (2003) |
| <i>Scaptotrigona polysticta</i> | SS | 4 | 2.63 | 4.50 | 1.55 | 0.57 | 23.42 | 0.25 | 0.11 | 19.89 | 25.37 | 38.32 | Yes | Aguilar (2004) |
| <i>Tetragona elongata</i> | RP | 3 | 2.51 | 3.89 | 1.48 | 0.64 | 25.10 | 1.88 | 0.07 | 12.43 | 42.43 | 319.52 | No | Jarau et al. (2003) |
| <i>Tetragonisca angustula</i> | RP | 3 | 1.69 | 1.85 | 1.10 | 0.69 | 9.59 | 0.64 | 0.02 | 3.98 | 14.18 | 23.58 | No | Nieh (2004) |
| <i>Trigona braueri</i> | RP | 2 | 2.61 | 4.17 | 1.54 | 0.61 | | 8.25 | 0.03 | 15.91 | 422.46 | 1504.21 | Yes | Grüter (2020) |
| <i>Trigona recursa</i> | RP | 2 | 2.34 | 3.14 | 1.32 | 0.57 | | 1.78 | 0.02 | 12.23 | 115.87 | 271.76 | Yes | Jarau et al. (2003) |
| <i>Trigonisca nataliae</i> | RP | 2 | 1.17 | 0.88 | 0.75 | 0.66 | | 0.15 | 0.14 | 1.47 | 9.95 | 143.96 | | |

unrestricted foraging traffic could be particularly beneficial for species with large colonies and mass-recruitment. These species predominantly use pheromone trails or chemical markings of food sources to recruit large numbers of nestmates to food sources (Barth et al., 2008; Hrncir, 2009; Hrncir & Maia-Silva, 2013; Jarau, 2009; Lindauer & Kerr, 1960; Nieh, 2004). Mass-recruitment can lead to rapid bursts of foraging activity after the discovery of a new food source (Roubik, 1989), which is likely to greatly increase peak traffic at entrances. This would increase the benefit of relatively larger entrances in mass-recruiting species. Entrance size and architecture can also affect landing speed and the risk of mid-air collisions, which in turn impact both foraging efficiency and predation risk (Shackleton et al., 2019; Tichit et al., 2020a).

Nest entrance architecture may also be affected by visual constraints and biases. For example, there is evidence that nest entrance shape in stingless bees has evolved convergently to resemble flowers (Biesmeijer et al., 2005). Indeed, it seems plausible that entrance appearance and size are linked to bee vision if, as seems likely, homing bees use entrances as a visual beacon for orientation. Species with poor visual acuity might have to build relatively larger or more ornate entrances than species with better vision. Alternatively, species with lower visual acuity could reduce their flying speed during the landing and entering process to avoid landing errors (Wheatley et al., 2018). Numerous predators hunt for returning foragers at entrances of stingless bee nests, including spiders, wasps, geckos and toads (Grüter, 2020; Halcroft et al., 2013; Penney & Gabriel, 2009; Roubik, 1989; Schwarz, 1948; Shackleton et al., 2019) and foragers that miss the entrance, in some cases bouncing off in an uncontrolled direction, are more likely to be captured (Penney & Gabriel, 2009; Shackleton et al., 2019). Thus, we hypothesise that the species-specific phenotypic traits of eye size, entrance size, landing speed and the proportion of returning foragers that make landing errors are likely to be interrelated.

Comparative studies facilitate understanding how traits are correlated and identify potential selection pressures that shape phenotypic trait variation in stingless bees (Couvillon et al., 2008; Grüter et al., 2017; l'Anson Price et al., 2021; Nunes et al., 2017; Rasmussen & Camargo, 2008). Until relatively recently, phylogenetically controlled comparative studies were hampered by uncertainties regarding the phylogenetic relationships within the stingless bees. However, an improved understanding of their phylogeny has made comparative studies more feasible (Rasmussen & Cameron, 2009). Here we combine phylogenetic information with our own measurements of entrance size, eye size, landing behaviour plus

literature-based information of the foraging strategy of 23 stingless bee species from Brazil to explore whether and how these traits are correlated. We predicted, for example, that species with smaller eyes would build relatively larger entrances and/or land at slower speeds. We also tested the prediction that species that use mass-recruitment build relatively larger entrances.

