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Journal

Insectes Sociaux, 63(4)

ISSN

0020-1812

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Publication Date

2016-11-01

DOI

10.1007/s00040-016-0491-1

Peer reviewed

1 The published version of this paper is:

2

3 Medina, R. G., Fairbairn, D. J., Bustillos, A., Montejo, E., Medina, S. and Quezada-Euán, J. J. 2016.

4 Variable patterns of intraspecific sexual size dimorphism and allometry in primitive and highly eusocial corbiculate bees (Hymenoptera: Apidae). *Insectes Sociaux* 63: 493-500. doi:10.1007/s00040-016-0491-1

Variable patterns of intraspecific sexual size dimorphism and allometry
in three species of eusocial corbiculate bees (Hymenoptera:Apidae)

3

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24 **SUMMARY**

25 Sexual size dimorphism (SSD), in which one sex is larger than the other, has
26 remained understudied in social insects, particularly bees. Using weight and linear
27 structural measurements, we quantified the magnitude of SSD and its variation across nests
28 in three species of corbiculate bees, two belonging to the highly eusocial Apini (*Apis*
29 *mellifera*) and Meliponini (*Melipona beecheii*), and one to the primitively eusocial
30 Euglossini (*Euglossa viridissima*). We asked if similar to most insects, including
31 Hymenoptera, SSD is female-biased in these eusocial species. Contrary to expectations, we
32 found that SSD was moderately male-biased in the two highly eusocial species and slightly
33 male-biased for weight and not significant for linear size in *E. viridissima*. The possible
34 roles of queen protogyny and reduced brood provisioning by queens in shaping these
35 patterns of SSD are discussed. The allometry of SSD among nests differed among species
36 as well, ranging from hypoallometry in *A. mellifera*, to isometry in *M. beecheii*, to
37 hyperallometry in *E. viridissima*. This variation indicates that the phenotypic response of
38 body size to differing conditions across nests differs both between sexes and among
39 species. The variation detected among the three studied species in both SSD and allometry
40 for SSD precludes any broad generalizations to other corbiculate bees. However, it does
41 suggest that corbiculate bees can provide a new and diverse framework to analyze the
42 effects of social environment on the evolution of animal sexual dimorphism.

43

44 **Keywords:** Body size, sexual dimorphism, allometry, social insect, bee.

45

46

47 INTRODUCTION

48 Sexual Size Dimorphism (SSD) refers to a consistent difference in mean body size
49 between males and females, and is often expressed as a ratio of mean sizes (Fairbairn
50 1997). In a majority of insect orders females are more commonly the larger sex ($F > M$)
51 and female size varies more than male size in response to environmental conditions (Teder
52 and Tammaru 2005). Female-biased SSD has been attributed to stronger selection for high
53 fecundity in females compared to sexual selection in males (Blanckenhorn 2000; Webb and
54 Freckleton 2007). Nonetheless, within a given clade, variance in SSD is also common, and
55 males can be larger in some species whilst females are the larger sex in others (Fairbairn
56 1997, 2013).

57 Surprisingly, SSD has remained understudied in social insects, particularly in bees
58 (Cueva del Castillo and Fairbairn 2007). Bees (Hymenoptera: Anthophila) are a key
59 ecosystem service group representing the most important pollinators worldwide. Most
60 eusocial bee species are found in the subfamily Apinae or corbiculate bees, a monophyletic
61 clade within the Apoidea (Michener 2000). Four tribes form the corbiculate bees:
62 bumblebees (Bombini), orchid bees (Euglossini), stingless bees (Meliponini) and
63 honeybees (Apini). Different levels of eusociality exist in Apinae: the Meliponini and Apini
64 are highly eusocial whilst the Bombini and a number of species in the Euglossini are
65 primitively eusocial. Female phenotypic and behavioral differentiation is extreme in the
66 highly eusocial Apini and Meliponini with two clear castes: reproductive queens and
67 mostly sterile workers (Michener 1974; Simpson et al. 2011). In contrast, in the Euglossini
68 and Bombini females are phenotypically similar.

69 With such contrasting levels of female reproductive differentiation, the
70 monophyletic Apinae represent a good model in which to test hypotheses regarding SSD

71 variation in relation to sociality. Parental care and food collection are activities that are
72 absent in queens of the highly eusocial species but still present in primitively eusocial ones
73 (Wilson 1971; Michener 1974). If the degree of parental care acts as a strong factor for
74 selection of female size in eusocial bees as it does in solitary species (Shreeves and Field
75 2008), females of eusocial species should be smaller relative to their males than females of
76 solitary species. Accordingly, as the sex gaining more from a large body size in terms of
77 fitness is presumed to evolve towards a larger size (Teder 2005), we would predict different
78 patterns of SSD in eusocial species compared to primitively social and solitary ones.

