

1 **Sociality in the North African small carpenter bee, *Ceratina albosticta***

2 Michael Mikát ^{1,2} and Sandra M. Rehan ¹

3 ¹ Department of Biology, York University, Toronto, Canada

4 ² Department of General Zoology, Martin Luther University, Halle, Germany

5 **ABSTRACT**

6 Small carpenter bees (genus *Ceratina*) are excellent taxa for studying early stages of social
7 evolution, as they have high within and between species variability in social and parental behavior.
8 Most species of *Ceratina* studied are facultatively social, with solitary and social nests in sympatry.
9 Here we examined the nesting and social biology of *Ceratina albosticta* from populations on the
10 edge of the Sahara Desert in Morocco. Although the majority of nests were solitary, social colonies
11 were relatively common and occurred in 16% of nests. Social nests typically contained two
12 females, however, nests possessing up to four females were also detected. Two female nests
13 contained four times more offspring on average than solitary nests; therefore, their nest
14 productivity per female was two times higher than in solitary nests. Social nests contained females
15 of similar body size, but the female with larger ovarian development also exhibited greater wing
16 wear. Ovarian dissections and wing wear data suggests that one female performs foraging and
17 reproduction tasks, while the other female serves as a guard. The brood productivity of this
18 facultatively social bee suggests a benefit to social nesting in this species. Moreover, the division
19 of labor observed is most like other Xylocopinae bees with some females monopolizing foraging
20 and reproduction while other remain on the nest as a guard. This is unlike the more traditional
21 queen and worker roles found in the corbiculate and halictid bees, but an interesting and relatively
22 understudied independent origin of eusociality.

23 **Keywords:** Facultative sociality, per capita productivity, reproductive division of labor, *Ceratina*,
24 Xylocopinae

25 INTRODUCTION

26 Social insects have evolved highly complex and organized societies, containing millions
27 of individuals and have keystone roles in some terrestrial ecosystems (Wilson and Hölldobler
28 2005). However, large and complex animal societies evolved from simple societies, and to
29 understand the origin of social behavior it is important to study species which are in simple stages
30 of social evolution (Schwarz et al. 2007; Shell and Rehan 2017). The most appropriate model
31 organisms are facultatively social species, in which solitary and social nesting strategies are
32 present in sympatry. This variability in sociality makes it is possible to directly compare the
33 biology while controlling for population and environmental variables (Smith et al. 2007; Prager
34 2014; Rehan et al. 2014). In Hymenoptera, the most important groups where facultatively social
35 species are present include taxa Halictidae, Xylocopinae, and Euglossini in bees, as well as
36 Stenogastrine and some Crabronidae wasps (Ross and Matthews 1989; Hogendoorn and Velthuis
37 1999; Schwarz et al. 2007; Turillazzi 2013; Faria and Melo 2020).

38 Small carpenter bees (genus *Ceratina*) are excellent for comparing solitary and social
39 lifestyle. They belong to family Apidae and subfamily Xylocopinae, therefore they are closely
40 related to other simple social bees - *Xylocopa* and allodapines. Although *Ceratina* bees was
41 traditionally considered solitary, there is growing evidence that most species are facultatively
42 social (Groom and Rehan 2018; Mikát et al. 2022). *Ceratina* species nest in broken stems with
43 soft pith (Sakagami and Laroca 1971; Sakagami and Maeta 1977; Rehan and Richards 2010;
44 Rehan 2020; Mikát et al. 2021). At the beginning of the nesting cycle, a female excavates a burrow
45 in the pith of a dead, broken stem (Sakagami and Laroca 1971; Rehan and Richards 2010). Later,
46 brood cells are provisioned with pollen and nectar, making a pollen ball on which an egg is laid
47 (Rehan and Richards 2010; Rehan 2020; Mikát et al. 2021). Brood cells are separated by partitions

48 constructed from pith scraped from the inner walls of the nest (Sakagami and Larooca 1971; Rehan
49 2020). When provisioning is completed, the mother usually guards her offspring until adulthood
50 (Sakagami and Larooca 1971; Sakagami and Maeta 1977; Rehan and Richards 2010; Mikát et al.
51 2016). When the offspring reach adulthood, the mother feeds them pollen and nectar (Sakagami
52 and Maeta 1977; Mikát et al. 2017, 2020b).

53 Social nests of *Ceratina* usually consist of only two females (Sakagami and Maeta 1984;
54 Okazaki 1992; Rehan et al. 2010), however, occasionally social nests can be composed of up to
55 six females (Mikát et al. 2022). Social nesting is strongly associated with nest reuse, in which some
56 offspring remain at the natal nest and do not disperse (Sakagami and Maeta 1984; Okazaki 1992;
57 Rehan et al. 2011). There is evidence for social nesting from approximately thirty-two out of forty-
58 two *Ceratina* species which were behaviorally examined (Groom and Rehan 2018; Mikát et al.
59 2022). Although sociality is present in most of the behaviorally studied species, social nesting is
60 generally scarce with the proportion of social nesting between 1-30% in facultatively social species
61 (Sakagami and Maeta 1984; Okazaki 1992; Rehan et al. 2010, 2015). As social nests are generally
62 scarce, there is a necessity for large datasets to compare solitary and social nesting strategies. Most
63 *Ceratina* species have limited data from only a few social nests which limits detailed comparisons
64 of solitary and social strategies. Extensive data for multifemale nests have been collected only for
65 a few focal species, e.g. *C. australensis* (Rehan et al. 2010, 2011, 2014), *C. okinawana* (Okazaki
66 1992), and *C. japonica* (Sakagami and Maeta 1984).