Materials and methods

Study species

We measured the entrance size area of 23 species of stingless bees in three Brazilian states (Table 1). They differed in their foraging method, entrance architecture, body size and general ecology. We studied both wild colonies and colonies kept in wooden hive boxes, 2 to 4 colonies per species. All colonies in hives included in this study had built their typical, species-specific nest entrances.

Landing behaviour

We quantified the foraging traffic of each colony by videoing the entrance. This foraging traffic (the number of bees entering or leaving the colony per second) provides a reliable estimate of relative colony size across species (Grüter et al., 2017; Leão, 2019). Videoing was done during days with good foraging conditions, using a Sony HDR-HC3 camera in front of the nest entrance, taking care not to obstruct the flight path of the returning bees. From the videos, we counted the traffic rate and determined the proportion of arrivals that ended in failed landing attempts. A landing attempt was considered a failure if the bee bounced off the nest entrance or missed the entrance entirely.

We then photographed each nest entrance from the front to estimate both the outer entrance size, that is, the total circumference of the entrance including any structural additions, which could be used as a visual target for returning foragers, and the inner entrance size, which is the actual area of the opening through which foragers enter and leave (see Figure S1a, b). We placed a ruler next to the nest entrances to be able to make accurate measurements from the photographs. The inner and the outer entrance areas were subsequently determined with ImageJ 1.46 and averaged for each species. We compared our species averages with those reported in Couvillon et al. (2008) to detect potential discrepancies. For the 12 species that were included in both studies, entrance size measurements (our inner entrance size measurements) were very similar, with an $R^2 = 0.93$ (see our Table 1 and Table 1 in