79 Intraspecific variation in body size is proximately mediated by variation in the
80 conditions that affect individual growth and development, and as a consequence, SSD
81 shows considerable variation among populations within species (Roff 1992; Teder and
82 Tamaru 2005, Blanckenhorn et al 2006, 2007a). Such spatial variation in SSD may be
83 purely phenotypic, reflecting sex-specific reaction norms to environmental conditions
84 experienced during development (Cueva del Castillo et al. 2015). Given that females are
85 generally the larger sex in insects, their greater phenotypic plasticity (steeper reaction
86 norms) often covaries with SSD and mean body size such that populations experiencing
87 benign conditions have both larger mean body sizes and greater SSD (Teder and Tammaru
88 2005). In social insects, thanks to group homeostasis, individual development can be
89 buffered against environmental fluctuations (Moritz and Southwick 1992) and this may
90 result in less intraspecific variation in body size and SSD than in solitary species. This
91 hypothesis has not been evaluated.

92 We quantified for the first time the magnitude of intraspecific variation in body size,
93 SSD and SSD allometry in three species of corbiculate bees, two belonging to the highly
94 eusocial Apini and Meliponini and one to the primitively eusocial Euglossini. We evaluated

95 if, as in solitary species, SSD is female-biased in eusocial bees. We compare SSD among
96 nests, which represent a new level of comparison akin to looking at variation among
97 families within a species (Blanckenhorn et al. 2007a). Both social entities are neither long
98 lasting, geographically separated populations (as in Fairbairn 2005 or Blanckenhorn et al
99 2006) nor purely environmental treatments (Teder and Tammaru 2005). We evaluate if
100 SSD varies allometrically at this level of comparison and if so, if the patterns of allometry
101 are similar to those found among-populations of other insects.

102

103

104 **MATERIALS AND METHODS**

105 **Sample collection and estimates of body size**

106 We studied three species representative of the tribes of tropical corbiculate bees:
107 *Euglossa viridissima* (Euglossini), *Melipona beecheii* (Meliponini) and Africanized *Apis*
108 *mellifera* (Apini). The study was conducted in the Yucatan Peninsula of Mexico. The nests
109 of all species were collected around the city of Mérida (20°58'04"N 89°37'18"W). The
110 maximum distance between nests of each species was a couple of kilometers and thus all
111 nests for a given species are considered to belong to the same population.

112 For *M. beecheii* and *A. mellifera* we aimed at obtaining 10 males and 10 gynes from
113 each of ten colonies of each species. Samples were obtained between June and August
114 2015, when colonies tend to produce more reproductives (Pech-May et al. 2012). *M.*
115 *beecheii* combs were extracted from each of ten colonies and kept in an incubator at 31°C
116 and 70% humidity. For *A. mellifera*, combs containing capped male cells and queen cells
117 were kept in an incubator at 34°C and 70% humidity. When individuals of both species

118 emerged, they were weighed and immediately frozen for later analyses. A total of 98 males
119 and 98 gynes were obtained for *M. beecheii* and a total of 100 individuals of each sex were
120 obtained for *A. mellifera*.

121 For *E. viridissima*, 28 males and 47 females were obtained from 11 nests in wooden
122 boxes (7 x 3 x 3 cm) between May and October. In this species solitary mothers colonize
123 and start a new nest by gradually constructing different numbers of resin-made brood cells
124 that can vary between 1 to a few dozen (Cocom-Pech et al. 2008). When the construction of
125 cells was finished, the box entrance was protected with a metallic mesh in order to collect
126 all individuals upon emergence. Each individual was collected and weighed on an
127 analytical scale and its sex determined. Immediately after, individuals were frozen to
128 preserve them for further analyses. In contrast to *M. beecheii* and *A. mellifera*, it was not
129 possible to obtain the same numbers of males and females per nest in *E. viridissima*
130 because offspring number and sex ratios varied between nests.

131 Apart from the mass trait represented by fresh weight of the individuals, four linear
132 structural traits associated with body size in bees were additionally recorded (Bullock 1999;
133 Greenleaf et al. 2007; Quezada-Euán et al. 2007). Specimens were dissected and the head,
134 thorax, right hind leg and right forewing were mounted on slides. Photographs of each
135 structure were taken with a microscope-mounted camera, and the endpoints delimiting four
136 morphometric traits marked: head width, intertegular width, forewing length and femur
137 length.

