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RESEARCH ARTICLE

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

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

Keywords Facultative sociality · Per capita productivity · Reproductive division of labor · *Ceratina* · Xylocopinae

Introduction

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

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

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the nest (Sakagami and Laroca 1971; Rehan 2020). When provisioning is completed, the mother usually guards her offspring until adulthood (Sakagami and Laroca 1971; Sakagami and Maeta 1977; Rehan and Richards 2010; Mikát et al. 2016). When the offspring reach adulthood, the mother feeds them pollen and nectar (Sakagami and Maeta 1977; Mikát et al. 2017, 2020b).

Social nests of *Ceratina* usually consist of only two females (Sakagami and Maeta 1984; Okazaki 1992; Rehan et al. 2010); however, occasionally social nests can be composed of up to six females (Mikát et al. 2022). Social nesting is strongly associated with nest reuse, in which some offspring remain at the natal nest and do not disperse (Sakagami and Maeta 1984; Okazaki 1992; Rehan et al. 2011). There is evidence for social nesting from approximately 32 out of 42 *Ceratina* species which were behaviorally examined (Groom and Rehan 2018; Mikát et al. 2022). Although sociality is present in most of the behaviorally studied species, social nesting is generally scarce with the proportion of social nesting between 1 and 30% in facultatively social species (Sakagami and Maeta 1984; Okazaki 1992; Rehan et al. 2010, 2015). As social nests are generally scarce, there is a necessity for large datasets to compare solitary and social nesting strategies. Most *Ceratina* species have limited data from only a few social nests which limits detailed comparisons of solitary and social strategies. Extensive data for multifemale nests have been collected only for a few focal species, e.g., *C. australensis* (Rehan et al. 2010, 2011, 2014), *C. okinawana* (Okazaki 1992), and *C. japonica* (Sakagami and Maeta 1984).

Social biology of *Ceratina* bees is dependent on climate, and tropical species are almost always facultatively social (Rehan et al. 2015; Groom and Rehan 2018). On the other hand, in temperate species, solitary nesting prevails (Groom and Rehan 2018), although facultative sociality was also detected (Sakagami and Maeta 1984). Here, we examine the social and nesting biology of *C. albosticta* in the warm and arid climates within the northern edge of the Sahara Desert in Morocco. We provide the first descriptions of social colonies in this species and perform comparisons between solitary and social nests. Moreover, we compared features between solitary nesting females including evidence for foraging and reproductive division of labor.

Methods

Nest collections

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

Stems which can contain *Ceratina* nests were collected from rose plantations and naturally dead broken stems which had visible burrows into the pith. Nests were collected during the morning (before 7:30 a.m.) or in evening (after 5 p.m.) to ensure that all inhabitants were present inside nests. Twigs were cut using clippers at the base of the stem and nest entrances were plugged with masking tape to prevent adult bees from escaping the nests. Nests were later opened lengthwise using clippers and nest contents were recorded. The vast majority of *C. albosticta* nests (84%, 302/359) were collected in stems of *Rosa damascena*. Other important nesting substrates were fennel *Foeniculum vulgare* (5%, 19/359), raspberry *Rubus* sp. (4%, 13/359), and various Asteraceae plants (3%, 9/359).

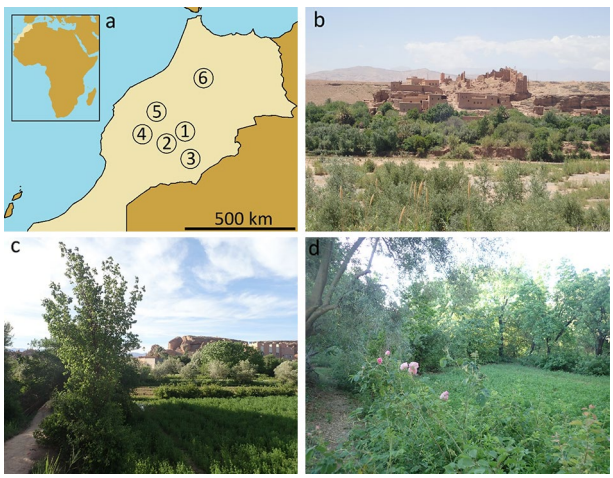

Fig. 1 **a** Position of Morocco within northwestern Africa and locations where nests were collected: 1 = Kalaat M'Gouna and Dades Ait Ben Ali, 2 = Ourzazatte, 3 = Zagora, 4 = Asni, 5 = El Kelaat Des Srangha, and 6 = Azrou. **b** Ecosystems in Kalaat M'Gouna Walley with agriculture, including rose plantations,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

