

Nesting biology and subsociality in *Ceratina calcarata* (Hymenoptera: Apidae)

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Abstract—To evaluate sociality in small carpenter bees (*Ceratina* Latreille), we studied the life history and nesting biology of a common eastern North American species, *Ceratina* (*Zadontomerus*) *calcarata* Robertson. Pan-trap and nest collections throughout the active season (May to September 2006) were used to assess seasonal phenology and nesting biology of *C. calcarata* in southern Ontario. Adults overwintered in their natal nests. Males emerged in early May and occupied preexisting hollows in twigs and stems. Females emerged from hibernacula 2 weeks later, founding new nests. Nest founding and provisioning occurred throughout the spring; females remained with developing brood through the summer. Complete nests contained, on average, 6.9 offspring, with egg-to-adult development averaging 46 days. *Ceratina calcarata* is subsocial rather than solitary: mothers are long-lived and nest-loyal, and care for offspring from egg to adulthood. Subsociality is found in all behaviourally classified small carpenter bees, while some species cross the boundary into social life, making *Ceratina* an important genus for the study of the transition between solitary and social life.

Résumé—Afin d'évaluer la socialité des petites fourmis charpentières (*Ceratina* Latreille), nous avons étudié le cycle biologique et la biologie de la nidification chez une espèce commune de l'est de l'Amérique du Nord, *C. (Zadontomerus) calcarata* Robertson. Nous avons utilisé des pièges à cuvette et des récoltes de nids durant toute la saison active (mai à septembre 2006) pour déterminer la phénologie saisonnière et la biologie de la nidification chez *C. calcarata* dans le sud de l'Ontario. Les adultes passent l'hiver dans le nid où ils sont nés. Les mâles émergent au début de mai et occupent des cavités préexistantes dans les ramilles et les tiges. Les femelles émergent des hibernacles deux semaines plus tard et fondent de nouveaux nids. La fondation et l'approvisionnement des nids se poursuivent pendant tout le printemps et les femelles demeurent avec le couvain en développement pendant tout l'été. Les nids complets contiennent en moyenne 6,9 rejetons et le développement de l'œuf à l'adulte prend en moyenne 46 jours. *Ceratina calcarata* est subsocial plutôt que solitaire; les femelles vivent longtemps, sont fidèles au nid et s'occupent des petits, de l'œuf à l'adulte. On retrouve de la subsocialité chez toutes les fourmis classées comme petites charpentières d'après leur comportement, bien que certaines espèces passent la frontière vers la vie sociale, ce qui fait de *Ceratina* un taxon important pour l'étude des transitions de la vie solitaire à la vie sociale.

[Traduit par la Rédaction]

Introduction

Subsociality is arguably the simplest form of social behaviour and is defined as prolonged parental care and parent–offspring interaction (Michener 1969; Wilson 1971; Tallamy and Wood 1986). Two preadaptations allow subsociality to arise: (1) nest loyalty, because it is difficult to defend or care for offspring

dispersed through time and space; and (2) parental longevity, because parents need to survive long enough to interact with their offspring throughout and (or) after development (Tallamy and Wood 1986). Once subsocial behaviours are in place, some organisms cross the boundary into social life and exhibit such behaviours as mutual tolerance and cooperative reproduction (Wilson 1971).

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Carpenter bees in the genus *Ceratina* Latreille (Hymenoptera: Apidae) are key taxa for understanding the transition from subsociality to sociality because they are long-lived and nest-loyal and tend to their young throughout development, sometimes even after they have eclosed as adults (Sakagami and Maeta 1977; Michener 1985). Species of this genus are generally categorized as solitary, although sociality occurs naturally in some species (Sakagami and Laroca 1971; Sakagami and Maeta 1984; Rehan *et al.* 2009) and can be induced artificially (Chandler 1975; Sakagami and Maeta 1987, 1989, 1995). This suggests two reasons for making a closer investigation of the nesting biology of *Ceratina* species. First, apparently solitary species may actually be facultatively social. Second, detailed information on the nesting biology of solitary and social species is required for comparative analyses that may lead to insights into the nature of evolutionary transitions between solitary behaviour, subsociality, and group-living.