138

139 **Intraspecific evaluation of SSD**

140 To test if SSD existed in the three species we used comparisons based on body
141 weight and linear measures. For linear comparisons, we used a single indicator of body size

142 represented by the first component from a Principal Component Analysis (PCA). Most of
 143 the variation related to body size is expressed in the first component (PC1) when highly
 144 positively correlated (Wiley 1981). The PCAs were conducted on the correlation matrix of
 145 the data set for each species and two principal components were obtained. To analyse the
 146 effect of nest on SSD, and to compare females and males, we used the mean fresh weight
 147 and PCA scores of each sex per nest. Intraspecific comparisons were done using t-tests. A
 148 Satterthwaite approximation was used to calculate the standard errors.

149 We estimated an index of SSD for each species using the weight and PC1 data of
 150 females and males as suggested by Lovich and Gibbons (1992):

$$151 \quad SSD = \frac{\bar{\chi}_{\text{trait value of males}}}{\bar{\chi}_{\text{trait value of females}}} - 1$$

152 The PC1 scores had to first be transformed by adding an arbitrary constant, given
 153 that some values were negative. The same constant (the absolute value of 2) was used to
 154 transform the scores for all species, nests and sexes. We used male values as the numerator
 155 because males are the larger sex in the studied species.

156

157 **Pattern of SSD allometry**

158 To evaluate the pattern of allometry in each species we used model II Major Axis
 159 (MA) regressions of the ln of weight and transformed PC1 scores. The values of males
 160 were regressed on those for females using the mean values of each sex per nest using the
 161 software PAST, version 3.06 (Hammer et al. 2001); 95% confidence intervals of the slopes
 162 were calculated too. The regression slopes were compared to the null expectation of
 163 isometry between sexes (i.e. 1). A slope significantly less than 1.0 would indicate that
 164 female size increased relatively faster than male size indicating the former being more

165 sensitive to environmental conditions. A slope significantly greater than 1.0 would indicate
166 the opposite tendency.

167

168

169 **RESULTS**

170 **Intraspecific evaluation of SSD**

171 For the three species, the loadings of all four linear traits for PC1 were positive
172 meaning that this component is a good indicator of overall body size (Supplementary Table
173 1). In the three species the loadings for PC2 had different signs indicating shape related
174 differences between males and females (Supplementary Table 1; Wiley 1981). However, in
175 all three species PC2 accounts for less than 25% of the variance (Supplementary Table 1)
176 which is less than the variance expected for one of the traits alone. Thus, PC2 was not
177 considered for comparisons between sexes.

178 Significant size differences were detected between the sexes for all three species.
179 For both *M. beecheii* and *A. mellifera*, males were significantly heavier and had
180 significantly higher PC1 scores than females (Table 1; Fig. 1). The magnitude of SSD in
181 these highly eusocial species was moderate, with males ranging from 26% to 52% larger
182 than females. For *E. viridissima*, males weighed significantly more than females, but the
183 difference was much smaller than in either of the other two species (10%), and the PC1
184 scores of the two sexes did not differ (Table 1; Fig. 1). For all three species SSD based on
185 linear size was greater than SSD based on weight, which is not typical when SSD is
186 estimated for both mass and linear measures (Fairbairn 2013). Although this pattern could
187 arise if females were more robust than males (i.e., had higher mass per unit length), this is
188 not the case for the species in our study because in *Apis* and *Melipona* drones are more

189 robust than females. The higher SSD for linear measures in our study is an artifact of
190 having used standardized PC1 scores rather than raw linear measures as our measure of
191 linear size. Our linear estimates can be compared among nests and among species, but are
192 not directly comparable to the SSD estimates based upon unstandardized weights. The SSD
193 estimations for each species varied among nests but were positive in all nests, meaning that
194 in all cases males were larger than females, although in the primitively eusocial species, *E.*
195 *viridissima*, the minimum SSD values approached zero and the overall SSD was not
196 significant.

197

198

199 **Pattern of SSD allometry**

200

201

For *M. beecheii* the MA regression slopes for male on female ln weight and ln size
202 were not significantly different from 1, indicating isometry for SSD, with intercepts greater
203 than 0 (Table 2). In this species males are larger than females and the size of both sexes
204 varies similarly among nests. For *A. mellifera* the intercept was again greater than 0, but in
205 contrast to *M. beecheii* the slopes for ln weight and ln size were significantly less than 1,
206 indicating significant hypoallometry for SSD and that female size varies more than male
207 size among nests. For *E. viridissima* the slope was greater than 1, for both weight and linear
208 size, but significantly so only for the latter. This indicates hyperallometry due to male linear
209 size varying more than female size among nests. Males are slightly larger than females (i.e.
210 the points fall above the 1:1 line) but this difference is much less pronounced than in the
211 two highly eusocial species.