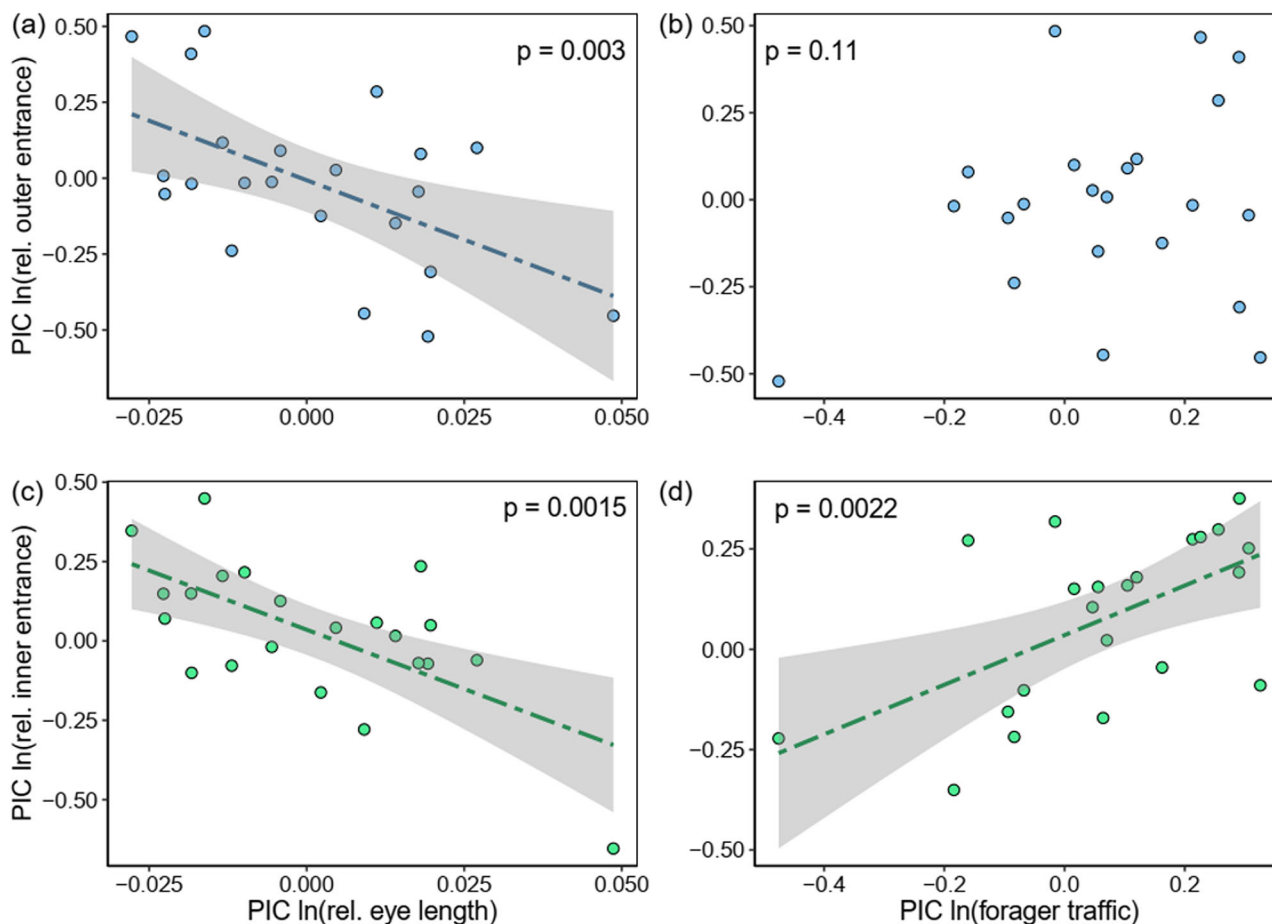


Figure 2. Relationship between relative inner and outer entrance size (entrance area divided by head area) and relative eye size (eye length divided by the cube root of the bee weight) (a, c) and forager traffic (b, d) for 23 species. Note that the p-values are based on phylogenetic generalised least squares (PGLS) models as described in the Materials and Methods section. The best fit lines are based on multiple linear regression of phylogenetically independent contrasts (PICs), which are mathematically equivalent to PGLS. To increase the visibility of the effects in c and d, the response variable (inner entrance) was corrected for the effect of, respectively, forager traffic and relative eye length. The grey shaded areas represent 95% confidence intervals.

Couvillon et al. (2008)), confirming that entrance size is a consistent trait.

To measure flight entry speed, we attached a toothpick beside the nest entrance, with the toothpick parallel to the flight path of arriving bees. The video camera was the same height as the entrance at 90 degrees to the toothpick at a distance of approximately 1.5 m. We videoed (25 frames/second) until we had recorded 15 landings per colony. Due to the positions of some wild nests and their entrances, videoing was possible for only 16 species. To quantify a consistent landing speed, we determined the distance travelled between the last two frames before the bee disappeared into the entrance hole. The distances were measured with ImageJ 1.46 and averaged for each species.

Size measurements

After videoing, we collected 5–6 foragers from each colony to measure bee weight, to 0.1 mg using a Sartorius TE64 high precision balance, head and eye

size. Eye size (see below) was an indicator of potential visual acuity. In bees and many other insects, visual acuity and sensitivity depend on eye morphology, principally eye size and ommatidia number (Jander & Jander, 2002; Kapustjanskij et al., 2007; Narendra et al., 2011; Somanathan et al., 2009; Streinzer et al., 2016).

We removed the head from the body and placed it onto 1 mm graph paper. We took photographs of each head with a Nikon D7000 digital camera with a macro lens (Nikon AF-S VR 105 mm) at a standard distance. From the photo, head width (HW) and height (HH) were determined with ImageJ 1.46. We estimated the head area (HA) of each bee using the formula for an ellipse: $HA = \pi \left(\frac{HW}{2}\right) \left(\frac{HH}{2}\right)$. The head area was used to calculate the relative entrance size of each species by dividing both inner and outer mean entrance area by the mean head area (Couvillon et al., 2008). The relative inner and outer entrance sizes correlated positively across species, i.e., species with larger inner entrances also tended to have larger outer entrances (model II regression,

