

# The body size of the oil-collecting bee *Tetrapedia diversipes* (Apidae)

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Academic editor: Jack Neff | Received 6 March 2015 | Accepted 13 November 2015 | Published 22 December 2015

<http://zoobank.org/11685432-4E55-4EE9-A405-7F77BFFD2BB0>

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**Citation:** Pinto CE, da Silva A, Cordeiro GD, Alves-dos-Santos I (2015) The body size of the oil-collecting bee *Tetrapedia diversipes* (Apidae). Journal of Hymenoptera Research 47: 103–113. doi: 10.3897/JHR.47.4837

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## Abstract

The body size of bees can affect their fitness in many ways. There is an indirect relationship between the size of the mother and the size of her progeny. This is so because large mothers use larger nests and brood cells and have higher foraging capacity than small mothers, and consequently large mothers supply a larger amount of food to their larvae, which grow larger. We analyzed the relationship between body size of individual oil-collecting bees of the species *Tetrapedia diversipes* and the size of their brood cells from Boracéia and Ilhabela, southeastern Brazil. In addition, we manipulated 26 brood cells of a population at the campus of Universidade de São Paulo by removing food from 13 brood cells. In this case, we checked the relationship between the body size of these bees and the amount of food consumed. We measured 241 individuals: 135 males and 106 females. No significant size difference was found between males and females. Only a weak relationship between body size and brood cell volume was detected, possibly due to the low variation in both female size and brood cell size. In the food manipulation experiment, the unmanipulated individuals were larger than individuals for whom part of the provisions were removed but no correlation was found between amount of food removed and offspring size.

## Keywords

Solitary bee, morphometry, cell provisions, parental investment, trap nest

## Introduction

The body size of bees strongly affects their fitness. Larger individuals can produce more eggs (Tengo and Baur 1993) and survive diapause better (Tepedino and Torchio 1982); larger males can defend more effectively their territories and have more mating opportunities (Alcock 1995); in social species larger females can become dominant (Buckle 1982). However, the size of bees is a balance between advantages and disadvantages that determine the range of optimal body size (Blanckenhorn 2000, Seidelmann 2014).

The body size of a bee is also correlated to the body size of its parents. However, size is probably not genetically inherited; when it occurs, the inheritance is very weak (Tepedino et al. 1984). The body size of parent bees and the body size of their progeny are correlated due to the parents' contribution to the amount of food supplied to their larvae (Johnson 1990, Ribeiro 1994). Larger individuals build larger nests with larger brood cells and larger amounts of food (Rooijackers and Sommeijer 2009, O'Neill et al. 2010). In bee species that nest in pre-existing cavities, the size of the brood cell is related to the diameter of the cavity, and the diameter of the cavity is related to the amount of food supplied (Klostermeyer et al. 1973).

Besides food resources (pollen and nectar), bees of the genus *Tetrapedia* (Tetrapediini, Apidae) collect floral oils and have morphological and behavioral adaptations to exploit this resource (Alves dos Santos et al. 2007). Females of this genus nest in pre-existing cavities such as bamboo hollows, and trap nests of several sizes (Camillo 2000, Garófalo et al. 2004). In general, the nests have between 6 and 15 cells and construction time varies from 3 to 6 weeks (Alves dos Santos et al. 2002). As obvious as it may seem few studies have analyzed the amount of food for the larvae and size of emerged bees (Klostermeyer et al. 1973, Danforth 1990, Johnson 1990). However, in none of them was removed food from brood cells.

This study examined variation in several morphometric measures in individuals of *Tetrapedia diversipes* in relation to population origins, gender, and brood cell size. For this proposal, the study consisted of two parts: In the first part we used data from trap nests from two populations and related the morphometric measurements of bees with their populations of origin, sex and brood cell volume. In the second part we used a third population to manipulate the amount of food that was available to the larvae and related that to measures of these bees.

## Methods

The specimens of *Tetrapedia diversipes* used in our analysis were reared from trap nests from areas within the Atlantic Forest in the state of Sao Paulo, Southeastern Brazil: (1) Ilhabela State Park (23°45'S – 45°27'W; 7 m a.s.l.); (2) Boracéia Biological Station (23°38'S – 45°52'W; 492 m a.s.l.). The individuals from Ilhabela and Boracéia were obtained in a trap nest inventory carried out by Cordeiro (2009). We obtained 730 individuals of *T. diversipes* from 347 nests (249 individuals from 116 nests in Boracéia