212

213

214 **DISCUSSION**

215 Our results in the three studied species contrast with those in most solitary species
216 and insect taxa, where females are usually the larger sex (Blanckenhorn et al. 2007a; Webb
217 and Freckleton 2007). In other social insects, the average female mass at the time of mating
218 can be up to 25 times larger than males mass (Boomsma et al. 2005). However, using both
219 fresh weight and linear size, we found no evidence of intraspecific female-biased SSD in
220 any of our three studied bee species. On the contrary, we found moderate male-biased SSD
221 in both highly eusocial species *M. beecheii* and *A. mellifera*, and minor sexual size
222 dimorphism for mass in the primitively eusocial species *E. viridissima*.

223 Regarding allometry, the three species show different trends. The allometric slope
224 does not differ from 1.0 in *M. beecheii*, indicating isometry for body size in the two sexes.
225 This means that the ratio of male to female linear size or weight does not vary
226 systematically with body size in this species. In contrast, the allometric slope for *A.*
227 *mellifera* is significantly less than 1.0 for both weight and linear size, indicating that the
228 female size varies more among colonies than male size and the ratio of male to female size
229 decreases as body size increases (hypoallometry). Yet a third pattern is seen in *E.*
230 *viridissima*. In this species the trend is hyperallometric, especially for linear size, indicating
231 that male size varies more than female size and SSD increases as size increases. This
232 diversity of results precludes generalities concerning allometric trends and suggests that the
233 balance of selection on body size in males and females, as well as patterns of sex-specific
234 phenotypic plasticity, are likely to differ among species in the eusocial Apinae. The bees
235 comprise around 20,000 species and thus, our results are not sufficient to indicate general
236 trends about SSD or allometry in the group. However, little information is available for the

237 eusocial species in the Apinae and our findings provide a starting point to test more general
238 hypotheses.

239 In most insects, females compete for resources that can be converted into offspring,
240 while males compete for females (Paxton 2005; Teder 2005). Typically, female fecundity
241 increases with body size (Honěk, 1993), and hence a major evolutionary force contributing
242 to female-biased SSD is fecundity selection favoring large size in females (Blanckenhorn,
243 2000; Beani et al. 2014). Females in highly eusocial species are released from the
244 constraints of foraging and nest building, and we might expect body size in these species to
245 respond more readily to fecundity selection, with resultant higher fecundity and larger size
246 than found in primitively eusocial species (Boomsma 2005; Beani et al. 2014). Contrary to
247 this expectation, we found male-biased SSD in *M. beecheii* and *A. mellifera*. We did not
248 measure abdominal size which seems to better indicate selection for fecundity in females
249 (Blanckenhorn et al. 2007a), but our finding of male-biased SSD in the other linear
250 measures and in weight is still unexpected. Female fecundity selection is not invariably
251 associated with female-biased size dimorphism (Olsson et al. 2002; Pincheira-Donoso and
252 Hunt 2016) because SSD is the result of the net selection acting on body size and its
253 components in both sexes (Preziosi and Fairbairn 2000; Blanckenhorn 2005, Fairbairn et al
254 2007; Fairbairn 2013). The relationship between body size and fitness in males and females
255 of the eusocial Apinae is likely complex and influenced by selective forces other than
256 fecundity.

257 In addition to fecundity, it has been shown that the level of parental care is
258 positively related to the degree of female-biased SSD in solitary bees (Shreeves and Field
259 2008). Highly eusocial bee queens are specialized egg-layers that produce hundreds to
260 thousands of offspring per day (Moritz and Southwick 1992). Queens in these species are

261 also not subject to the physical requirements of transporting larval provisions. In contrast,
262 in the primitively eusocial tribes, females start nests on their own, which comprise an
263 obligate phase when they have to collect all nest materials and caring for the brood
264 (Michener 1974). Dominant females in eusocial Euglossines act as workers during a period
265 in their early life and then act like queens, coercing their daughters to rear their offspring
266 (Cocom-Pech et al. 2008). Possibly nest construction and provisioning exert stronger
267 selection on the body size of reproductive females in primitively eusocial species than in
268 highly eusocial ones, but this selection is weaker than in solitary species in which SSD is
269 clearly female-biased. Our results are consistent with this hypothesis: we found SSD to be
270 only slightly male-biased for weight and not significant for linear measures in *E.*
271 *viridissima*. This magnitude and direction of SSD is intermediate between the moderately
272 male-biased SSD in our two highly eusocial species and the strong female-biased SSD in
273 solitary species (Shreeves and Field 2008). However, in the bumble bees, the other
274 primitively eusocial clade, females are by norm the larger sex (Cueva del Castillo and
275 Fairbairn 2011), and gynes of some *Trigona* stingless bees seem to have similar or larger
276 body size than males (personal observation), so factors other than parental care may also be
277 involved in explaining the absence of female biased SSD in the eusocial Apinae. It has been
278 argued that body size differs little between female castes in wasps and bees due to selection
279 for flight ability during swarm formation (Peeters and Ito 2015). The constraints of flight
280 may thus impact the evolution of body size in females and hence contribute to patterns of
281 SSD in this group. The possible effects of female flight on SSD in the Apinae remain to be
282 investigated.