67 Social biology of *Ceratina* bees is dependent on climate, and tropical species are almost
68 always facultatively social (Rehan et al. 2015; Groom and Rehan 2018). On the other hand, in
69 temperate species solitary nesting prevails (Groom and Rehan 2018), although facultative sociality
70 was also detected (Sakagami and Maeta 1984). Here, we examine the social and nesting biology

71 of *C. albosticta* in the warm and arid climates within the northern edge of the Sahara Desert in
72 Morocco. We provide the first descriptions of social colonies in this species and perform
73 comparisons between solitary and social nests. Moreover, we compared features between solitary
74 nesting females including evidence for foraging and reproductive division of labor.

75

76 METHODS

77 Nest collections

78 *Ceratina albosticta* nests were collected in May (18-25), September (27-30) and October
79 (2 and 22) 2019 in Morocco. We collected 359 nests in total. Most nests were collected around the
80 city of Kalaat M'Gouna (N=295, 31.2365256N, 6.1347164W) (Fig 1). Additional nests were
81 collected near cities: Asni (N = 11, 31.2481761N, 7.9790867W), Azrou (N = 2, 33.4363111N,
82 5.2305825W), Dades Ait Ben Ali (N = 23, 31.4376036N, 6.0112125W), El Kelaat Des Srangha
83 (N = 8, 32.0459144N, 7.4122411W), Ourzazatte (N = 18, 30.9258386N, 6.9415847W) and Zagora
84 (N = 2, 30.3235361N, 5.8258306W). Kalaat M'Gouna is in the Dades Valley, south of the High
85 Atlas Mountains at an elevation of 1450 meters above sea level. The main agricultural plant is
86 Damask rose *Rosa damascena*, which is cultivated primarily for rose oil (Figs. 1d, S1). Rose plants
87 are regularly cut, establishing a high density of dead edges of twigs with accessible pith. These
88 twigs provide optimal opportunities for nesting of *Ceratina* bees.

89 Stems which can contain *Ceratina* nests were collected from rose plantations and naturally
90 dead broken stems which had visible burrows into the pith. Nests were collected during the
91 morning (before 7:30 a.m.) or in evening (after 5 p.m.) to ensure that all inhabitants were present
92 inside nests. Twigs were cut using clippers at the base of the stem and nest entrances were plugged
93 with masking tape to prevent adult bees from escaping the nests. Nests were later opened

94 lengthwise using clippers and nest contents were recorded. The vast majority of *C. albosticta* nests
95 (84%, 302/359) were collected in stems of *Rosa damascena*. Other important nesting substrates
96 were fennel *Foeniculum vulgare* (5%, 19/359), raspberry *Rubus* sp. (4%, 13/359) and various
97 Asteraceae plants (3%, 9/359)

98 Identification of *C. albosticta* and distinction of sympatric similar species (e.g. *C.*
99 *maghrebensis*) was performed using the keys (Daly 1983; Terzo and Rasmont 1997) and by
100 comparison of collected individuals with material identified by Michaël Terzo within the
101 collection in Oberösterreichische Landesmuseen in Linz, Austria.

102

103 Nests contents

104 For each nest, the following features were recorded: length of nest, length of entrance
105 burrow (distance between nest entrance and outermost brood cell partition), width of twig, width
106 of nest, number and sex of adults, number and stage of offspring, and number of empty cells. The
107 presence of dead offspring or parasites, primarily *Gasteruption* (Hymenoptera: Gasteruptionidae),
108 was also recorded. Nest reuse was indicated by the presence of frass, soiled pith and nest walls.
109 Adults and offspring were preserved in 96% ethanol immediately after nest dissection for
110 subsequent analyses.

111 *Ceratina* behavior varies throughout the nesting cycle, making classification of nest stage
112 necessary for the proper understanding of *Ceratina* natural history (Daly 1966). We distinguished
113 following categories of nests: **Burrows**, which contained *Ceratina* adult(s) and no apparent relics
114 of current *Ceratina* nesting, can be used for overwintering, overnight, or in addition to being new
115 founded nests; however it is difficult to distinguish between these possibilities. **Active brood** nests
116 contained an egg or incompletely provisioned pollen ball in the outermost brood cell, as female(s)

117 actively perform brood cell provisioning in these nests (Fig. 2). **Full brood** nests contained a larva
118 or pupa in outermost brood cell and the adult female(s) performs nest guarding at this stage. **Full-**
119 **mature brood** nests contained young adults which have crawled through nest partitions together
120 with immature offspring. In **mature brood** nests, all offspring were fully eclosed adults. In
121 contrast with burrows usually multiple individuals were present and there were excrement, residua
122 of cell walls, or dead offspring in the bottom of nest .

123 Only active and full brood nests were included for the analysis of social nesting, because
124 in non-reproductive nest stages (mature brood nests) it is not possible to distinguish reproductive
125 development among colony members. For reproductive (active and full brood) nests, we calculated
126 the number of brood cells provisioned and proportion of offspring survived. Active brood nests
127 and full brood nests were placed into following categories: **solitary nests** (Figs. 2, S2), which
128 contained only one adult female, **multifemale (=social) nests** which contained two or more
129 females (Figs. 2, S3), **bisex nests** which containing male and female adults, and **orphaned nests**
130 brood but no adults.

131 We measured head width, ovarian development, and wing wear for females from active
132 and full brood nests. All measurements were performed using a Nikon SMZ 800 stereomicroscope
133 integrated with an ocular scale at the Rehan Laboratory at York University, Toronto. Head width
134 is a commonly used as a measure of bee body size (Rehan et al. 2011). Head width was measured
135 as the distance between the outer margins of the compound eyes. For assessment of ovarian
136 development, the bee's abdomen was dissected and the length of the three largest oocytes was
137 measured. The length of these three oocytes from each bee was summed and reported as ovarian
138 development. In two-female nests, we defined social classes based on ovarian development: social
139 primary (female with larger ovarian development) and social secondary (female with smaller

140 ovarian development). Wing wear was classified using a relative scale from zero to six with zero
141 indicating pristine wing margins with no nicks or tears and six being completely shredded with no
142 remaining apical margin (Mueller and Wolf-Mueller 1993). Some bees had wing wear much
143 exceeding six on the scale of Mueller and Wolf-Mueller (1993), and a degree seven was stated for
144 such situations. Wing wear was averaged across both wings to produce the final score for each
145 adult bee.