Ceratina is a large, cosmopolitan genus (Michener 2007), and its species provide numerous evolutionary contrasts through their diverse sociobiology (Michener 1985), ecology, and biogeography (Michener 1979). *Ceratina* species are xylophilous mass-provisioners that form their nests in the pith of dead, broken twigs. Nest-founding consists of chewing out the pith to excavate a long burrow inside the twig. Following nest formation, a foundress uses foraged pollen and nectar to form a pollen mass upon which she lays a single egg. After oviposition she caps the brood cell with a round septum formed by scraping pith tissue from the walls of the nest burrow. This process is repeated for further brood cells in a series such that brood is aligned in order of oviposition within a single unbranched burrow. Females invest their entire reproductive effort in a single nest and remain in the nest after completing oviposition to guard against predators and parasites (Michener 1985).

The eastern Canadian *Ceratina* species *C. calcarata* Robertson, *C. dupla* Say, and *C. strenua* Smith belong to the subgenus *Zadontomerus* Ashmead (Daly 1973). The

nesting biology of *C. calcarata* has been studied in southern portions of its range, including Indiana, (Grothaus 1962; Johnson 1988, 1990), Missouri (Rau 1928), and Georgia (Kislow 1976) in the United States of America. No studies have focused on northern populations, which experience shorter breeding seasons and harsher overwintering conditions, both of which potentially influence nesting biology and social behaviour (Richards 2001; Soucy 2002). The objectives of this study were to (i) document the seasonal phenology and nesting biology of *C. calcarata* in the Niagara region of southern Ontario, and (ii) present evidence of maternal care and subsociality in this species.

Materials and methods

Pan-trap collections

To characterize foraging and emergence phenology, bees were collected using pan traps. Pan traps are useful for determining emergence dates and abundance of bees throughout the season and providing large samples for exploring variation in size and age of bees through indirect measures (Packer *et al.* 2007). Six collection sites, each at least 1 ha in size, were selected in sunny fields and meadows on the Brock University campus and the adjacent Glenridge Quarry Naturalization Site in St. Catharines, Ontario (49°7'N, 79°14'W). All sites had remained unmowed for 5–40 years and had a typical southern Ontario mix of native and introduced plants. Each site was sampled weekly using 30 pan traps consisting of blue, white, and yellow plastic bowls (6 oz SOLO PS6-0099) arranged in an alternating pattern and filled with soapy water. At each site, bowls were placed 10 m apart along two parallel 140 m long transects, also 10 m apart. Pan traps were set out at 0900 and collected at 1500. Each site was sampled weekly from 10 May to 30 August 2005 and from 1 May to 4 September 2006. All collected specimens were preserved in 70% ethanol and sorted in the laboratory, separating the *Ceratina* specimens and identifying them to species (Rehan and Richards 2008) and sex. Voucher specimens are retained at Brock University in the collections of M.H. Richards. As an approximation of body size

(Rust 1991), head width was measured across the widest part of the face, including both compound eyes. Wing wear was scored to estimate age and foraging effort (Cartar 1992): undamaged (“unworn”) bees with no nicks or tears along the apical margins of their forewings were assigned a score of 0 and highly damaged (“worn”) bees with completely shredded apical forewing margins a score of 5. Bees collected in pan traps between May and June of a given year are “spring” samples and those from August through September “summer” samples.

Nest collections

A total of 563 *C. calcarata* nests were collected in 2006 from twigs of American red raspberry, *Rubus idaeus* L. (Rosaceae), and staghorn sumac, *Rhus typhina* L. (Anacardiaceae), growing on the Brock University campus and at the Glenridge Quarry Naturalization Site. In March the ends of numerous dead branches were clipped to expose fresh pith as nesting substrate for bees to excavate that spring. From these and other broken twigs a minimum of 10 nests were collected each week from 1 May through 4 September.

Nests were collected early in the morning (prior to 8 a.m.) to ensure that all occupants were present. Nests were collected by clipping branches with pruning shears at the base of a shoot and then covering the nest entrance with masking tape to ensure that occupants were contained within the nest until dissection. Twigs collected in the field were dissected in the laboratory the same day. Nests were carefully split lengthwise to avoid injuring immature bees or destroying cell septa. Nest contents were recorded, including brood-cell number, brood-cell contents, number of parasites, and location of adult females in the twig. Nest-architecture measurements, including nest length, nest width, entrance width, brood-cell length, brood-cell width, and cell-septum thickness, were made using digital calipers (accuracy ± 0.01 mm).