283 In many insect species males are both smaller and emerge earlier on average than
284 females. In such species, selection favoring protandry could contribute to female-biased

285 size dimorphism because early emerging males may have a higher mating success but are
286 smaller in size (Singer, 1982; Wiklund & Solbreck, 1982; Zonneveld, 1996; but see
287 Blanckenhorn et al., 2007b). However, in the three species of corbiculate bees studied here,
288 males have longer development times than females. In *E. viridissima* the species with the
289 least SSD, males emerge on average 4 days later than females (May-Itzá et al. 2014), whilst
290 in the two species with clear male-biased SSD the gap between female and male emergence
291 is of 3-4 days in *M. beecheii* (Moo-Valle et al. 2004) and 8-9 days in *A. mellifera* (Winston
292 1987). In contrast, in bumblebees, queens take on average 4 days longer to develop than
293 males (Duchateau and Velthuis 1988). In addition, it is known that honey bee queens
294 receive more food during larval development than drones (Winston 1987) and that gynes
295 and drones in *M. beecheii* may receive similar amounts of food (Moo-Valle et al. 2001). In
296 spite of this, males are larger in both species suggesting that protogyny may be one
297 additional factor contributing to the absence of female-biased SSD in the studied species.
298 The adaptive significance, if any, of later emergence by males remains to be discerned.

299 We have referred mainly to factors that may contribute to the absence of female-
300 biased SSD in our studied species because in the Hymenoptera males seem to be under
301 weak sexual selection (Beani et al. 2014). This may relate to the fact that males are
302 normally unable to monopolize groups of females by preventing female dispersal
303 (Boomsma et al. 2005). Moreover, there is likely to be little or no mating advantage to large
304 male size in species that practice male scramble competition in this group. Males in the
305 Apini and Meliponini compete against conspecifics, typically by chasing females in
306 congregation areas, and there is no physical contest competition among males (Paxton
307 2005). This likely reduces the selection favoring large males and could even favor smaller
308 (possibly more agile) males. However, large male size can confer some advantages to

309 males of the eusocial bees, as sperm load has been positively correlated with body size in
310 some species (Garófalo et al. 1986; Schlüns et al. 2003; Pech-May et al. 2012). Whether
311 this is true for Euglossine species is yet to be determined. Reduced sexual size dimorphism
312 in Euglossines could also be due to their particular courtship and mating processes.
313 Euglossine males usually establish leks in which they presumably use chemicals to attract
314 females (Kimsey 1980). Males actively collect fragrances from different sources and the
315 amounts collected are not related to male body size (Eltz et al. 2015). Nonetheless,
316 territoriality may involve some type of defense of the male displaying spots or chemical
317 sources, and body size may confer some type of premating advantage in this competition.

318 Noteworthy, for the three studied species the magnitude of SSD varied amongst
319 nests and showed that SSD in eusocial Apinae did not move in a narrow range as is
320 commonly assumed for species (Blanckenhorn et al. 2007a). Therefore, nests seem to be
321 more reasonably considered as populations (Teder and Tammaru 2005) in which SSD
322 allometry is possibly generated by phenotypic responses to internal variation. In this
323 respect, a trade-off between individual size and colony size (presumably related to food
324 provisions) is suggested to influence the pattern of SSD in the bumble bees (Cueva del
325 Castillo et al. 2015) and body size in stingless bees (Quezada-Euán et al. 2011; 2015). Our
326 results highlight that intraspecific SSD varies among eusocial species, and that for more
327 accurate interspecific and population comparisons in eusocial clades it would be therefore
328 advised to derive SSD from a range of colonies.

329 The variation of social organization and reproductive strategies in the monophyletic
330 clade of the corbiculate bees seems to have created different conditions for the evolution of
331 intraspecific SSD (Table 3). The complex relation between SSD and social environment

332 remains poorly understood but models like that of corbiculate bees in which patterns of
 333 intraspecific (among-family) SSD can be readily discerned provide a new scale in
 334 which to partition the effects of phenotypic plasticity, sexual selection and natural
 335 selection on the evolution of insect sexual dimorphism.