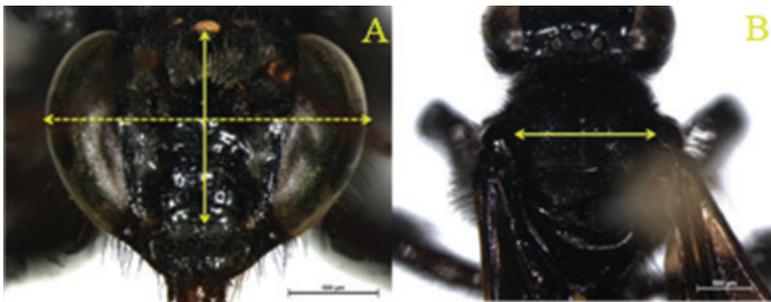
and 481 individuals from 231 nests in Ilhabela). We used part of this material. The trap nests consisted of were composed of perforated wood blocks filled with black cardboard, each 0.6 cm in diameter and 5.8 cm in length (two nests, one from Ilhabela and other from Boracéia had a diameter of 0.8 cm).

### Morphometry of individuals and cells of two populations

The measurements taken from the specimens were: head width, the distance from the central ocellus to the fissure of the labrum, and intertegular span (Fig. 1). To estimate the dry mass of bees, we used the following formula:  $ITS = 0.77 DM^{0.405}$ , where ITS is the intertegular distance and DM is the dry mass (Bullock 1999). The bees were photographed with a digital camera coupled to a stereomicroscope and the structures were measured with Gimp® software. The individuals were separated by place of collection, sex, and nest of origin. In total, 135 males and 106 females from Ilhabela (105 males and 69 females) and Boracéia (30 males and 37 females) were measured. Brood cell length was measured with a digital caliper, and the volume of the cells was estimated (considering the nest diameter, as described in the previous topic, the cells are cylindrical). The body size measures were analyzed by PCA (Principal component analysis) and with the PCA scores we performed ANOVAs to do the comparison of body sizes between populations. We used the estimated dry weight in the analysis. The relationship between PCA scores and brood cell volume was estimated for individuals from Ilhabela and Boracéia using a regression test. The statistical analysis was performed in R (R Development Core Team 2009).

### Food manipulation experiment and morphometry

We tested the influence of the amount of food available on the size of the individual in the campus at the University of São Paulo (23°33'S, 46°43'W) at the Laboratory of Bees, in the state of Sao Paulo, Southeast Brazil. For this, we used individuals obtained



**Figure 1.** Measurements taken from individual *Tetrapedia diversipes*. **A** Head width between eyes (dotted arrow) and head length (from the central ocellus to the fissure of the labrum) **B** Intertegular distance.

from trap nests maintained permanently at the Laboratory of Bees. For four months, from November 2010 to February 2011, we monitored trap-nests that were occupied by *Tetrapedia diversipes* females. When the construction of one cell was concluded (after monitoring the behavior of the female for some days), the tube containing the nest was removed from the wooden block and examined. The space occupied by the provisions in each cell was measured with a digital caliper, and the last cell of the series had part of its provisions removed. The pollen removed portions of the provisions were weighed (fresh weights) on a high-precision scale (Explorer OHAUS) and stored in Eppendorf tubes in the freezer. All the provisions from five cells was removed and to obtain the amount of food deposited for one larva (N = 5). The manipulated nests were placed in laboratory tubes and monitored daily until emergence (N = 13), other 13 cells of immatures were unmanipulated. After emergence, individual *T. diversipes* were killed with ethyl acetate, pinned, labeled, and deposited at the Paulo Nogueira Neto Entomological Collection (CEPANN). The same measurements cited in the previous item were taken from these individuals (Fig. 1).

The measures of body sizes used in this work are correlated, thus, the body measures were analyzed by PCA (Principal component analysis). We used the PCA scores we to perform t tests to evaluate the morphometric differences among individuals that had their food manipulated and those that did not. The regression analysis was made to test the influence of the amount of food removed on bee size.