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

Nests' contents

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

Ceratina behavior varies throughout the nesting cycle, making classification of nest stage necessary for the proper understanding of *Ceratina* natural history (Daly 1966). We distinguished the following categories of nests: *burrows*, which contained *Ceratina* adult(s) and no apparent relics of current *Ceratina* nesting, can be used for overwintering, overnight, or in addition to being new founded nests; however, it is difficult to distinguish between these possibilities. *Active brood* nests contained an egg or incompletely provisioned pollen ball in the outermost brood cell, as female(s) actively perform brood cell provisioning in these nests (Fig. 2). *Full brood* nests contained a larva or pupa in outermost brood cell and the adult female(s) performs nest guarding at this stage. *Full-mature brood* nests contained young adults which have crawled through nest partitions together with immature offspring. In *mature brood* nests, all offspring were fully eclosed adults. This is in contrast with burrows as mature brood nests usually have multiple individuals present with excrement and residua of cell walls.

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

We measured head width, ovarian development, and wing wear for females from active and full brood nests. All measurements were performed using a Nikon SMZ 800 stereomicroscope integrated with an ocular scale at the Rehan Laboratory at York University, Toronto. Head width is a commonly used as a measure of bee body size (Rehan et al. 2011). Head width was measured as the distance between the outer margins of the compound eyes. For assessment of ovarian development, the bee's abdomen was dissected and the length of the three largest oocytes was measured. The length of these three oocytes from each bee was summed and reported as ovarian development. In two-female nests, we defined social classes based on ovarian development: social primary (female with larger ovarian development) and social secondary (female with smaller ovarian development). Wing wear was classified using a relative scale from zero to six with zero indicating pristine wing margins with no nicks or tears and six being completely shredded with no remaining apical margin (Mueller and Wolf-Mueller 1993). Some bees had wing wear much exceeding six on the scale of Mueller and Wolf-Mueller (1993), and a degree seven was stated for

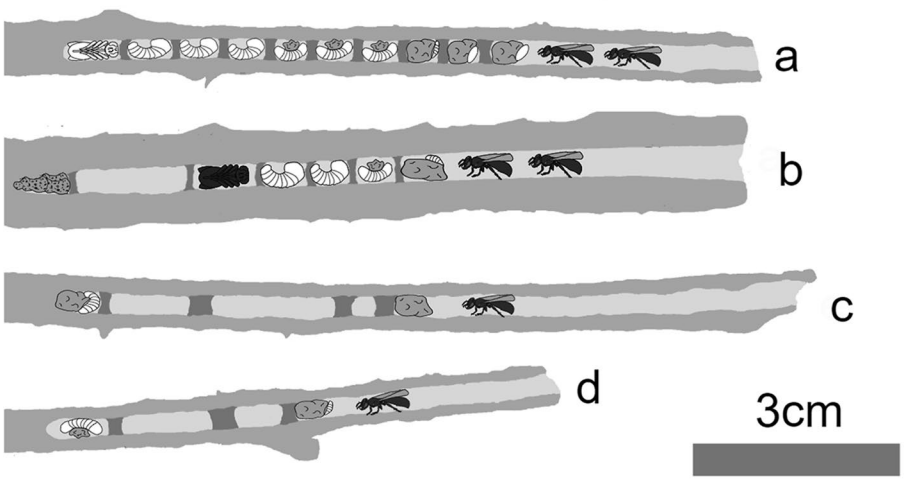

Fig. 2 Examples of nests of *C. albosticta*: **a** social active brood nests, **b** social full brood nests, **c** solitary active brood nest, and **d** solitary full brood nest. Oldest offspring are in the bottom (*left*), while youngest offspring or currently provisioned brood cell is the outermost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

such situations. Wing wear was averaged across both wings to produce the final score for each adult bee.