146

147 Analyses

148 All statistical analyses were performed in the R 4.0.4 (R Core Team 2014). For general
149 description of *C. albosticta* natural history (phenology, proportion of social nests and description
150 of full brood nest structure) we used nests sampled in all period and locations. For analysis of
151 phenology, we used all nests and divided them to two sample periods (May vs September and
152 October). To calculate the proportion of social nests, we used all active brood nests and full brood
153 nests. In data with quantitative dependent variable, linear model or ANOVA analysis was fitted
154 firstly and normality of residuals was checked using diagnostic plots. If residuals were not normal,
155 data were transformed, or appropriate generalized linear model was used.

156 We performed a comparison of the features of solitary and two-female social nests. Other
157 multifemale (nests containing 3-4 females) and bisex nests were not included in the analysis due
158 to small sample sizes. As the vast majority of active brood nests and full brood nests were collected
159 in Kalaat M'Gouna in May, we included only nests from this period and location for comparisons
160 between solitary and two-female nests. For these analyses, we included nest stage (active vs full
161 brood nest) as a covariate. In results section, we present only effect of sociality, however, full
162 Anova tables of model where nest stage and interaction between sociality and are present in

163 supplementary materials (table S1). A linear model was used for testing differences in nest length
164 between solitary and two-female nests. A Poisson generalized linear model was used for testing
165 number of brood cells. Binomial generalized linear models were used for testing the proportion of
166 empty cells (from total number of cells including brood cells) and also for association between
167 nest reuse and sociality.

168 Effect of sociality on current nest productivity (number of eggs and incompletely
169 provisioned pollen balls) was tested using Poisson generalized linear model. As only active brood
170 nests were included to this analysis, nest stage was not included as covariate. Proportion of dead
171 brood cells, proportion of brood cells damaged by *Gasteruption* wasps and by unknown reasons
172 were tested by a Chi square test.

173 The existence of non-random differentiation of ovarian development was tested using a
174 randomization test. First, we calculated the average difference in ovarian development between
175 females from 11 two-female active brood nests. Later, we randomly selected 11 pairs of females
176 from 52 solitary active brood nests. We compared difference in ovarian development between
177 females in two-female nests and randomly selected pairs of solitary females. We repeated this
178 procedure 10,000 times. For full script see supplementary materials.

179 Differences among solitary females and females from two-female nests were tested by
180 ANOVA and TukeyHSD post-hoc tests with nest stage (active brood nest vs full brood nest) as
181 covariate. For wing wear, we used logarithmic transformation of data ($\log(\text{wing wear} + 1)$),
182 because original data had strongly non-normal (positive skewed) distribution and not normal
183 distribution of residuals. Lastly, we performed paired t-test for comparisons between females from
184 two-female nests within one nest.

185

186 RESULTS

187 Phenology of nest stages

188 In May, active brood nests (46%) were prevalent, burrows (28%) and full brood nests
189 (20%) were also common. No full-mature and mature brood nests were found in May. In
190 September and October combined, mature brood nests (48%) and burrows (31%) were common.
191 Full brood nests were rare (8%) and active brood nests were very rare (1%) (Table S2).

192 Adult sex ratio was female-biased in May (82% females, N = 202 females and 45 males).
193 Conversely, adult sex ratio was male biased in September and October combined (44% of females,
194 N = 174 females and 227 males). Adult sex ratio significantly differed between May and
195 September + October (Chi square test, $\chi^2 = 90.92$, $df = 1$, $p < 2.2e-16$).

196

197 Proportion of solitary and multifemale nests

198 Most nests (79%) were solitary, 16% were multifemale (Table S3), 2% were bisex and 3%
199 were orphaned. Most multifemale nests (84%, 21/25) contained only two females, but we found
200 two nests containing three females and two nests containing four females.

201

202 Description of full brood nest structure

203 At least one female was present in 96% (52/54) of full brood nests. This female was never
204 observed inspecting brood cells. Nests were 9.75 cm long on average (N = 54, range 2.5-34.7 cm,
205 SD = 5.62). The entrance burrow (distance between nest entrance and outermost brood cell
206 partition) was 7.17 cm long on average (N = 54, range 1.4-28.7 cm, SD = 4.68). The number of
207 brood cells provisioned was 2.6 on average (N = 54, range 1-8, SD = 1.792). The last brood cell
208 was open in 94% of nests (51/54, Fig 2). About one third of nests (31%, 17/54) contained only one

209 provisioned brood cell, which was open. Empty cells were often present in nests (Fig. 2). There
210 were on average 0.5 empty cells per nest (N = 52, range 0 - 3, SD = 0.87). Empty cells were less
211 common than brood cells, present in 17 % (27/158) of all nest cells.

212 In May, the number of provisioned brood cells was 2.7 on average (N = 42, range 1-8, SD
213 = 1.92). In September, the number provisioned of brood cells was 2.2 on average (N = 12, range 1
214 - 4, SD = 1.93). The difference between periods was not statistically significant (Poisson GLM, N
215 = 54, deviance = 1.13, residual deviance = 56.62, p = 0.29).

216

217 Brood cell mortality

218 In total, 83% (361/433) of brood cells contained live offspring. *Gasteruption* wasps
219 damaged 9% (38/433) of brood cells. One *Gasteruption* larva commonly damaged multiple brood
220 cells in one nest. Other parasites damaged less than 1% (3/433) of brood cells. Seven percent of
221 brood cells (31/433) contained dead brood or only pollen balls and cause of brood death was
222 unknown. Offspring survival in active brood nests was 83% (246/293) while offspring survival in
223 full brood nests was 82% (115/140).