336

337 **ACKNOWLEDGEMENTS**

338 Our sincere thanks to Professor Wolf U Blanckenhorn for the constructive comments and
 339 discussion. We also appreciate the comments and suggestions of two anonymous reviewers
 340 which greatly improved our manuscript. Grants to RGM and AB were provided through
 341 project SEP-Conacyt 103341 “Conservación de las abejas sin aguijón de México”. Eduardo
 342 Montejo helped during data collection.

343

344

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515 **Table and Figure Captions**

516 Table 1. Species values and t-tests for fresh weight and linear traits represented by principal
517 components (PC) between males and females for three species of corbiculate bees using
518 mean values per nest. Intraspecific SSD and their range calculated from fresh weight and
519 PC1 are presented. N represents the number of nests

520 Table 2. Estimation of MA regression parameters for three species of corbiculate bees. N
521 represents the number of nests. PC1 is the transformed PC1 score (see text for explanation)

522 Table 3. Some aspects of the sociality and reproductive strategies found in the corbiculate
523 bees. The results on intraspecific SSD from the present study are included to show the
524 variation in this regard for the clade.

525 Supplementary Table 1. Statistics of Principal Component Analysis of linear traits in three
526 species of corbiculate bees. FWL=Forewing length; HW=Head width; IW=Inter-tegular
527 width; FL=Femur length

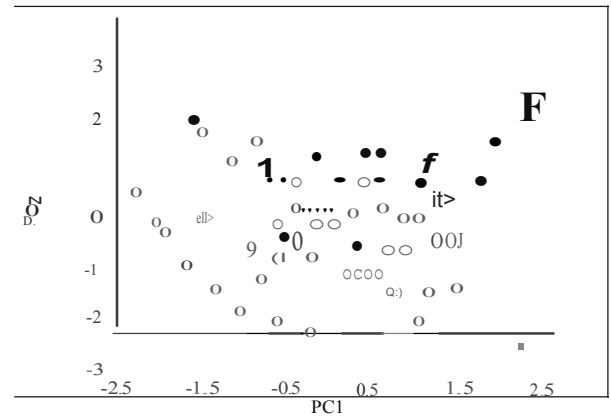
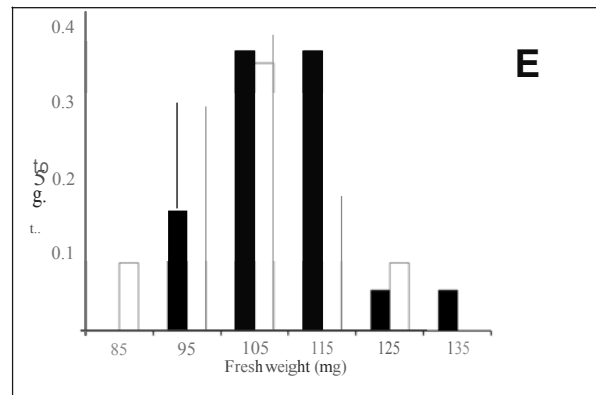
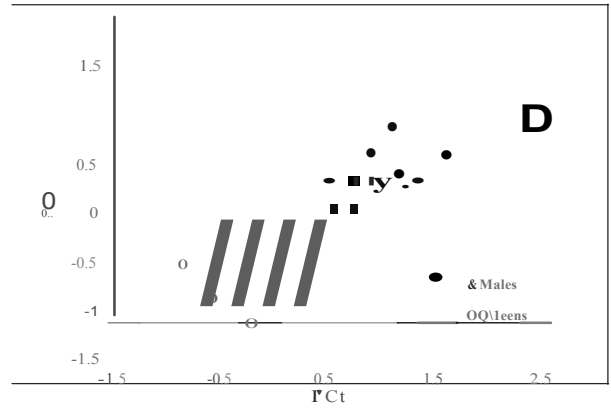
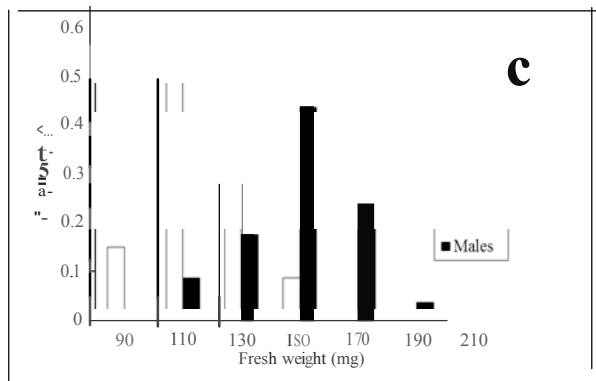
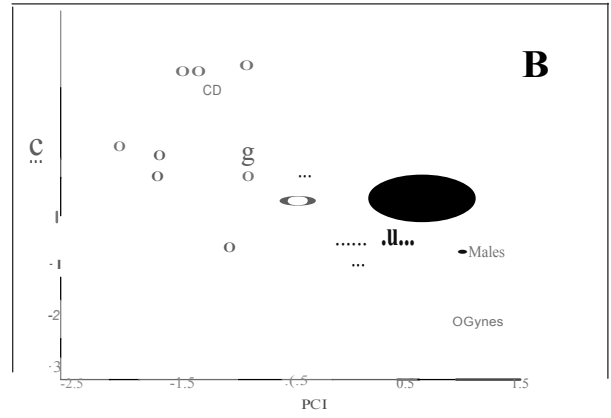
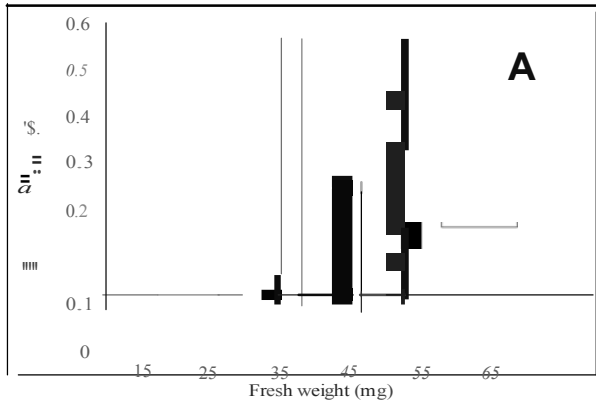
528 Fig 1. Frequency distribution of male and female fresh weight and principal component
529 scores of linear structural measurements (PC1 and PC2) for *M. beecheii* (A and B), *A.*
530 *mellifera* (C and D) and *E. viridissima* (E and F), respectively. Frequencies are based on
531 individual weights.