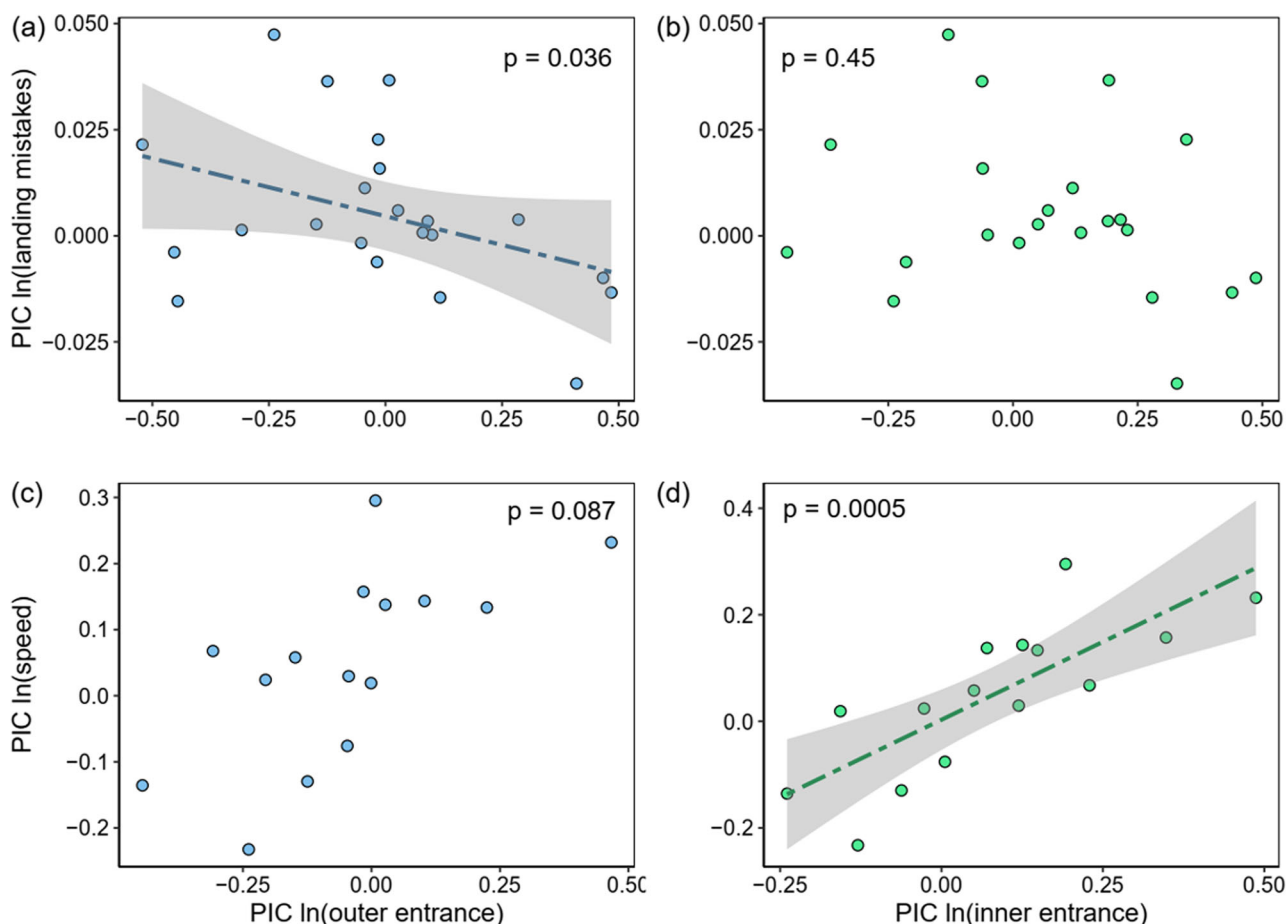


Figure 3. Relationship between relative inner and outer entrance size (entrance area divided by head area) and landing error rate (a, b) and approach flight speed (c, d) for 23 and 16 species respectively. As in Figure 2, the p-values are based on phylogenetically corrected generalised least squares (PGLS) models. The best fit lines are based on multiple linear regression of phylogenetically independent contrasts (PICs). The grey shaded areas represent 95% confidence intervals.

$R^2 = 0.41$, slope = 0.86, 95% confidence interval (C.I.) of slope = 0.61-1.21, $p = 0.0009$.

Eye length and width were measured by taking the maximum length and width of the eye. Eye length was highly correlated with eye width ($R^2 = 0.96$) and so was used as a measure of eye size (Figure S1c, line 3). We also checked whether eye length scales isometrically with bee size (see below) because bee size is the major determinant (97% of variation explained) of ommatidia number and visual sensitivity in many bees (Jander & Jander, 2002; Streinzer et al., 2016). To calculate a species-specific value of eye length relative to bee size, we divided the mean eye length by the cube root of the mean bee weight (because of the cubic relationship between length and weight) (see e.g., Grüter et al., 2012).