All nests were categorized using a modification of Daly’s (1966) classification (Rehan *et al.* 2009). *Hibernacula* are nests with darkened interior walls containing fecal pellets or pollen residue from the previous breeding season and

one or multiple adult bees. *Founding* nests are formed in newly excavated pith, as indicated by light interior walls. They are devoid of fecal pellets or pollen residue and do not yet contain brood cells or larval provisions. *Active brood* nests contain one or more brood cells under construction or pollen masses with eggs or small larvae, but clutches are not yet complete. In *complete* or *full brood* nests, the outermost cell (closest to the nest entrance) contains a larva or pupa; because eggs take about 5 days to hatch (Johnson 1988), we assumed that finding such a nest indicated that the mother had finished her nest for the season. *Mature brood* nests contain only adult bees, the youngest of which are callow offspring.

Immature stages and development rates

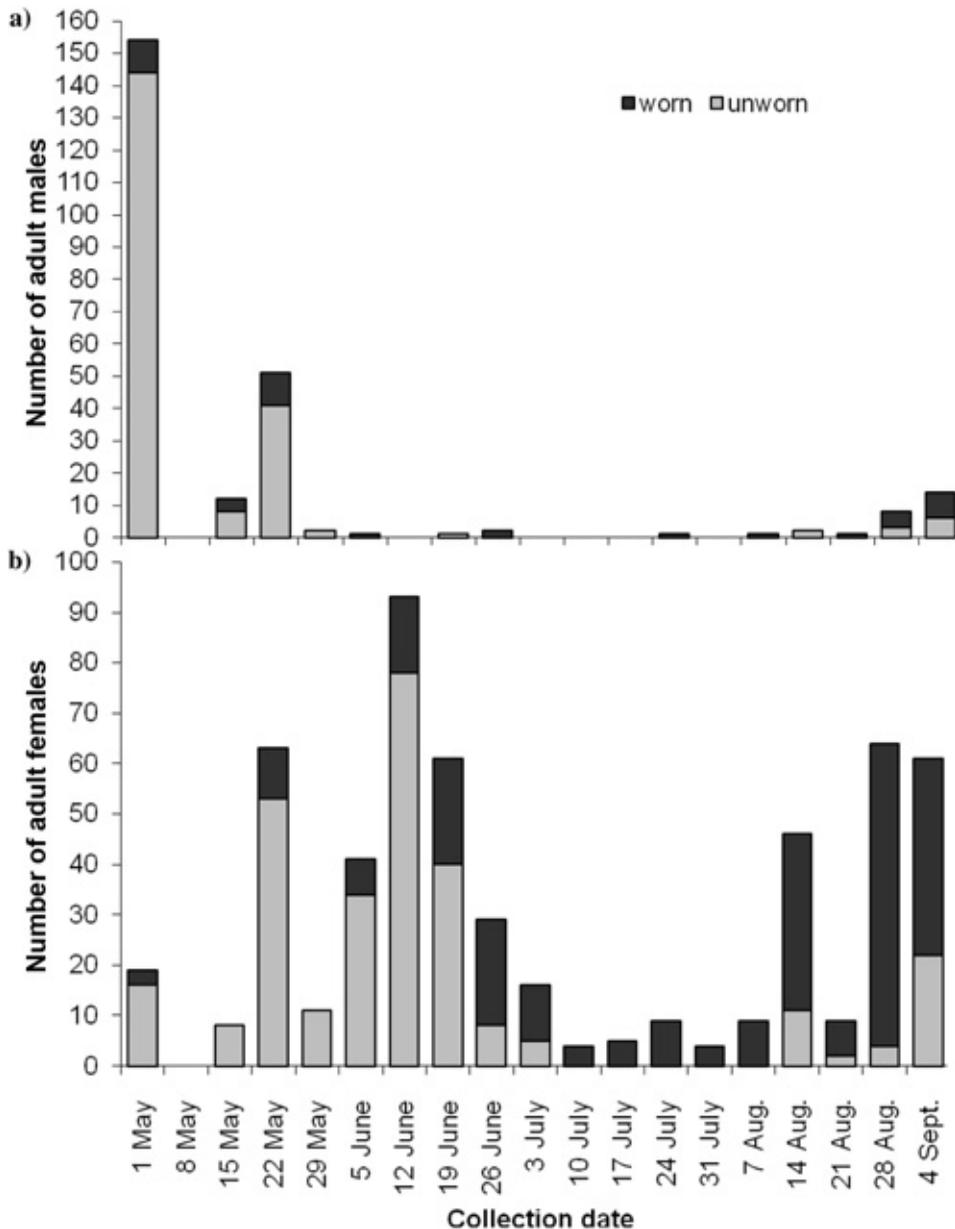
All larvae and pupae collected from nests were placed individually in 200 μ L microcentrifuge tubes each with an air hole in the lid, reared in a laboratory incubator at 25–27 °C, and observed daily. Eighteen development stages from egg to adult were distinguished, based on morphology and pigmentation (Daly 1966). No eggs hatched in the laboratory so we used Johnson’s (1988) observation that eggs take, on average, 5 days to hatch into larvae and begin feeding on the pollen mass. Larval stages are described in terms of the size of the larva relative to the remainder of its pollen mass (*e.g.*, 1/3 means that the larva was 1/3 the length of its pollen mass). Fully grown larvae have consumed their entire pollen mass and are round and fat, whereas prepupae are post-defecatory and longer and skinnier than fully grown larvae. Prepupae metamorphose into white-eyed pupae; the eyes subsequently darken to pink, red, brown, and then black. After the black-eyed stage, the entire body becomes pigmented, the pigmentation being described in terms of the proportion of black integument (1/4, 1/2, 3/4, and fully pigmented). Following full pigmentation, pupae moult into milky-winged adults.