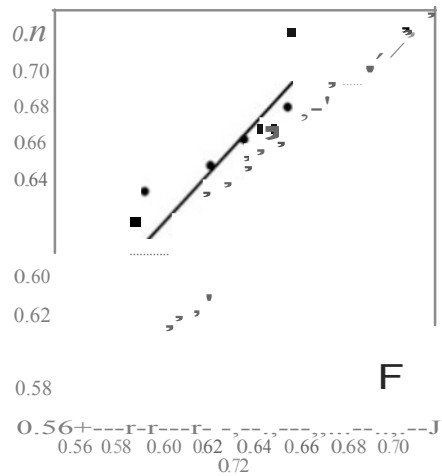
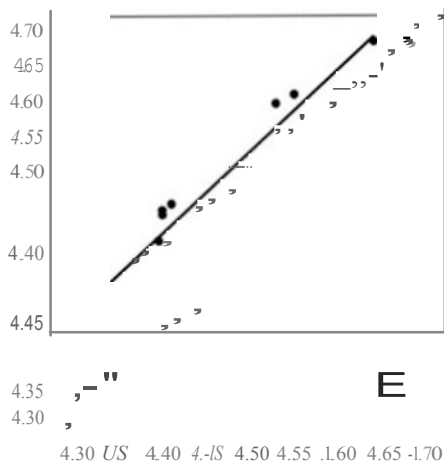
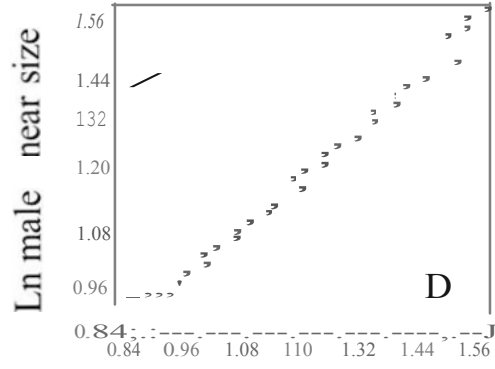
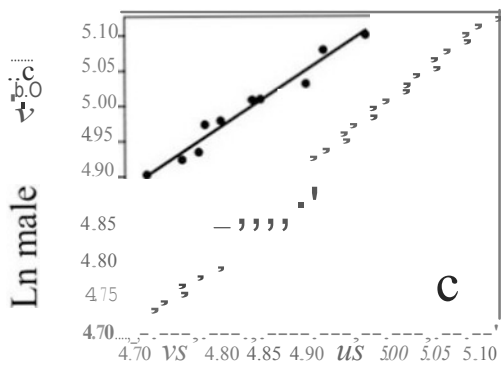
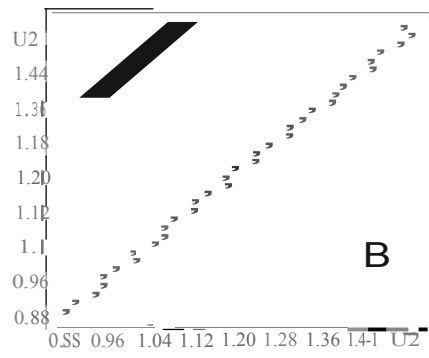
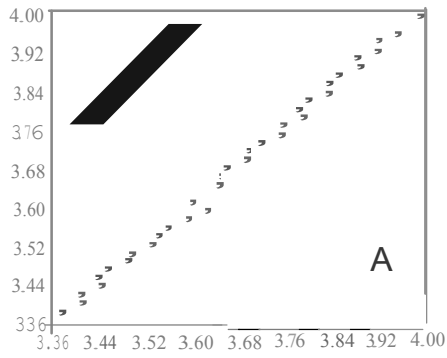
532 Fig 2. MA regression of ln male weight and size (ordinate axis) on female ln weight and
533 size (abscissa axis) for *M. beecheii* (A and B), *A. mellifera* (C and D) and *E. viridissima* (E
534 and F), respectively. The dotted line represents isometry.