224

225 Comparison between solitary and two-female nests

226 Nest reuse was not a significant influence on the probability of sociality (binomial GLM,
227 N = 131, deviance = 2.47, residual deviance = 109.49, p = 0.12, Table 1). Two-female nests had a
228 significantly higher number of brood cells than solitary nests (Poisson GLM, N = 132, deviance =
229 136.25, residual deviance = 125.40, p < 2e-16; Fig. S4). Two-female nests also had a higher
230 number of recently provisioned brood cells (cells containing eggs or incompletely provisioned
231 pollen ball) than solitary nests (Poisson GLM, N = 91 deviance = 9.42, residual deviance = 9.42,

232 p = 0.002). This difference remained significant, when only older nests (already containing at least
233 one larva) were included (Poisson GLM, N = 39, deviance = 6.39, residual deviance= 6.06, p =
234 0.012). Two-female nests were significantly longer than solitary nests (linear model, N = 132, F =
235 9.32, p = 0.0028; Fig. S4) and had a significantly lower proportion of empty cells (Binomial GLM,
236 N = 126, deviance = 40.28, residual deviance = 148.51, p = 2.205e-10; Fig. S4). The proportion
237 of dead offspring did not significantly differ between solitary and two-female nests (Chi square
238 test, $\chi^2 = 0.91$, df = 1, p = 0.34). There was also no significant difference in mortality caused by
239 *Gasteruption* (Chi square test, $\chi^2 = 1.11$, df = 1, p = 0.29) as well as unknown reasons (Chi square
240 test, $\chi^2 = 0$, df = 1, p = 1). Brood stages in higher development (pupae, full grown larvae) were
241 more common in social nests, whereas early developmental stages (partially provisioned pollen
242 balls, eggs) were more common in solitary nests (Fig. S5). The difference in proportion of brood
243 stages between solitary and two-female nests was statistically significant (Chi square test, $\chi^2 =$
244 23.41, df = 4, p = 0.00010).

245

246 Three and four female nests

247 We detected two three-female nests and two four-female nests. These nests had 8.75
248 provisioned brood cells on average (N = 4, range 4 - 13, SD = 3.77). Nests were on average 18.13
249 cm long (N = 4, SD = 1.46, range = 16.4 – 19.7). Empty cells were not found in any of these nests.
250 In three of these nests had female with largest ovarian development also the largest head width
251 and wing wear. Detailed nest descriptions are in supplementary materials.

252

253 Per capita productivity

254 In solitary nests, the average number of brood cells per female was 2.23 (N = 112, SD
255 =1.67, range =1 – 9; Fig. 3). In two-female nests, the average number of brood cells provisioned
256 per female was 3.98 (N = 20, SD = 1.25, range 1.5 – 6.5), the average number of three-female and
257 four-female nests combined was 2.62 (N = 4, SD = 1.36, range 1 – 4.33). Variance between
258 solitary, two-female and larger nests was statistically significant (ANOVA, df = 2, F = 9.83, p =
259 0.00010) There was a significant difference between solitary and two-female nests (TukeyHSD
260 test, diff = 1.65, p = 0.000053). Three + four female nests had no significant difference from
261 solitary nests (TukeyHSD, diff = 0.39, p = 0.87) nor two female nests (TukeyHSD, diff = -1.26, p
262 = 0.31) in number of brood cells per female.

263

264 Reproductive division of labor

265 We evaluated the reproductive status of females based on ovarian development. Sum of
266 three largest oocytes was significantly larger in females from active brood nests than in females
267 from full brood nests (linear model, N =100, F = 16.70, p = 8.93e-05). The average sum of the
268 three largest oocytes was 1.78 mm in active brood nests (N = 74, range = 0 - 3.75, SD = 0.92),
269 while the average sum of the three largest oocytes in full brood nests was 0.97 mm (N = 26, range
270 0 - 2.38, SD = 0.72). As full brood nests have generally reduced ovarian development (as they are
271 post-reproductive), we only used active brood nests for examination of reproductive division of
272 labor.

273 The average difference between females in ovarian development in two-female nests was
274 1.710 mm. Average simulated difference in ovarian development between two-randomly selected
275 females was 0.914 mm (10000 simulations of 11 randomly selected pairs from pool of solitary
276 nests, SD= 0.192, range = 0.328 - 1.675). Therefore, in all of 10000 cases simulated, difference in

277 ovarian development in two random solitary females was lower than difference in ovarian
278 development within two-female nests.

279 In two-female nests, we defined females with larger ovarian development as social primary
280 and females with smaller ovarian development as social secondary. There was significant variance
281 between solitary females, social primaries and social secondaries (ANOVA, $df = 2$, $F = 13.51$, $p =$
282 0.00005) Social primaries had significantly larger ovarian development than social secondaries
283 (Tukey HSD test, $diff = -1.71$, $p = 0.000010$; Fig. 4, Table 2). Solitary females had larger ovarian
284 development than social secondaries (Tukey HSD test, $diff = 1.12$, $p = 0.00021$) There was no
285 difference between social primaries and solitary females (Tukey HSD test, $diff = -0.60$, $p = 0.069$).

286 There was no significant variance in head width among solitary females, social primaries
287 and social secondaries (ANOVA, $N = 74$, $df = 2$, $F = 1.35$, $p = 0.26$) and there was no significant
288 difference when social primary and social secondary pairs within social nests were compared
289 (paired t-test, $t = 1.82$, $N = 11$, $p = 0.098$).

290 There was significant variance in wing wear between solitary females, social primaries
291 and social secondaries (ANOVA, $df = 2$, $F = 4.80$, $p = 0.01$). Social primaries had significantly
292 more wing wear than social secondaries (TukeyHSD test, $diff = -0.60$, $p = 0.0087$). Differences
293 between solitary females and social primaries was not significant (Tukey HSD test, $diff = -0.24$, p
294 $= 0.26$). Furthermore, the difference between solitary females and social secondaries was nearly
295 significant (TukeyHSD test, $diff = 0.35$, $p = 0.055$). Wing wear of social primaries was
296 significantly greater than social secondaries when pairs within two-female nests were compared
297 (paired t-test, $t = 2.61$, $N = 11$, $p = 0.026$).