Results and discussion

Seasonal phenology in southern Ontario

Ceratina calcarata had three distinct activity periods at our field sites in 2006, based on

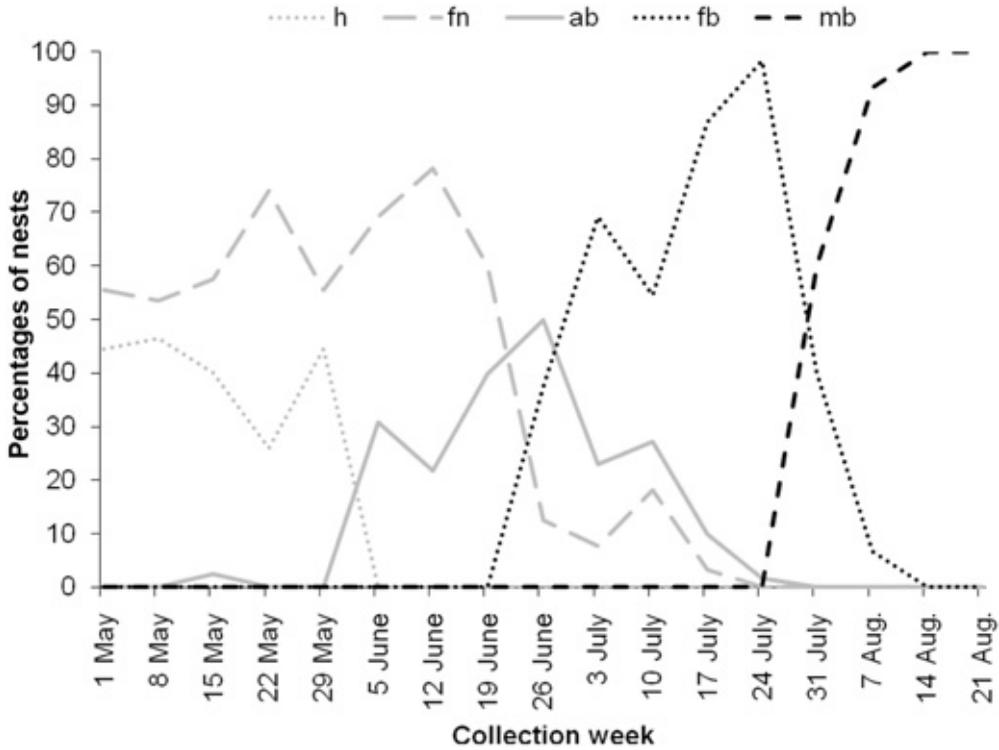
Fig. 1. Total numbers of male and female *Ceratina calcarata* in weekly pan-trap samples collected in St. Catharines, Ontario, in 2006. (a) Emergence of overwintered males in early May is protandrous. Males, most with undamaged (unworn) wings, appear in May. Very few males are collected between June and mid-August. Males with damaged (worn) wings appear in late August. (b) Females' wing wear increases steadily throughout the season. Females disappear from collections from mid-July to August and reappear in late August (with damaged and undamaged wings).