Forager recruitment method

We divided the study species into two broad foraging-recruitment categories based on data available in the literature (Grüter, 2020; l'Anson Price et al., 2021; Jarau & Hrncir, 2009; Lindauer & Kerr, 1960; Nieh, 2004): (1) species that use mass-recruitment,

mostly based on chemical trails, that are able to recruit large numbers of nestmates to a food source within a short time period; (2) species that show weak or no recruitment to food sources (see Table 1). Of the 23 study species, 19 could be classified. Since *Trigona braueri* belongs to the *T. fulviventris* species group (Rasmussen & Camargo, 2008), we assumed that it uses chemical trails, like all other studied *Trigona* (Grüter, 2020). Mass-recruitment is typically location-specific recruitment and results in rapid burst-like increases in foraging (Hrncir & Maia-Silva, 2013; Lindauer & Kerr, 1960; Roubik, 1989). Some species not classified as mass-recruiters may show a limited ability to recruit to food source locations, but recruitment is slow and imprecise (Hrncir, 2009; Jarau et al., 2003; Peng et al., 2021).

Statistical analysis

All statistical tests used R 3.6 (R Development Core Team, 2013). We used phylogenetic generalised least squares (PGLS) models (R package *nlme*) while assuming that traits evolve under a Brownian motion model (Paradis, 2011) with the *corBrownian* function, as implemented in the R package *ape* (Paradis &

Schliep, 2019). Variables were logarithmically transformed (natural logarithm) before analyses (Paradis, 2011). To correct the data for phylogenetic dependence before plotting we used phylogenetically independent contrasts (PICs), which are mathematically equivalent to GLS.

The phylogenetic framework for the comparative analysis of our species relied on the tree of Rasmussen and Cameron (2009), complemented with information from Ramírez et al. (2010). The chronogram from Rasmussen and Cameron (2009) was pruned to include only the taxa relevant for this study (see Figure S2). For *Trigona braueri* and *T. recursa* we assumed a divergence time of 18 million years, since *T. braueri* is considered to be part of the *Trigona fulviventris* species group which diverged from the *T. recursa* branch an estimated 18 million years ago (Rasmussen & Camargo, 2008; Rasmussen & Cameron, 2009). We note that *Tetragona elongata* corresponds to the form often called *Tetragona clavipes* in south-eastern Brazil (Pedro, 2014).

We tested whether relative eye length, landing speed and foraging method predict entrance size. While we considered relative eye size to be particularly interesting because relatively large eyes could indicate selection for better vision, we also tested the role of absolute eye size (statistical values for absolute eye size are provided between braces, “[]”). We also tested whether entrance size predicts the probability of landing errors. We ran separate models for the outer and the inner relative entrance sizes because these two entrance features might have different functions, with the outer entrance primarily functioning as a visual beacon. To avoid over parameterization, we did not include more than 2 predictor variables per model. Figure S3 summarises the traits studied in relation to relative inner and outer entrance size and our results.

To check whether eye length scales isometrically with bee size (and thus can be expected to predict ommatidia number, Jander & Jander, 2002) we used reduced major axis regression (model II) (Laws & Archie, 1981) to test whether the slope b of the relationship $\ln(\text{eye length}) = \ln(a) + b \times \ln(\sqrt[3]{\text{body weight}})$ differs from 1 (Grüter et al., 2012; Hölldobler & Wilson, 2009; Wilson, 1953).

Results

Data from the 23 species are summarised in Table 1. We tested whether eye size increases or decreases disproportionally with body size across species. This could occur if, for example, smaller species compensate for reduced visual acuity by having disproportionately larger eyes. However, the 95%-confidence interval for the slope of the relationship between

the natural logarithm of the eye length and the natural logarithm of the cube root of body weight is not significantly different from 1 (model II regression, $R^2 = 0.93$, slope = 0.92, 95% confidence interval (C.I.) of slope = 0.81–1.03), indicating that eye length and bee size scale isometrically.

We tested whether the relative eye length was related to the relative size of the inner or outer entrance area. Since colony size is also likely to affect the relative size of the entrance (Biesmeijer et al., 2007; Couvillon et al., 2008), foraging traffic was included as a second predictor. We found a significant negative relationship between relative eye length and both outer and inner entrance size (Figure 2a and b) (outer entrance: PGLS, $t = -3.38$, $p = 0.003$ [absolute eye length: $t = 0.71$, $p = 0.49$]; inner entrance: $t = -3.67$, $p = 0.0015$ [$t = 0.20$, $p = 0.84$]). Higher foraging traffic was not associated with the outer entrance size (Figure 2c) (PGLS, $t = 1.67$, $p = 0.11$), but was significantly and positively associated with inner entrance size (Figure 2d) ($t = 3.51$, $p = 0.0022$).