298

299

300 DISCUSSION

301 North African *Ceratina albosticta* exhibit facultatively social behavior. Most of the
302 multifemale nests examined contained only two females, but nests containing up to four females
303 were also collected. Solitary and two-female nests differ in many aspects, such as number of brood
304 cells provisioned, nest length and the proportion of empty cells. Non-random differentiation of
305 ovarian size in two-female nests suggests that reproductive division of labor is present in this
306 species.

307 **Phenology:** As we obtained data only from beginning and end of the season, our ability to assess
308 nesting phenology is limited. However, as we detected active brood and full brood nests in both
309 May and September, this suggests a bivoltine or possibly multivoltine colony cycles. In May, ,
310 active and full brood nesting stages were prevalent (no mature brood nests were found at this time),
311 while in September/October, mature brood and burrow nesting stages were most common. These
312 data support seasonality and a lack of continuous nesting year round. Multifemale active brood
313 nests were present in May and mature brood nests were not found at this time, therefore this
314 supports that all adult females which we collected in May were most likely overwintered from the
315 previous year and no newly emerged females were present in May samples. This suggests that
316 possible differences in wing wear are mainly caused by difference in foraging activity not in age.

317 **Nesting biology:** Adult female(s) were present almost always (96%) in full brood nests.
318 Therefore, we suggest that facultative nest abandonment is not present in *C. albosticta*. This
319 contrasts with other species belonging to same subgenus (*Euceratina*), where the possibility of
320 nest abandonment after provisioning completion was detected (Mikát et al. 2016, 2021). We
321 suppose that nest without mother were only accidentally orphaned. However, we never observed
322 females inspecting brood cells, and brood cell partitions appeared to be well preserved. Therefore,

323 we propose that *C. albosticta* may not perform inspecting of brood inside brood cells, as is known
324 in several *Ceratina* species (also Mediterranean *C. cucurbitina*) (Sakagami and Maeta 1977; Rehan
325 and Richards 2010; Mikát et al. 2020a), but was not reported in other species belonging to the
326 shared subgenus *Euceratina* (Mikát et al. 2019a, 2021). The average number of brood cells
327 provisioned in full brood nests (2.6) is much lower than what is known from most *Ceratina* bees
328 studied to date, which is typically between 4 and 12 offspring (Sakagami and Laroca 1971;
329 Vickruck et al. 2011; Mikát et al. 2016, 2021). However, this number of provisioned brood cells
330 is similar to some species present in Cyprus, particularly *C. cypriaca* and *C. mandibularis*, which
331 belongs also to subgenus *Euceratina* (Mikát et al. 2022). A total of 31% of full brood *C. albosticta*
332 nests contained only one offspring, which was not separated from its mother by a brood cell
333 partition and therefore the mother was still in contact with this offspring in an open nest. This
334 suggests that strong pressure of natural enemies probably limits number of brood cells provisioned
335 per nest. The most important cause of brood cell mortality, which we detected was *Gasteruption*
336 wasps, which destroyed around 9% of brood cells. However, our sampling method is not able to
337 detect totally destroyed nests and total nest failure, especially as unguarded *Ceratina* nests are
338 vulnerable to natural enemies, such as ants, which destroy whole nests (Mikát et al. 2016).

339 **Sociality:** Although solitary nests were most prevalent in *Ceratina albosticta*, multifemale nests
340 were commonly detected and comprised 16% of nests. Most of the multifemale nests contained
341 two females, but three and four female nests were also found. This is similar to other facultatively
342 social *Ceratina*, where multifemale nests usually contain two females, but larger nests were also
343 collected (Sakagami and Maeta 1984; Okazaki 1992; Oppenheimer and Rehan 2020; Mikát et al.
344 2022). Males were detected in active brood nests and full brood nests extremely rarely; therefore
345 we do not propose that they have an important role unlike social *C. chalybea* and biparental *C.*

346 *nigrolabiata* (Mikát et al. 2019b, 2021), but future long term studies are needed to determine their
347 prevalence and possible social function.

348 The number of brood cells was around four times higher in two-female nests in comparison
349 with solitary nests. Solitary nests often had only one to three provisioned brood cells , even in full
350 brood nests where provisioning was complete. The number of brood cells in solitary nests is much
351 lower than is usual for *Ceratina* bees, but two-female nests contained usually 5-8 brood cells which
352 is consistent with former studies on this genus (Sakagami and Laroca 1971; Vickruck et al. 2011;
353 Mikát et al. 2016, 2021). Therefore, our data suggest that there is a strong factor which limits the
354 number of brood cells provisioned in solitary nests of *C. albosticta*. This is probably connected
355 with risk of total nest destruction as *Ceratina* nests are vulnerable to natural enemies when they
356 are unguarded (Sakagami and Maeta 1977; Rehan et al. 2011; Mikát et al. 2016). Solitary females
357 perhaps provision fewer brood cells and invest more in nest guarding to offset the risks total nest
358 failure.