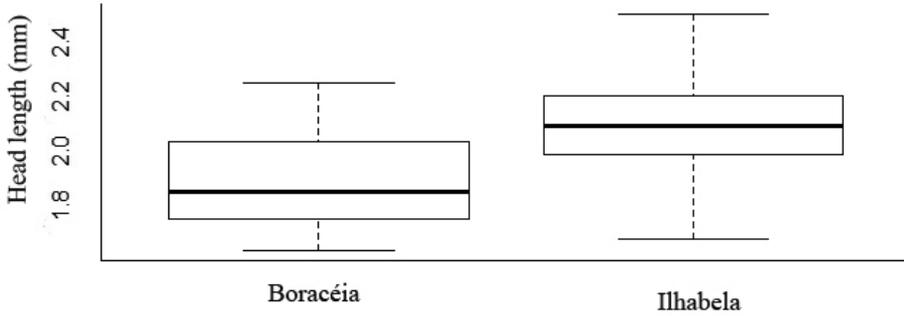
## Results

### Morphometry of individuals from Ilhabela and Boracéia

The PCA analysis showed that about 70% of the measures variation was explained for the first axis of the PCA (PC1) (70% in Ilhabela and 69% in Boracéia). In 241 individuals measured (67 from Boracéia Biological Station and 174 from Ilhabela State Park, Table 1) we observed a difference in the head length of bees between populations ( $F = 69.39$ ; d.f. = 1;  $p = 0.0001$ ) (Fig. 2). In the Ilhabela and Boracéia populations there were not significant difference between sexes and the PC1 ( $F = 3.12$ ; d.f. = 1;  $p = 0.07$  and  $F = 2.53$ ; d.f. = 1;  $p = 0.11$ , respectively).

**Table 1.** Mean  $\pm$  standard deviation of the measurements taken from *Tetrapedia diversipes* males and females from Ilhabela and Boracéia.

Locality	Sex	N	Head length (mm)	Head width (mm)	Intertegular distance (mm)	Estimated dry mass (mg)
Ilhabela	♂	105	2.07 $\pm$ 0.13	2.73 $\pm$ 0.10	2.09 $\pm$ 0.11	22.98 $\pm$ 0.11
	♀	69	2.11 $\pm$ 0.16	2.74 $\pm$ 0.11	2.13 $\pm$ 0.12	23.02 $\pm$ 0.12
Boracéia	♂	30	1.86 $\pm$ 0.17	2.7 $\pm$ 0.11	2.07 $\pm$ 0.12	22.96 $\pm$ 0.12
	♀	37	1.92 $\pm$ 0.09	2.74 $\pm$ 0.18	2.09 $\pm$ 0.10	22.99 $\pm$ 0.10



**Figure 2.** Head length of emergent individual *Tetrapedia diversipes* from the studied populations. The box plot shows the median, the quartiles, and the maximum and minimum of the values measured.

**Table 2.** Measurements of *T. diversipes* brood cells, from which the studied individuals emerged.

Locality	Number of cells	Mean length of cells (cm)	Mean volume of cells (cm <sup>3</sup> )
Boracéia	64*	0.97 ± 0.07	0.27 ± 0.035
Ilhabela	171*	0.89 ± 0.09	0.25 ± 0.03

\*Four cells from Boracéia and three from Ilhabela, whose nest diameter was 0.8 cm, were removed from this analysis.

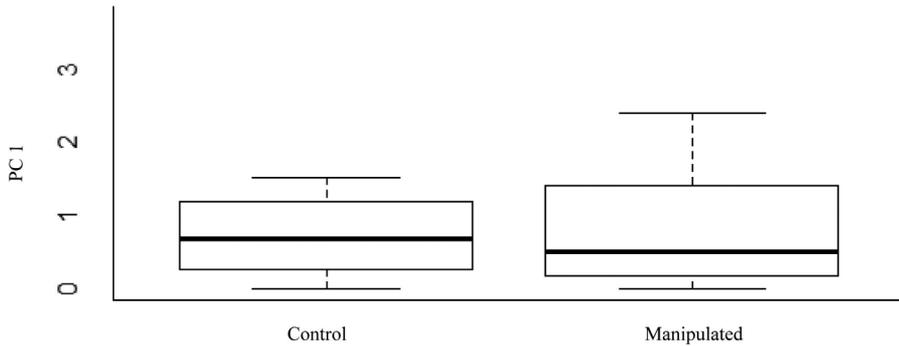
The 241 cells of *Tetrapedia diversipes* from Ilhabela (174) and Boracéia (67) populations had similar volumes (Table 2). In both populations, most cells (> 80%) had a volume close to the mean value (between 0.22 cm<sup>3</sup> and 0.30 cm<sup>3</sup>).

No relationship was observed between PC1 and brood cell volume for the Ilhabela population ( $F = 0.027$ ; d.f. = 172;  $p = 0.86$ ,  $R^2 = -0.005$ ). For the Boracéia population, there was a positive relation between PC1 and brood cell volume ( $F = 5.89$ ; d.f. = 65;  $p = 0.01$ ,  $R^2 = 0.06$ ).