their abundance in pan-trap samples (Fig. 1). The first activity period was in early spring, with abundant overwintered adult males appearing by the first week of May. Male

emergence peaked about 3 weeks earlier than female emergence; adult females were not abundant until the fourth week of May, whereas most males had disappeared by the

Fig. 2. Phenology of nest development in *Ceratina calcarata*, based on 563 nests collected in St. Catharines, Ontario, from 1 May to 4 September 2006. Hibernacula (h) and founding nests (fn) were collected throughout May. Active brood (ab) nests were collected throughout June and full brood (fb) nests in July. By the second week of August, all collected nests contained mature brood (mb).



end of May. For females, the first activity period likely represented initial dispersal from their natal nest to feed, mate, and search for a new nest site. Slightly less than half of all nests collected in May were hibernacula, while the remainder were founding nests (Fig. 2). The majority of females collected in May had unworn wings, indicating that they were born in late 2005, but a small number had worn wings (13 of 90 (14%) females collected in pan traps and 8 of 131 (6%) females found in hibernacula and founding nests; Fig. 1), suggesting that they had been foragers in 2005. This shows that females occasionally overwinter a second time together with their adult offspring.

The second period of activity, which entailed brood-provisioning and oviposition by adult females, began at the end of May and all broods were complete by the fourth week of July (Fig. 2). During the brood-provisioning

period, females were abundant in pan traps, but as broods were completed, the numbers of females collected declined and a period of relative quiescence ensued in midsummer (Fig. 1). Nest collections indicated that during the quiescent period, mothers remained in their nests with their brood, while adult males rested in twigs containing natural hollows or cavities excavated by other insects (including abandoned *C. calcarata* nests).

A third period of activity began in mid-August, when first females and then males were caught with increasing frequency in pan traps (Fig. 1). A majority of these bees were heavily worn and must have been overwintered adults that had been active earlier in the season. Worn females collected in August must have been mothers that had remained in the nest while their brood developed, whereas the unworn females would have been newly emerged daughters (Fig. 1). The difference in

the proportions of worn females *versus* worn males (210 of 249 (84%) females and 14 of 25 (56%) males; likelihood-ratio χ^2 , $G = 6.56$, $P = 0.010$) suggests that adult females have a considerably higher probability of surviving through the summer than males. That both sexes of *C. calcarata* often overwinter in their natal nest is indicated by the fact that only mature brood nests and no founding nests were collected in September (Fig. 2). However, some new adults do disperse prior to overwintering, because mature brood nests contained significantly fewer occupants than full brood nests ($F_{1,173} = 19.79$, $P < 0.001$).

Brood survival and development

Of 563 brood nests collected over the season, 110 were complete. These were collected between 26 June and 27 July 2006 and contained 805 brood cells. Complete nests contained 1–14 brood cells, with 6.9 ± 2.98 (mean \pm SD) and a mode of 8 per nest. Only 1 of 805 brood cells was unprovisioned (the mother formed the cell septum and left the space typical of a single brood cell, but omitted the pollen mass and egg). Seventy (9%) brood cells contained pollen balls with no egg deposited on them and 42 (5%) contained brood that had died prior to collection. One hundred and seventeen larvae (15%) in 22 nests were parasitized and killed by female mites (*Pyemotes* Amerling; Acari: Actinedida: Pyemotidae) and chalcid wasp larvae (identified by DNA sequencing; GenBank accession No. EU157965), and 96 (12%) died from unknown causes in the laboratory during maturation. Finally, 479 (59%) brood were successfully reared to adulthood.

From daily developmental observations based on all juveniles reared in the laboratory at 25–27 °C, *C. calcarata* take, on average, 46 days to develop from egg to adulthood (Table 1). Eighteen development stages were distinguishable: 1 egg, 8 larval, and 9 pupal. Immatures collected as eggs died shortly after nest dissection in the laboratory, so there are no direct observations on egg eclosion rates. Larvae develop for 19 days then pupate for an additional 22 days.