359 When we calculate per capita nest productivity, two female nests are two times more
360 productive than solitary nests. This is in contrast with previously studied facultatively social
361 *Ceratina*, where per capita productivity usually remains stable (Mikát et al. 2022) or decreases in
362 social nests (Rehan et al. 2014; Dew et al. 2018a). Additionally, this same trend can be found in
363 *Xylocopa* bees (Prager 2014). However, increase of per capita productivity from solitary to two-
364 female nests is commonly detected in allodapine bees (Bull and Schwarz 2001; Joyce and Schwarz
365 2006; Chenoweth and Schwarz 2007; Bernauer et al. 2021), but not all (Dew et al. 2018b; Jeanne
366 et al. 2022). We showed increased per capita brood productivity from one to two female nests.
367 Although our data for larger nests are limited, we observed that three and four-female nests were
368 not as productive as two female nests. Additionally, we found a higher number of freshly

369 provisioned brood cells in two-female than in solitary nests. Therefore, this suggests that sociality
370 has a positive effect on provisioning rate. Moreover, we found a lower proportion of empty cells
371 in two-female nests than in solitary nests. As empty cells are considered as protection against
372 parasites (Münster-Swendsen and Calabuig 2000), it is possible that social nests can invest less in
373 this protection, because one female guards the nest when the other female is on a foraging trip.
374 However, we did not find a difference in overall brood cell mortality between solitary and two-
375 female nests, and when we separated the effects of *Gasteruption* and unknown reasons, mortality
376 also did not differ between solitary and two-female nests. The reason is that brood cell mortality
377 is generally low (17%) for this species, therefore is difficult to detect any potential effect. Taken
378 together, two-female *C. albosticta* nests are more productive than solitary nests, however larger
379 increases of colony size to more than two females are probably not beneficial. Unimodal optimum
380 of per-capita productivity was reported also for several allodapine bees (Joyce and Schwarz 2006;
381 Chenoweth and Schwarz 2007; Bernauer et al. 2021). *Ceratina* nests are vulnerable, when are not
382 protected by adults (Mikát et al. 2016, 2019b) and presence of a second female allows for full-
383 time guarding, while the other more dominant female is on foraging trip. *Ceratina* have a linear
384 nest architecture which limits females to provisioning one brood cell at a time and precludes work
385 on multiple brood cells or establishing branched burrows as common in social *Megalopta* and
386 *Xylocopa* bees (Smith et al. 2007; Hogendoorn and Velthuis 1999). The difficulties of navigating
387 and passing along a linear corridor (Sakagami and Maeta 1987) as well as brood provisioning
388 considerations limits the efficiency of more females cooperating in a nest.

389

390 **Reproductive division of labor**

391 Ovarian development of solitary females was similar to social primaries, and higher than
392 social secondaries in *C. albosticta*. However, social secondaries had at least some ovarian
393 development in almost all nests. Therefore, this suggests that both females are capable of egg-
394 laying. This situation is in *Ceratina australensis*, where both females are capable of egg laying,
395 but the secondary female only reproduces in the absence of the primary (Rehan et al. 2014). Similar
396 reproductive queueing is known in *Xylocopa* bees and stenogastrine and *Ropalidia* wasps (Stark
397 1992; Bridge and Field 2007; Bang and Gadagkar 2012; Vickruck and Richards 2018) .

398 Ovarian rank was not significantly associated with head width, but was significantly
399 associated with wing wear - females with larger wing wear also had higher ovarian development.
400 This is similar to the social structure observed in *C. australensis* and *C. mandibularis*, in which
401 ovarian development is also associated with wing wear, but not head width (Rehan et al. 2010;
402 Mikát et al. 2022). Greater wing wear is generally attributable to higher foraging activity (Foster
403 and Cartar 2011). This puts into question if the social primary has larger wing wear because she
404 performed greater foraging activity in the present brood rearing season, or because she is older and
405 performed more foraging activity in a past season. As the wing wear and ovarian development of
406 solitary females was most similar to social primaries, this suggests that most probably social
407 primaries monopolize foraging and reproduction much like solitary females, while social
408 secondaries remain on the nest as a guard and hopefully inherit the nest for future reproduction.
409 Females that monopolize foraging and reproduction, while others remain in the nest as non-
410 foraging and non-reproductive guards is a recurrent form of division of labor in bees across tribes
411 of the Xylocopinae (Xylocopini: Hogendoorn and Velthuis, 1999; Ceratinini: Rehan et al., 2010;
412 Allodapini: Schwarz et al., 2011).

413

414 **Conclusions**

415 We detected social nesting in the desert inhabiting small carpenter bee, *Ceratina albosticta*.
416 Multifemale nests usually contained two females, but instances of up to four females were
417 observed. Two-female nests had high per capita brood productivity in comparison with solitary
418 nests, which indicate a benefit of social nesting. Reproductive dominance is associated with wing
419 wear, but not head width. Generally, *C. albosticta* seems behaviorally similar to the social primary
420 and secondary division of labor observed in the semisocial congener, *Ceratina australensis*. Unlike
421 former studies in this genus, *C. albosticta* has a greater per capita brood productivity in two female
422 nest in comparison with solitary nests. Future studies are needed to determine the relatedness
423 within colonies and between social females and to examine the costs and benefits of social nesting
424 in this species.

425

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438

439

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582

583 **Table 1:** Comparison between solitary nests and two-female nests.

	Solitary nests	Two-female nests
N of nests analyzed	111	20
Number of brood cells		
Average	2.2	8
Range	1-9	3-13
SD	1.67	2.6
Length of nest		
Average	9.78	12.91
Range	2.2-25.6	6.7-20.3
SD	4.18	4.55
Proportion of nests reused	27.03%	45.00%
Proportion of empty cells	24.70%	4.22%
Proportion of dead offspring	16.91%	12.67%
- killed by <i>Gasteruption</i>	9.66%	4.00%
- killed by another parasite	0.48%	0.00%
-dead by unknown reason	6.76%	6.67%
N brood cells analyzed	207	150
Stages of not-dead brood cells		
partial provision	19.63%	7.75%
Egg	25.70%	17.61%
feeding larvae	36.45%	38.03%
full grown larvae	14.95%	26.06%
Pupae	3.27%	10.56%
N brood cells analyzed	213	142