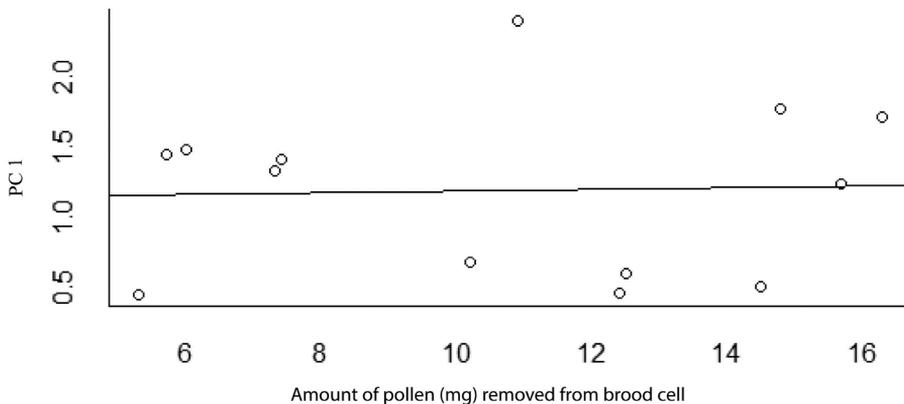
### Food manipulation experiment and morphometry

Twenty-six individual *T. diversipes* emerged from the monitored cells: 13 from cells that had the food manipulated and 13 from unmanipulated cells (Suppl. material 1). Individuals from unmanipulated cells were significantly larger than individuals from manipulated cells in all measurements analyzed: head width ( $F = 55.53$ ; d.f. = 25;  $p = 0.0001$ ), head length ( $F = 31.03$ ; d.f. = 25;  $p = 0.0001$ ), and estimated dry mass ( $F = 59.11$ ; d.f. = 25;  $p = 0.0001$ ) (Fig. 4). The food from unmanipulated cells weighed, on average,  $89.28 \pm 8.13$  mg (max. = 92.04 mg; min. = 70.53 mg).

The PC1 and the second component (PC2) of PCA explained 63% and 20%, respectively, of all variation on the measures manipulated bees and 62% and 25% of all variation on the measures unmanipulated bees. Thus, we used the PC1 and the PC2 to compare manipulated and unmanipulated bees. The scores of the PC1 and the PC2 of



**Figure 3.** Comparison of body measurements of individual *T. diversipes* emergent from the Laboratory of Bees, Sao Paulo, in the food manipulation experiment (n = 26: 13 unmanipulated and 13 manipulated). The box plot shows the median, the quartiles, and the maximum and minimum values of the PC1 scores.



**Figure 4.** Relationship between scores of the PC 1 of body measurements of emergent individual *T. diversipes* (n = 13) and the weight of the pollen removed from their cells.

the unmanipulated bees were significantly larger than the manipulated bees ( $t = 7.94$ ;  $d.f. = 51$ ;  $p = 0.0001$ ).

No correlation was found between PC1 and the amount of food removed from a cell ( $R^2 = -0.08$ ;  $d.f. = 11$ ;  $p = 0.88$ ).

## Discussion

There was difference in head length between the two populations of *Tetrapedia diversipes* studied. In general, morphometric differences are expected in bee populations that do not maintain a gene flow and are separated into different subspecies (Amssalu et al. 2004, Borsuk and Olszewski 2010). The studied populations are 52 km apart, Boracéia in the mountains (499 m a.s.l.) and Ilhabela in the coast (7 m a.s.l.), further-

more Ilhabela is an oceanic island. Therefore, there is probably little or no gene flow between them. This could explain the difference in head length between populations. Neves (2012) observed that three populations of *T. diversipes* in Bahia, separated by up to 500 m, differed in wing morphometry. The author suggested that low gene flow between populations may explain the difference found.

We found a positive correlation between bee size and brood cells volume in one of the populations studied (Boracéia), however, there was a poor fit of the data to the straight line correlation. This may be a reflection of both the small size variation of the female bees and lack of variation among the size of the cells built. Although, the trap nests offered have a standardized diameter (0.6 cm), the bees could adjust the available space cells by making cells longer or shorter. Nonetheless, even for bees that emerged from the seven cells (two nests) whose nest diameter was 0.8 cm, we did not find a significant difference. The body sizes of individuals that emerged from these cells were similar to the population mean (Suppl. material 2). The amount of food supplied may vary if the females build longer cells. Nevertheless, we do not have data on the amount of food available for the bees from Ilhabela and Boracéia. This becomes evident if we analyze the volumes of the cells built. In both areas most cells built (approximately 80%) had a volume close to the mean. Hence, the weak relationship found may be a consequence of most cells having similar volumes.