Analyses

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

We performed a comparison of the features of solitary and two-female social nests. Other multifemale (nests containing 3–4 females) and bisex nests were not included in the analysis due to small sample sizes. As the vast majority of active brood nests and full brood nests were collected in Kalaat M'Gouna in May, we included only nests from this period and location for comparisons between solitary and two-female nests. For these analyses, we included nest stage (active vs full brood nest) as a covariate. In results section, we present only effect of sociality; however, full Anova tables of model where nest stage and interaction between sociality and are present in supplementary materials (Table S1). A linear model was used for testing differences in nest length between solitary and two-female nests. A Poisson generalized linear model was used for testing number of brood cells. Binomial generalized linear models were used for testing the proportion of empty cells (from total number of cells including brood cells) and also for association between nest reuse and sociality.

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

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

Differences among solitary females and females from two-female nests were tested by ANOVA and TukeyHSD post hoc tests with nest stage (active brood nest vs full brood nest) as covariate. For wing wear, we used non-parametric tests (Kruskal–Wallis test and Dunn's post hoc tests) due to strongly non-normal distribution of residuals.

Results

Phenology of nest stages

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

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

Proportion of solitary and multifemale nests

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

Description of full brood nest structure

At least one female was present in 96% (52/54) of full brood nests. This female was never observed inspecting brood cells. Nests were 9.75 cm long on average ($N = 54$, range 2.5–34.7 cm, SD = 5.62). The entrance burrow (distance between nest entrance and outermost brood cell partition) was 7.17 cm long on average ($N = 54$, range 1.4–28.7 cm, SD = 4.68). The number of brood cells provisioned was 2.6 on average ($N = 54$, range 1–8, SD = 1.792). The last brood cell was open in 94% of nests (51/54, Fig. 2). About one-third of nests (31%, 17/54) contained only one provisioned brood cell, which was open. Empty cells were often present in nests (Fig. 2). There were on average 0.5 empty cells per nest ($N = 52$, range 0—3, SD = 0.87). Empty cells were less common than brood cells, present in 17% (27/158) of all nest cells.

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

Brood cell mortality

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

Comparison between solitary and two-female nests

Nest reuse was not a significant influence on the probability of sociality (binomial GLM, $N = 131$, deviance = 2.47, residual deviance = 109.49, $p = 0.12$, Table 1). Two-female nests had a significantly higher number of brood cells than solitary nests (Poisson GLM, $N = 132$, deviance = 136.25, residual deviance = 125.40, $p < 2e{-}16$; Fig. S4). Two-female nests also had a higher number of recently provisioned brood cells (cells containing eggs or incompletely provisioned pollen ball) than solitary nests (Poisson GLM, $N = 91$ deviance = 9.42, residual deviance = 9.42, $p = 0.002$). This difference remained significant, when only older nests (already containing at least one larva) were included (Poisson GLM, $N = 39$, deviance = 6.39, residual deviance = 6.06, $p = 0.012$). Two-female nests were significantly longer than solitary nests (linear model, $N = 132$, $F = 9.32$, $p = 0.0028$; Fig. S4) and had a significantly lower proportion of empty cells (Binomial GLM, $N = 126$, deviance = 40.28, residual deviance = 148.51, $p = 2.205e\text{-}10$; Fig. S4). The proportion of dead offspring did not significantly differ between solitary and two-female nests (Chi-square test, $\chi^2 = 0.91$, $df = 1$, $p = 0.34$). There was also no significant difference in mortality caused by *Gasteruption* (Chi-square test, $\chi^2 = 1.11$, $df = 1$, $p = 0.29$) as well as unknown reasons (Chi-square test, $\chi^2 = 0$, $df = 1$, $p = 1$). Brood stages in higher development (pupae, full grown larvae) were more common in social nests, whereas early developmental stages (partially provisioned pollen balls, eggs) were more common in solitary nests (Fig. S5). The difference in proportion of brood stages between solitary and two-female nests was statistically significant (Chi-square test, $\chi^2 = 23.41$, $df = 4$, $p = 0.00010$).