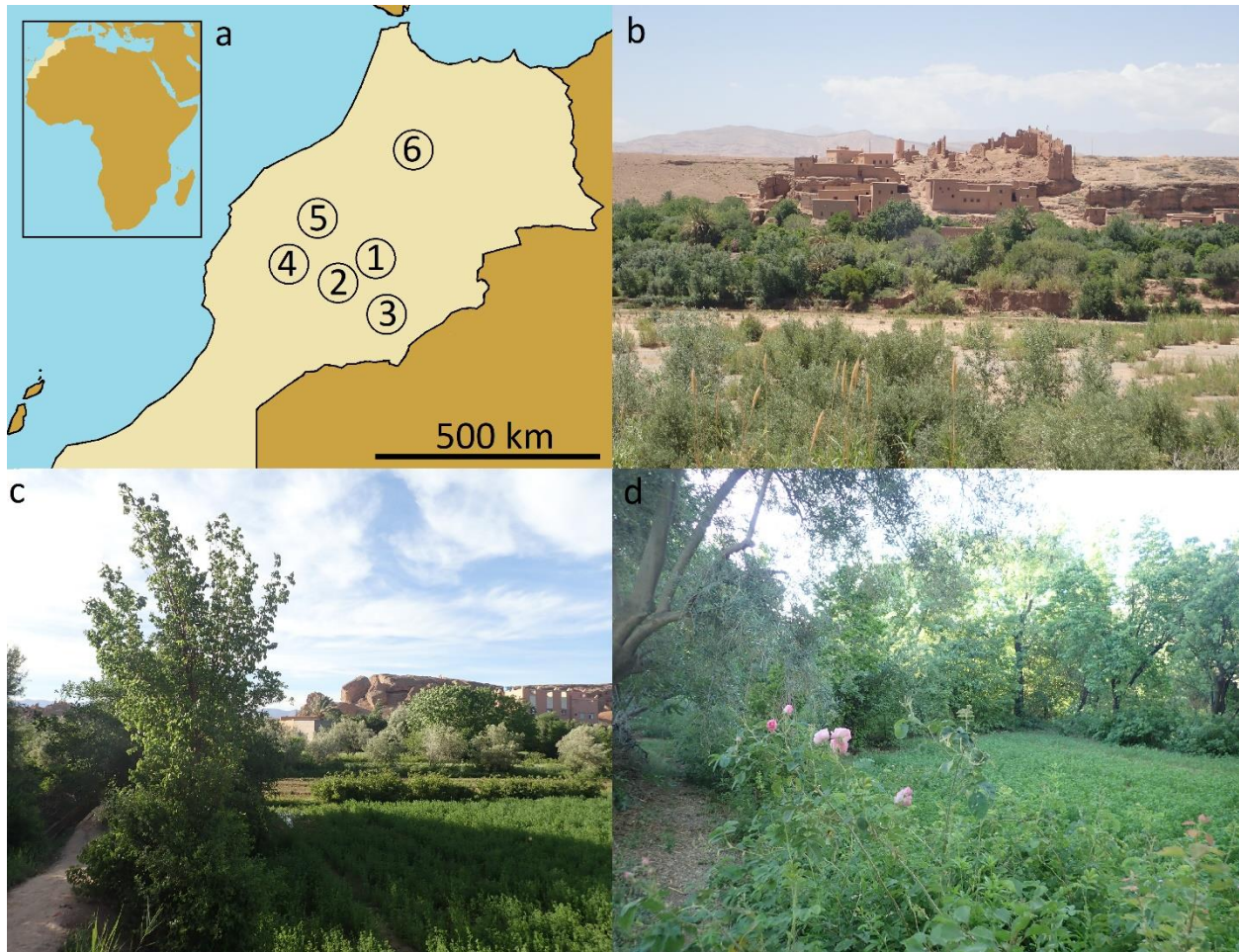
584

585 **Table 2:** Comparison of features of solitary females, social primaries and social secondaries.

	Solitary females	Social primaries	Social secondaries
N females	52	11	11
sum of three largest oocytes (mm)			
Mean	1.86	2.46	0.75
Range	0.00 - 3.75	1.18 - 3.61	0.00 - 0.54
SD	0.83	0.84	0.54
head width (mm)			
Mean	1.79	1.83	1.77
Range	1.59 - 2.00	1.65 - 1.98	1.63 - 1.90
SD	0.08	0.10	0.07
wing wear score			

Mean	1.7	2.4	0.9
Range	0.0 - 7.0	0.0 - 5.0	0.0 - 4.5
SD	1.4	1.5	1.2

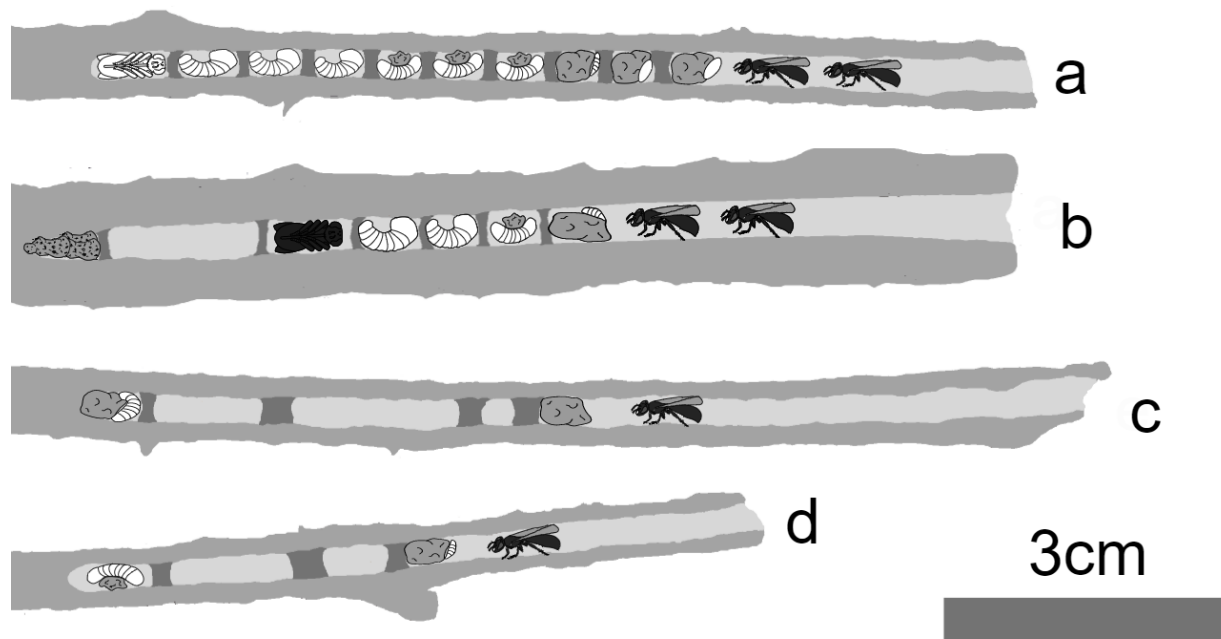
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587