Table 1. Development rates of immature *Ceratina calcarata* collected in St. Catharines, Ontario, in 2006.

Stage	Development rate (days)		<i>n</i>
	Mean	SD	
Egg	5.00	na	na
Larva			
1/3–2/3 pb	4.50	3.12	8
2/3–7/8 pb	3.38	2.58	24
1 \times pb	1.83	1.18	31
Larva			
1.5 \times pb	1.89	0.87	35
2 \times pb	2.33	1.51	51
Small bit pb	2.25	1.48	68
Fully grown larva	2.33	1.66	108
Prepupae	5.24	1.81	134
Pupa			
White	2.65	1.28	178
Pink	1.80	0.86	184
Red	1.98	0.96	189
Brown	2.70	1.36	142
Black	3.95	1.51	125
1/4	1.53	1.22	51
1/2	1.64	0.88	56
3/4	2.34	0.95	142
Fully pigmented	3.68	1.54	223
Total	46.04	1.46	1749

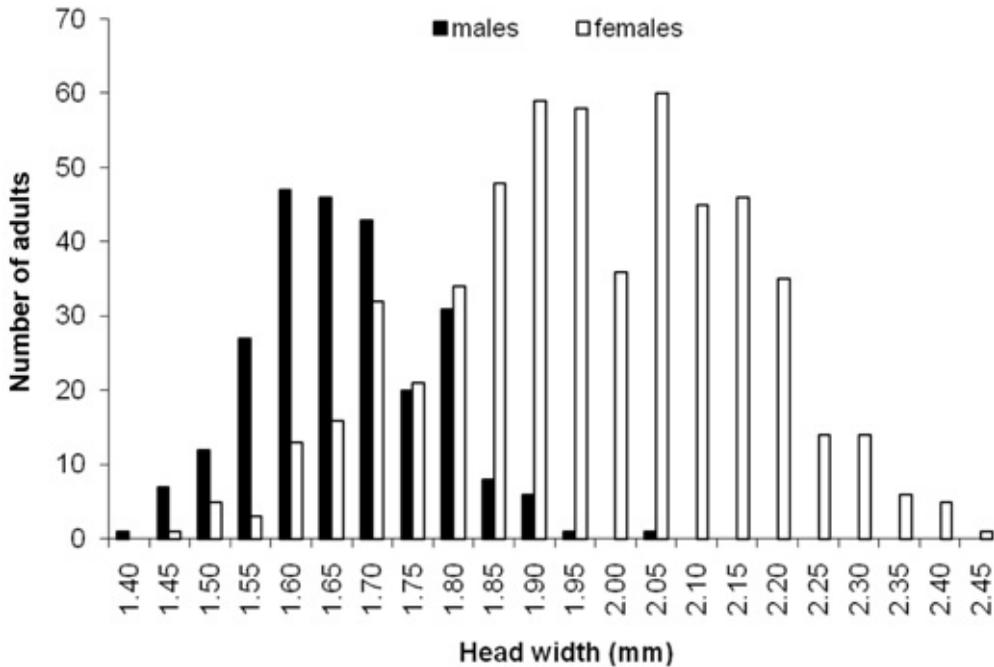
Note: Values for most larval stages are presented as the ratio of the length of the larva to the length of the pollen mass (pb); “small bit pb” indicates that the larva is more than 2 \times longer than the remaining pollen mass. Pupal stages from “white” to “black” describe changes in eye pigmentation and pupal stages “1/4” to “fully pigmented” describe changes in body pigmentation.

Influence of adult body size on survival

Pan traps yielded a large sample of adults of both sexes for the study of body-size range and variation in this species (Fig. 3). Mean female and male head widths were 1.94 mm (range 1.41–2.83 mm; CV = 9.6%) and 1.65 mm (range 1.38–2.04 mm; CV = 6.8%), respectively.