Table 1 Comparison between solitary nests and two-female nests

	Solitary nests	Two-female nests
No. of nests analyzed		
Number of brood cells	111	20
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 *Gasteruption*	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

Three- and four-female nests

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

Per capita productivity

In solitary nests, the average number of brood cells per female was 2.23 ($N = 112$, SD = 1.67, range = 1–9; Fig. 3). In two-female nests, the average number of brood cells provisioned per female was 3.98 ($N = 20$, SD = 1.25, range 1.5–6.5), and the average number of three-female and four-female nests combined was 2.62 ($N = 4$, SD = 1.36, range 1–4.33). Variance between solitary, two-female, and larger nests was statistically significant (ANOVA, $df = 2$, $F = 9.83$, p = 0.00010). There was a significant difference between solitary and two-female nests (TukeyHSD test, diff = 1.65, $p = 0.000053$). Three and four-female nests had no significant difference from solitary nests (TukeyHSD, diff = 0.39,

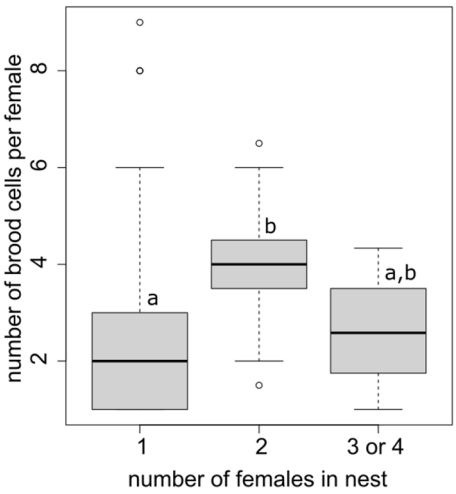

Fig. 3 Per capita brood productivity in relationship with number of females per nest in *C. albosticta*

$p = 0.87$) nor two-female nests (TukeyHSD, diff = − 1.26, $p = 0.31$) in number of brood cells per female.

Reproductive division of labor

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

The average difference between females in ovarian development in two-female nests was 1.71 mm. Average simulated difference in ovarian development between two-randomly selected females was 0.91 mm (10,000 simulations of 11 randomly selected pairs from pool of solitary nests, SD = 0.19, range = 0.33–1.68). Therefore, in all of the 10,000 cases simulated, the difference in ovarian development in two random solitary females was lower than difference in ovarian development within two-female nests.

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

There was no significant variance in head width among solitary females, social primaries, and social secondaries (ANOVA, $N = 74$, $df = 2$, $F = 1.35$, $p = 0.26$), and there was no significant difference when social primary and social