588 **Figure 1.** a) Position of Morocco within northwestern Africa and locations where nests were
589 collected: 1 = Kalaat M'Gouna and Dades Ait Ben Ali, 2 = Ourzazatte, 3 = Zagora, 4 = Asni, 5 =
590 El Kelaat Des Srangha, 6 = Azrou. b) Ecosystems in Kalaat M'Gouna Walley with agriculture,
591 including rose plantations, and semi-desert. c) Landscape in Kalaat M'Gouna where rose
592 plantations provide ample nesting opportunities for *C. albosticta*. d) Rose agriculture at Kalaat
593 M'Gouna.

594



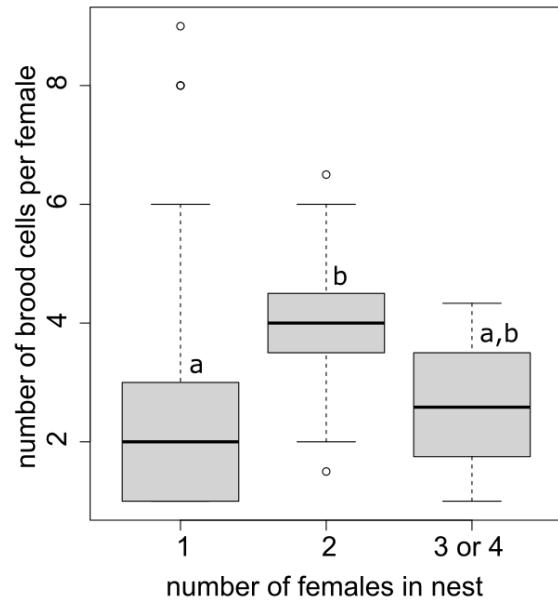
595

596 **Figure 2.** Examples of nests of *C. albosticta*: a) social active brood nests, b) social full brood nests,
 597 c) solitary active brood nest, and d) solitary full brood nest. Oldest offspring are in the bottom
 598 (left) while youngest offspring or currently provisioned brood cell is the outermost (right). Adult
 599 females are in the nest entrance. Empty cells can be present between cells with offspring. All
 600 drawings are based on real nests. Illustrations by: Eva Matoušková and Michael Mikát

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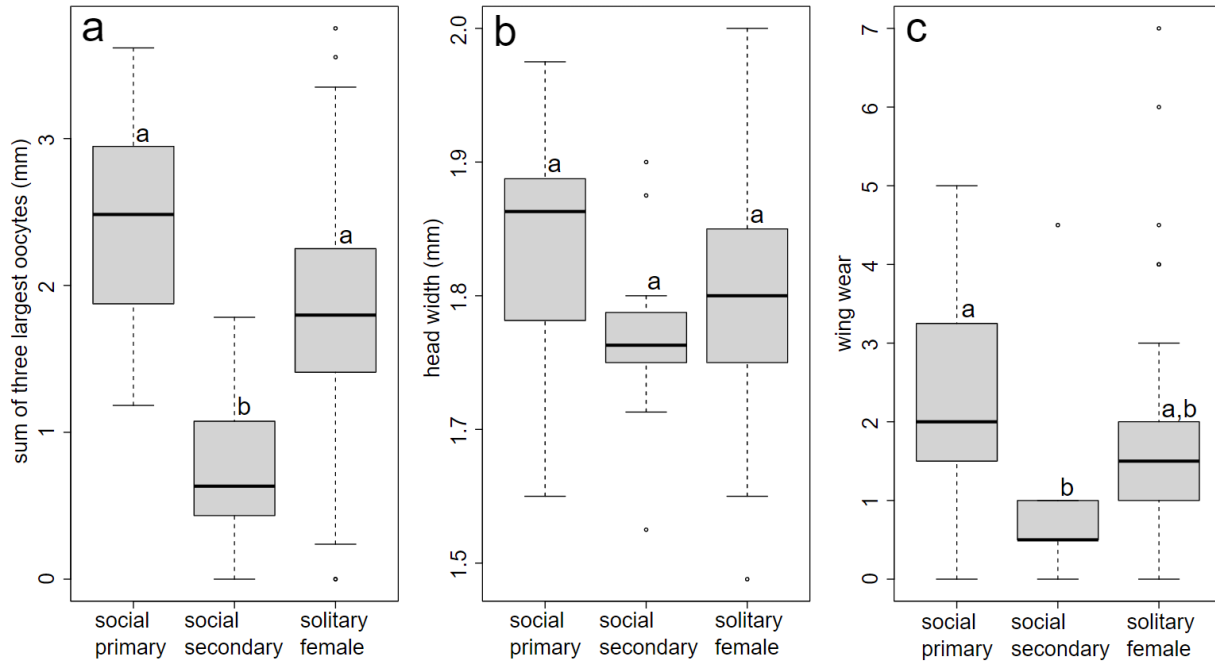
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605 **Figure 3.** Per capita brood productivity in relationship with number of females per nest in *C.*

606 *albosticta*.

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610 **Figure 4.** Features of social primary (female with larger ovarian development from two-female
 611 nest), social secondary (female with lower ovarian development from two-female nests) and
 612 females from solitary nests. a) Sum of three largest oocytes, b) head width, and c) wing wear
 613 scores.

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