The distribution of head widths of unworn males did not differ between summer 2005 (newly eclosed adults: head width 1.62 ± 0.12 (mean \pm SD)) and spring 2006 (the same cohort emerging from hibernation: head width 1.65 ± 0.11 ($F_{1,206} = 2.36$, ns), suggesting no influence of size on over-winter survival of

Fig. 3. Body-size distributions based on head widths of male and female *Ceratina calcarata* from pan-trap samples collected in St. Catharines, Ontario, in 2006.



males. Unworn, newly eclosed females collected in summer 2005 (head width 1.86 ± 0.19) were significantly smaller than those collected in spring 2006 (head width 1.93 ± 0.18 ; $F_{1,286} = 3.97$, $P = 0.04$). Similarly, unworn females collected in summer 2006 (head width 1.86 ± 0.19) were significantly smaller than those collected in spring 2006 (head width 1.93 ± 0.18 ; $F_{1,291} = 3.75$, $P = 0.05$). Overall, these patterns suggest size-differential mortality in females but not in males: small females are produced in late summer, but tend not to survive winter.

Nest architecture

The architecture of *C. calcarata* nests follows the description by Michener (1985). We found the dimensions of 302 nests to be as follows: total nest length = 108.41 ± 78.23 mm (mean \pm SD); nest width = 2.90 ± 0.53 mm; nest-entrance width = 3.35 ± 0.60 mm. The dimensions of 271 brood cells were as follows: brood-cell length = 7.13 ± 4.51 mm; cell width = 3.31 ± 0.55 mm; septum thickness =

3.09 ± 2.23 mm. The nest entrance was significantly wider than the burrow (paired t test: $t = 15.42$, $n = 298$, $P < 0.0001$).

After the nest tunnel is constructed and provisioning of brood cells begins, the nest is not lengthened, so nest length provides an upper limit to the number of brood cells that can be constructed. Complete nests varied in length from 21 to 138 mm and were not limited by knots in the twig. Nest length was slightly but not significantly correlated with clutch size in complete nests ($r = 0.17$, $n = 110$, $P = 0.07$); some exceptionally long nests contained few brood cells and some short nests contained many. Thus, nest length did provide an upper limit to potential clutch size but long nests were no more fecund than short nests.

Maternal longevity and brood care

An adult female assumed to be the brood mother was found in all 156 founding and active brood nests and in 108 of 110 full brood nests, suggesting that nests are founded by a single female and that almost all nest foundresses survive at least until brood completion. Of 38

mature brood nests, 11 contained a worn adult female, suggesting that about 1/4 of mothers live past the time when some of their adult brood have dispersed from the natal nest, sometimes even surviving a second winter, as noted above. Despite surviving winter, no worn females were collected in founding nests, suggesting that females in this population rarely, if ever, produce a second brood.

Mothers inspect brood cells and interact with juveniles during development. At the time of nest dissection, most mothers were found in the gallery between the nest entrance and the first brood cell, often in a defensive position with their abdomen blocking the nest entrance. However, 14 of 108 (13%) mothers were found inside a brood cell containing a larva or pupa, having broken down the septa separating brood cells. Cells occupied by these mothers ranged from inner to outermost positions. Evidently, mothers reconstruct broken septa after inspecting brood cells because cell septa were intact in nests in which the mother was found in the entrance. In one nest, two pupae were found in the basal brood cell. Their mother likely did not repair the septum after brood-cell inspection because pollen masses and larvae were always found singly within a brood cell. Only one of the two orphaned full brood nests contained parasitized brood (6 of 12 brood), but this sample is insufficient to assess the effectiveness of maternal behaviour in preventing parasitism.

Latitudinal variation in *C. calcarata* nesting biology

Comparisons with populations in other geographical areas suggest consistency in the annual nesting cycle of *C. calcarata*, with some latitudinal variation induced by differences in season length. In Georgia and Indiana, as in Ontario, the life cycle is univoltine but major events occur about a month earlier (Grothaus 1962; Kislow 1976). The earlier phenology in southern populations is undoubtedly related to milder spring weather, but may also be influenced by faster juvenile development. In Georgia, egg-to-adult development takes about 43 days (Kislow 1976) and possibly as few as 34 days in Indiana (Johnson 1988); we estimated that it takes about 46 days in southern Ontario.