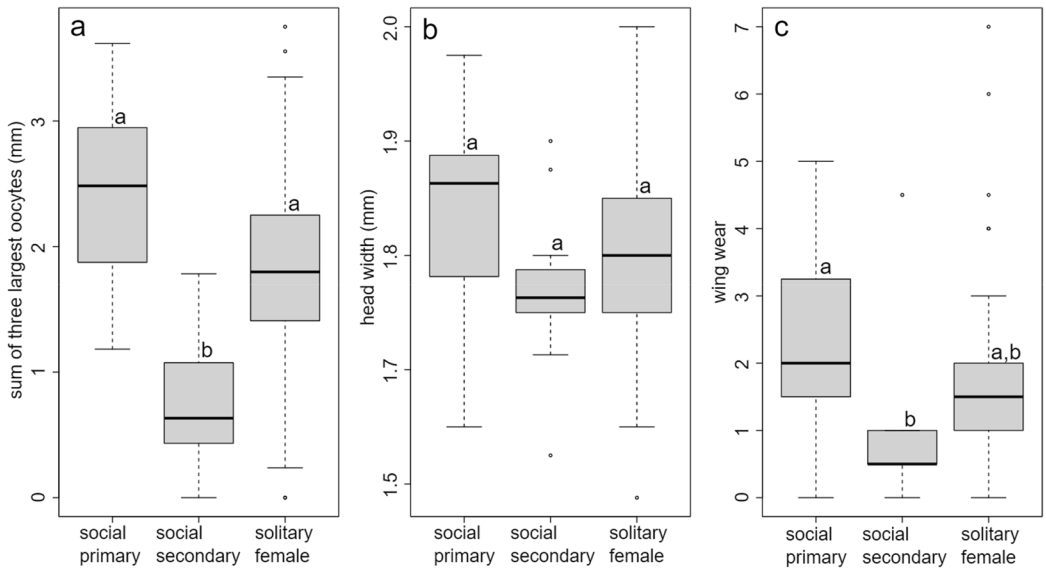

Fig. 4 Features of social primary (female with larger ovarian development from two-female nest), social secondary (female with lower ovarian development from two-female nests), and females from solitary nests. **a** Sum of three largest oocytes, **b** head width, and **c** wing wear scores

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

secondary pairs within social nests were compared (paired *t* test, $t = 1.82$, $N = 11$, $p = 0.098$).

There was significant variance in wing wear among solitary females, social primaries and social secondaries (Kruskal–Wallis test, chi = 9.96, $df = 2$, $p = 0.0069$). Social primaries had significantly more wing wear than social secondaries (Dunn's test, $z = 3.12$, $p = 0.0054$). Differences between solitary females and social primaries were not significant (Dunn's test, $z = 1.64$ $p = 0.30$). Furthermore, the difference between solitary females and social secondaries was nearly significant (Dunn's test, $z = -2.36$, $p = 0.053$). Wing wear of social primaries was significantly greater than social secondaries when pairs within two-female nests were compared (paired *t* test, $t = 2.61$, $N = 11$, $p = 0.026$).

Discussion

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

Phenology

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

Nesting biology

Adult female(s) were present almost always (96%) in full brood nests. Therefore, we suggest that facultative nest abandonment is not present in *C. albosticta*. This contrasts with other species belonging to same subgenus (*Euceratina)*, where the possibility of nest abandonment after provisioning completion was detected (Mikát et al. 2016, 2021b). We suppose that nest without mother were only accidentally orphaned. However, we never observed females inspecting brood cells, and brood cell partitions appeared to be well preserved. Therefore, we propose that *C. albosticta* may not perform inspecting of brood inside brood cells, as is known in several *Ceratina* species (also Mediterranean *C. cucurbitina*) (Sakagami and Maeta 1977; Rehan and Richards 2010; Mikát et al. 2020a), but was not reported in other species belonging to the shared subgenus *Euceratina* (Mikát et al. 2019a, 2021b). The average number of brood cells provisioned in full brood nests (2.6) is much lower than what is known from most *Ceratina* bees studied to date, which is typically between 4 and 12 offspring (Sakagami and Laroca 1971; Vickruck et al. 2011; Mikát et al. 2016, 2021b). However, this number of provisioned brood cells is similar to some species present in Cyprus, particularly *C. cypriaca* and *C. mandibularis*, which belongs also to the subgenus *Euceratina* (Mikát et al. 2022). A total of 31% of full brood *C. albosticta* nests contained only one offspring, which was not separated from its mother by a brood cell partition, and therefore, the mother was still in contact with this offspring in an open nest. This suggests that strong pressure of natural enemies probably limits the number of brood cells provisioned per nest. The most important cause of brood cell mortality which we detected was *Gasteruption* wasps, which destroyed around 9% of brood cells. However, our sampling method is not able to detect totally destroyed nests and total nest failure, especially as unguarded *Ceratina* nests are vulnerable to natural enemies, such as ants, which destroy whole nests (Mikát et al. 2016).