We then tested whether relative entrance size predicted the probability that returning foragers make landing errors. Because this might also depend on visual acuity, we included relative eye length as a second predictor in the model. We found that species with relatively smaller outer entrances made significantly more errors (Figure 3a) (PGLS, $t = -2.24$, $p = 0.036$), whereas relative eye length did not affect the error rate (PGLS, $t = -1.11$, $p = 0.28$ [$t = -0.71$, $p = 0.49$]). A separate model was run to test for the role of inner entrance size, which showed no significant relationship with error rate (Figure 3b) (PGLS, $t = -0.78$, $p = 0.45$; relative eye length: $t = -0.26$, $p = 0.80$ [$t = -0.91$, $p = 0.38$]).

Because we only had landing speed data for 16 species, we analysed this separately. We first tested whether the speed of bees on the final approach to the entrance affected the probability of landing errors, but found no significant relationship (PGLS, $t = -0.42$, $p = 0.68$). We then tested whether relative entrance size predicts landing speed. Since this might also depend on the relative eye size, we included this variable as a second predictor. There was a positive trend, but no significant relationship between outer entrance size and approach flight speed and no significant relationship with relative eye length (Figure 3c) (PGLS, outer entrance: $t = 1.85$, $p = 0.087$; relative eye length: $t = -0.47$, $p = 0.65$ [$t = 0.60$, $p = 0.56$]). However, foragers of species with larger inner entrance sizes landed at significantly faster speeds (Figure 3d) (PGLS, inner entrance: $t = 4.59$, $p = 0.0005$; relative eye length: $t = -0.59$, $p = 0.56$ [$t = 1.44$, $p = 0.17$]).

Mass-recruiting species had larger inner entrances (Figure S4a) (PGLS, $t = 2.45$, $p = 0.025$), but foraging method was not related to the size of the outer entrances ($t = 1.05$, $p = 0.31$). We also tested whether mass-recruiting species have smaller eyes or larger colonies than species that mostly use a solitary foraging strategy, but we found no relationship between mass-recruitment and relative eye length (Figure S4b) (PGLS, $t = -0.85$, $p = 0.41$ [$t = 0.97$, $p = 0.35$]) or colony size ($t = 0.90$, $p = 0.38$).

Discussion

Our results show both significant and non-significant relationships among behavioural and morphological traits connected to foraging and nest-entrance architecture. This highlights the value of comparative studies using this diverse and variable group of eusocial bees. Species with relatively smaller eyes build relatively larger entrances (Figure S3). This was true for both outer and inner entrances, and is consistent with the hypothesis that stingless bee nest entrances provide a visual target for approaching bees (Figure 2) (Camargo & Pedro, 2003). Entrance features are likely to guide returning bees in the immediate vicinity of the nest (<1 m), whereas landmarks are thought to be more important at greater distances (Zeil & Wittmann, 1993). Eye size is closely related to ommatidia number and bee size, and has been shown to determine visual acuity and light sensitivity in many insect groups (Jander & Jander, 2002; Moser et al., 2004; Greiner et al., 2007; Kapustjanskij et al., 2007; Somanathan et al., 2009; Wcislo & Tierney, 2009; Narendra et al., 2011; Streinzer et al., 2016). Interestingly, we found that relative eye size (eye length divided by the cube root of bee weight), rather than absolute eye size was linked to entrance size. This suggests that species that invest less in visual perception might need to build larger entrances to compensate. Our results are consistent with the hypothesis of Biesmeijer et al. (2005) that visual perception in stingless bees affects entrance architecture. Their findings indicate that both flowers and entrances frequently feature stripes, dark centres and peripheral dots and they argue that these traits evolve convergently due to sensory biases. Our results provide further support for a link between stingless bee vision and entrance architecture.