Longer growing seasons at lower latitudes are also associated with larger clutches: in Indiana and Georgia, complete nests contained, on average, 10 (Grothaus 1962; Johnson 1990) and 14 (Kislow 1976) offspring, respectively; in southern Ontario we found that the mean clutch size was about 7. Prolonged active seasons for southern populations likely enhance foraging opportunities, owing to protracted floral availability, apparently allowing mothers to provision more brood than in northern populations that experience shorter seasons. The earlier phenology, longer active season, and faster development of *C. calcarata* in Georgia and Indiana than in Ontario provide support for Rau's (1928) suggestion that *C. calcarata* could be bivoltine in Missouri.

Maternal and social behaviour in the genus *Ceratina*

In our study of *C. calcarata* in Ontario, as in Georgia (Kislow 1976), Indiana (Grothaus 1962; Johnson 1988), and Missouri (Rau 1928), all nests were founded by a single female, confirming that this species is obligately solitary across its range. Other notable observations consistent across populations concern maternal longevity and nest loyalty. As in our study, it was noted in earlier studies that adult females were usually (Grothaus 1962) or always (Rau 1928; Johnson 1988) found with completed broods. Thus, maternal longevity is combined with a habit of "maternal solicitude" (Rau 1928): females frequently open brood cells to inspect and groom the developing offspring, chew up failed brood cells and incorporate them into pith partitions, and rebuild brood cells after inspection, except occasionally when brood cells are occupied by late-stage pupae (Kislow 1976; this study). This suggests that *C. calcarata* is a subsocial rather than a solitary insect.

Subsocial traits of maternal longevity, nest loyalty, and brood care are typical of all *Ceratina* species studied to date (Michener 1985; Sakagami and Maeta 1977), including several Asian species that exhibit a low frequency of social nesting such as *Ceratina smaragdula* (Fabricius) (25% of nests), *C. nigrolateralis* Cockerell (6%), and *C. dentipes* Friese (5%) (Rehan *et al.* 2009) and *C. okinawana* Matsumura and Uchida

(15%), *C. japonica* Cockerell (10%), and *C. flavipes* Smith (1%) (Sakagami and Maeta 1987, 1989). Our observations of the subsocial behaviour of solitary female *C. calcarata* provide an important comparison with the subsocial maternal behaviour of other *Ceratina* species and may help to reveal the ecological pressures that drive the transition to sociality in this genus.

Ceratina species have numerous natural enemies (Daly 1967), but *C. calcarata* experiences moderate parasitism rates of 15%–33% of surveyed brood cells (Kislow 1976; this study) and a low brood-orphaning rate of 2%. In comparison, studied Asian *Ceratina* species experience 20%–50% brood parasitism, and brood-orphaning rates as high as 25% (Sakagami and Maeta 1987; Rehan *et al.* 2009). Cooperative nesting has two advantages in the face of high parasite pressure: nests can be guarded when a female is foraging, and a replacement adult can care for brood of a dead female. The association between parasite pressure and cooperative nesting, even at low frequency, suggests that increased adult mortality and brood parasitism are likely causes of subsocial nesting in *Ceratina* (Lin and Michener 1972; Evans 1977; Andersson 1984; Crespi 1994).

The evolution of sociality requires cohabitation and mutual tolerance, after which cooperative reproduction can occur (Michener 1969; Wilson 1971). All reported *Ceratina* (*Zadontomerus*) species establish new nests each spring (Kislow 1976). Although females cohabit as mature brood prior to winter, in spring they disperse and establish solitary nests. The univoltine life history of *C. calcarata* in southern Ontario (this study), Indiana (Grothaus 1962), and Georgia (Kislow 1976) precludes matrilineal cohabitation during the breeding season and multifemale nest provisioning. However, it would be interesting to study southern populations such as those described by Rau (1928) in Missouri to determine whether a bivoltine colony cycle (and therefore potential generational overlap and matrilineal cooperation) and reuse of old nests occur. Old World species frequently reuse nests, and even univoltine species such as *C. japonica* and *C. flavipes* have a low frequency of social nesting, predominantly in reused nests (Sakagami and Maeta 1984, 1989).

Conclusions

Ceratina calcarata is a subsocial bee with prolonged maternal care and parent–offspring interaction. At lower latitudes this species has faster development, a prolonged active season, and larger clutches. At the southern extent of its range, multiple generations per year could present opportunities for multifemale nest provisioning and subsocial life. Further study of this and additional *Ceratina* species from other populations and subgenera is needed to review the social potential and life-cycle variation across the genus.

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