Sociality

Although solitary nests were most prevalent in *Ceratina albosticta*, multifemale nests were commonly detected and comprised 16% of nests. Most of the multifemale nests contained two females, but three- and four-female nests were also found. This is similar to other facultatively social *Ceratina*, where multifemale nests usually contain two females, but larger nests were also collected (Sakagami and Maeta 1984; Okazaki 1992; Oppenheimer and Rehan 2020; Mikát et al. 2022). Males were detected in active brood nests and full brood nests extremely rarely; therefore, we do not propose that they have an important role unlike social *C. chalybea* and biparental *C. nigrolabiata* (Mikát et al. 2019b, 2021a), but future long-term studies are needed to determine their prevalence and possible social function.

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

When we calculate per-capita nest productivity, two-female nests are two times more productive than solitary nests. This is in contrast with previously studied facultatively social *Ceratina*, where per-capita productivity usually remains stable (Mikát et al. 2022) or decreases in social nests (Rehan et al. 2014; Dew et al. 2018a). Additionally, this same trend can be found in *Xylocopa* bees (Prager 2014). However, increase of per-capita productivity from solitary to two-female nests is commonly detected in allodapine bees (Bull and Schwarz 2001; Joyce and Schwarz 2006; Chenoweth and Schwarz 2007; Bernauer et al. 2021), but not all (Dew et al. 2018b; Jeanne et al. 2022). We showed increased per-capita brood productivity from one to two-female nests. Although our data for larger nests are limited, we observed that three- and four-female nests were not as productive as two-female nests. Additionally, we found a higher number of freshly provisioned brood cells in two-female than in solitary nests. Therefore, this suggests that sociality has a positive effect on provisioning rate. Moreover, we found a lower proportion of empty cells in two-female nests than in solitary nests. As empty cells are considered as protection against parasites (Münster-Swendsen and Calabuig 2000), it is possible that social nests can invest less in this protection, because one female guards the nest when the other female is on a foraging trip. However, we did not find a difference in overall brood cell mortality between solitary and two-female nests, and when we separated the effects of *Gasteruption* and unknown reasons, mortality also did not differ between solitary and two-female nests. The reason is that brood cell mortality is generally low (17%) for this species; therefore, it is difficult detect any potential effect. Taken together, two-female *C. albosticta* nests are more productive than solitary nests; however, larger increases of colony size to more than two females are probably not beneficial. Unimodal optimum of per-capita productivity was reported also for several allodapine bees (Joyce and Schwarz 2006; Chenoweth and Schwarz 2007; Bernauer et al. 2021). *Ceratina* nests are vulnerable when they are not protected by adults (Mikát et al. 2016, 2019b) and presence of a second female allows for full-time guarding, while the other more dominant female is on a foraging trip. *Ceratina* have a linear nest architecture which limits females to provisioning one brood cell at a time and precludes work on multiple brood cells or establishing branched burrows as common in social *Megalopta* and *Xylocopa* bees (Smith et al. 2007; Hogendoorn and Velthuis 1999). The difficulties of navigating and passing along a linear corridor (Sakagami and Maeta 1987) as well as brood provisioning considerations limit the efficiency of more females cooperating in a nest.

Reproductive division of labor

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

Ovarian rank was not significantly associated with head width, but was significantly associated with wing wear, females with larger wing wear also had higher ovarian development. This is similar to the social structure observed in *C. australensis* and *C. mandibularis*, in which ovarian development is also associated with wing wear, but not head width (Rehan et al. 2010; Mikát et al. 2022). Greater wing wear is generally attributable to higher foraging activity (Foster and Cartar 2011). This

puts into question if the social primary has larger wing wear, because she performed greater foraging activity in the present brood rearing season, or because she is older and performed more foraging activity in a past season. As the wing wear and ovarian development of solitary females was most similar to social primaries, this suggests that most probably social primaries monopolize foraging and reproduction much like solitary females, while social secondaries remain on the nest as a guard and hopefully inherit the nest for future reproduction. Females that monopolize foraging and reproduction, while others remain in the nest as non-foraging and non-reproductive guards are a recurrent form of division of labor in bees across tribes of the Xylocopinae (Xylocopini: Hogendoorn and Velthuis, 1999; Ceratinini: Rehan et al. 2010; Allodapini: Schwarz et al., 2011).

Conclusions

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

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