Returning bees of species with smaller inner entrances also approach the entrance more slowly (Figure 3), possibly to reduce errors. The link between entrance size and speed is exemplified by *Partamona helleri*. This species builds the characteristic “toad mouth” entrance, i.e., with a large outer entrance combined with a small inner funnel (Figure

11), that evolved within *Partamona* and which occurs in many species of this genus (Camargo & Pedro, 2003; Couvillon et al., 2008; Shackleton et al., 2019). This remarkable architectural invention allows bees to speed up in their final approach to the entrance and crash in, while bees of species with smaller entrances have to slow down to land and enter their nest on foot (Couvillon et al., 2008; Shackleton et al., 2019). Shackleton et al. (2019) measured *P. helleri* workers entering their nests at a speed of 90–130 cm/sec, which is more than twice as fast as the fastest of the 16 species whose speed we measured (Table 1). Adjusting the landing speed according to entrance size does, however, not seem to fully reduce landing mistakes in species with smaller entrances, as we still found a negative relationship between the size of the outer entrance and probability of making landing errors, such as by bouncing off the outer entrance or missing the entrance entirely. On the other hand, the rate of landing errors was not related to eye size, probably because species with smaller eye size compensate by building relatively larger entrances. The costs of landing mistakes have not been determined in the field, but it is known that a number of predators hunt for returning and outgoing bees at the entrances of stingless bees. Jumping spiders (Salticidae), in particular, are often observed hunting for foragers close to the entrance (Schwarz, 1948; Sakagami et al., 1983) and Penney and Gabriel (2009) describe how spiders prey on bees that miss the entrance. Strikingly, when Shackleton et al. (2019) placed freeze-killed jumping spiders on the edge of the entrances of *Partamona helleri* colonies, approaching foragers accelerated more before entering their nest. Acceleration shortly before entering the entrance tube has also occurs in other species (Tichit et al., 2020a,2020b) and might be common in stingless bees that have relatively larger entrances. The evolutionary causations of the correlations between landing speed, entrance size, and landing mistakes, which we describe here, could be examined by studies that manipulate nest entrance architecture and quantify the effects thereof on stingless bee forager behaviour.

As found in previous studies, species with greater foraging traffic, which is indicative of a larger colony size, build relatively larger entrances (Biesmeijer et al., 2007; Couvillon et al., 2008). In our study, this relationship was only significant for the inner entrance (Figure S4). This makes sense as the inner rather than the outer entrance size should be the limiting factor for traffic flow. In addition, by having more entrance guards, larger colonies may also be less vulnerable to invading enemies, such as robbers and predators, and so can more easily afford to have

a larger entrance (Biesmeijer et al., 2007; Couvillon et al., 2008). A relatively larger entrance would also allow a large number of defenders to exit the nest quickly in case of an attack, which might be beneficial for large colonies, but not species with small colony sizes.

Our data suggest a link between the size of the inner (but not outer) entrance and foraging method. Numerous stingless bee species use chemical sent marks to recruit large numbers of nestmate foragers to food sources (Grüter, 2020; Hrncir & Maia-Silva, 2013; Jarau, 2009; Jarau et al., 2003; Lindauer & Kerr, 1960; Nieh, 2004). Species with this mass-recruitment have been observed to collect a significant proportion of their food during relatively short bursts of foraging activity (Roubik, 1989; Roubik et al., 1986). A relatively larger inner entrance would be expected to facilitate large numbers of foragers to leave and return to the nest in short time periods.

Social insects are well known for their building skills, ranging from the double-sided wax combs of honey bees, which arrange hexagonal cells in the most efficient manner (Tautz, 2008; Winston, 1987), to the truly massive nests of some termites with passive air conditioning and gas exchange (Jones & Oldroyd, 2006). Compared to the closest relatives, the honey bees and bumble bees, stingless bees have remarkably diverse nest architecture and great variation in colony and bee size (Grüter, 2020; Roubik, 2006). Our results are a step towards understanding how these three major traits, which include the individual, the colony, and the nest interrelate and are adaptive. More generally, our study further highlights the value of a comparative approach that simultaneously analyses and connects multiple phenotypic traits.

Acknowledgements

We are greatly indebted to the late Dr. Paulo Nogueira-Neto (1922–2019) for the use of his hives and facilities at Fazenda Aretuzina. Additionally, we would like to thank Túlio Nunes for helping us study *Trigonisca nataliae* and Tomer Czaczkas for his companionship and support during field trips.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

C. G. was supported by a Science without Borders fellowship from the Brazilian CNPq (Process-number: 400664/2012-7).

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Data availability

Upon publication the data for all colonies will be made publicly available on FigShare (10.6084/m9.figshare.18093875).

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