535

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537





\ln female weight

\ln female linear size

1 Table 1

Species	Trait	Females Mean (Std.err.)	Males Mean (Std.err.)	t value	P	SSD	SSD range
<i>M. beecheii</i> (N=10)	Fresh weight (mg)	33.98 (0.497)	48.61 (0.919)	14	0.001	0.43	0.29 - 0.57
	PC1	-1.309 (0.049)	0.333 (0.051)	23.19	0.001	0.61	0.36 - 0.75
<i>A. mellifera</i> (N=10)	Fresh weight (mg)	126.01 (3.888)	158.8 (5.504)	4.86	0.003	0.26	0.11 - 0.53
	PC1	-0.173 (0.079)	1.219 (0.076)	12.61	0.001	0.52	0.36 - 0.77
<i>E. viridissima</i> (N=11)	Fresh weight (mg)	88.09 (0.02)	95.89 (0.02)	2.29	0.034	0.08	0.03 - 0.22
	PC1	-0.074 (0.096)	0.174 (0.130)	1.53	0.142	0.10	0.01 - 0.35

2

3

4 Table 2

Species	Variable	Slope	BCI [95%]	Intercept	BCI [95%]	r²
<i>M. beechii</i> (N=10)	Weight	0.815	(0.7368, 1.0287)	0.8995	(0.2832, 1.2987)	0.959
	PC1	0.7941	(0.5727, 1.0027)	0.9282	(0.7604, 1.0054)	0.944
<i>A. mellifera</i> (N=10)	Weight	0.8133	(0.6834, 0.9193)	1.0680	(0.5491, 1.6908)	0.964
	PC1	0.7503	(0.6661, 0.7884)	0.6801	(0.6412, 0.7609)	0.985
<i>E. viridissima</i> (N=11)	Weight	1.1354	(0.9971, 1.2126)	-0.0392	(-0.0643, 0.0208)	0.919
	PC1	1.2943	(1.0478, 1.58)	-0.1639	(-0.3426, -0.0129)	0.897

5

6

7 Table 3

Tribe	Female reproductive division of labor	Colony longevity and reproduction	Mating females	Mating Males	Protogyny	SSD	Intraspecific Allometry
Apini	All species highly eusocial (Queens do not engage in nest activities or food collection)	Perennial Fission by swarming	Polyandrous	Monogamous	Yes	Yes- male biased (this study)	Hypoallometry
Meliponini	All species highly eusocial (Queens do not engage in nest activities or food collection)	Perennial Fission by swarming	Predominantly Monoandrous	Monogamous	Yes	Yes – male biased (this study)	No
Euglossini	Some species primitively eusocial (Females initially engage in nest activities and food collection)	Seasonal Females start colonies on their own	Monoandrous	Polygynous (?)	Yes	No- This study	Hyperallometry
Bombini	All species primitively eusocial (Queens	Seasonal Queens start colonies on	Monoandrous	Polygynous	No	Yes –female biased (Castillo & Fairbairn 2011)	?

	initially engage in nest activities food collection)	their own					
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