Differences in body sizes are probably not hereditary (Tepedino et al. 1984), but rather are related to the size of the mother through non-genetic mechanisms. There are positive correlations of mother size and brood cell size (Tepedino and Torchio 1989), mother size and amount of food supplied (Boomsma and Eickwort 1993), brood cell size and amount of food supplied (Krombein 1967, Johnson 1990), amount of food supplied and size of emergent bees (Klostermeyer et al. 1973, Danforth 1990, Johnson 1990), and brood cell size and size of emergent bees (Klostermeyer et al. 1973, Kamm 1974, Alcock 1979, 1999, Tepedino and Torchio 1982). In *Lasioglossum zephyrum* bee size is correlated with brood cell size: the larger bees construct larger cells and larger bees emerge from larger cells (Kamm 1974). For this same species, offspring body size appears to result from a combination amount of food and pollen protein concentration (Roulston and Cane 2002). There was a relation between larger brood cells and amount of food supplied and between the amount of food weight of emergent bees in *Megachile rotundata* (Klostermeyer et al. 1973) the relation between amount of food and size of emergent bees was also verified in *Caliopsis persimilis* (Danforth 1990) and in *Ceratina calcarata* (Johnson 1990). Larger female *Centris palida* showed higher supply capacity (Alcock 1979). A higher foraging capacity of larger bees was observed in six Meliponini species, in which larger bees covered larger flight distances (Araújo et al. 2004).

The individuals from the unmanipulated cells were larger than those that had some provisions removed. However, there were no significant differences among individuals from manipulated cells as bees from cells where more food was removed were not significantly smaller than those where less was removed. Those that received more food did not grow larger. Roulston and Cane (2000) suggest that, for bee species that nest in natural cavities, the size of the cavity used is strongly related to the amount of food supplied. Studies that compared resource availability and dry mass showed that bees with

access more food are bigger (Peterson and Roitberg 2006) and there is a positive relation between adult dry mass and food provisioned (Bosch and Vicens 2002). We did not find a correlation between PC1 and food supplied, but when we used just the measures from estimated dry mass there is a correlation between estimated dry mass and food supplied ( $R^2 = 0.72$ ; d.f. = 11;  $p = 0.0001$ ). Thus, the nonsignificant relation between PC1 and amount of provisions removed may be due to the other two size measures (head width and head height). An influence of the amount of food ingested and the size of emergent bees was already reported for other species. In *Megachile rotundata* there is a strong relationship between the weight of the food supply and the weight and sex of the resulting progeny (Klostermeyer et al. 1973, O'Neill et al. 2010), in this case females emerged from cells with larger provisions. A similar result was found for *Calliopsis persimilis* (Danforth 1990). For *Ceratina calcarata* larger bees were those that received more food when larvae and larger females had larger foraging capacity and built cells with more food (Johnson 1990). Our food manipulation experiment on *T. diversipes* corroborated that larger bees ingested more food in the larval phase.

## Conclusion

We conclude that in *Tetrapedia diversipes*, removing some of the provisions produces results in smaller offspring than bees from cells with intact provisions. We also found a weak positive correlation between relationship brood cell volume and body size, in one of the populations studied.

## Acknowledgments

We thank the Brazilian Research Council (CNPq) for the scholarship granted to Carlos Eduardo Pinto da Silva (143001/2009–4) and the São Paulo Research Foundation (FAPESP) for the scholarship granted to Guaraci Duran Cordeiro (2007/51911–2) and the fellowship granted to Isabel Alves dos Santos (2004/00274–4). The Laboratory of Bees provided us with infrastructure. Dr. Tiago M. Franco allowed the use of his laboratory to take photographs. MSc. Katia Aleixo took the photos used in diagram 1. Claudia Ines da Silva, Helena Maura Torezan Silingardi, Julia Astegiano and Maria Cristina Gaglianone provided useful comments on earlier versions of this manuscript.

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## **Supplementary material 1**

### **Individual *Tetrapedia diversipes* emerged from trap nests at the Campus of the University of São Paulo**

Authors: Carlos Eduardo Pinto, Adriana da Silva, Guaraci Duran Cordeiro, Isabel Alves-dos-Santos

Data type: MS Word doc file

Explanation note: Of 26 emergent individuals, 13 did not have their food manipulated (control) and 13 part of their food removed (manipulated). The bees were measured and the value of pollen weight refers to the amount of pollen mass removed from each cell.

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## **Supplementary material 2**

### **Bees measures that emerged in seven brood cell with 0.8 cm diameter**

Authors: Carlos Eduardo Pinto, Adriana da Silva, Guaraci Duran Cordeiro, Isabel Alves-dos-Santos

Data type: MS Word doc file

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