Behav Ecol Sociobiol (2017) 71: 135
DOI 10.1007/s00265-017-2365-6

ORIGINAL ARTICLE

Sociodemographic variation in foraging behavior and the adaptive significance of worker production in the facultatively social small carpenter bee, *Ceratina calcarata*

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Received: 17 March 2017 / Revised: 20 July 2017 / Accepted: 7 August 2017 / Published online: 17 August 2017

Abstract
Provisioning for young offspring is an archetypical form of parental investment. *Ceratina calcarata* bees provide extended maternal care to their young and demonstrate an unusual strategy of dual-phase pollen provisioning. Most bees first gather provisions as they establish nests in spring. However, *C. calcarata* mothers will also feed their newly eclosed young a second time, perhaps ensuring their survival during a long winter diapause. Some mothers rear a small, worker-like daughter to assist them during this second provisioning phase. We studied provisioning behavior in *C. calcarata* to examine patterns of maternal investment and foraging dynamics throughout the breeding season. Mothers typically made a high number of short-duration foraging trips each day, whereas late-season females tended to make fewer and longer trips. This difference in foraging duration may indicate a lower risk of brood loss in those nests where mature offspring are present. Nest demographic data revealed that an offspring laid in the first brood cell position is typically female and usually smaller than her siblings. In 29% of the nests, this small daughter was observed to adopt a forager role at maturity and provisioned for her siblings. Dwarf daughters had a higher number of active days and foraging trips per day in orphaned nests than in nests where a mother was present. The foraging behaviors of worker-like daughters were similar in length of foraging trip and handling time to mothers during this second provisioning period. We hypothesize that incipiently social foraging by this smallest daughter may act as a form of insurance against brood loss during occasions when a mother is unable to sufficiently provision for her eclosed offspring during the second phase.

Significance statement
Parental investment in the size and sex of offspring is under strong selection for assured fitness returns. For example, many social insect mothers make an initial investment in small offspring to take on risky foraging behavior while they specialize on future reproduction. Solitary and facultatively social species provide an important baseline to understand the evolution of social complexity from natural variation in maternal care and foraging behavior. Here, we characterize the parental investment strategies of a subsocial small carpenter bee and reveal the potential adaptive significance of prolonged maternal care and worker production in this species. Mothers provide an initial investment that is extended by workers providing alloparental care to siblings. Maternal manipulation of dwarf eldest daughters may serve as an insurance mechanism in the event of maternal mortality to assure the survival of siblings.

Keywords Hymenoptera · Parental investment · Sex allocation · Foraging ecology · Maternal manipulation · Overwintering survival

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Communicated by J. Field

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-017-2365-6) contains supplementary material, which is available to authorized users.

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Introduction

Offspring provisioning is one of the main forms of parental investment (Tallamy and Wood 1986; Mas and Kölliker 2008). In Hymenoptera, brood provisioning may be an almost constant activity, and one that is highly costly (Willmer and Stone 2004; Morato and Martins 2006). There are two main provisioning strategies in bees: mass provisioning, when all supply of food for young offspring is collected before hatching of egg; and progressive provisioning, in which parents feed offspring directly (Field 2005; Michener 2007). When mass provisioning, a parent can optimize resource allocation among multiple brood, allowing her to decide exactly how much pollen and nectar to distribute to each individual offspring (Michener 1974; Danforth 1990). These brood investments are easily assessed, either through measurement of the provision mass (Johnson 1988; Tomkins et al. 2001; Lawson et al. 2016) or the body mass of a mature offspring (Strohm and Linsenmair 1999; Bosch and Vicens 2002; Rehan and Richards 2010a). As a mother invests more in any individual offspring, she effectively increases that offspring's probability of survival (Cowan 1981; Strohm and Linsenmair 2000). Life-history theory predicts that there is an optimal means of dividing resources among offspring, such that a balance is struck regarding the tradeoff between brood count and brood body size in any given species (Smith and Fretwell 1974).

Mothers may also optimize their brood investment by carefully controlling the allocation of brood sex (Charnov 1982). At a total population level, sex investment is expected to be an equal male to female ratio (Fisher 1930). Most animal species are sexually dimorphic, and optimal brood investment may vary between male and female offspring (Charnov 1982; Fisher 1930). This optimization strategy is especially common in Hymenoptera (Molumby 1997; Rehan and Richards 2010a), in which mothers can directly control which sex they will produce through selective insemination of their eggs (Gerber and Klostermeyer 1970).

In social Hymenoptera, offspring composition and subsequent resource allocation may be strongly influenced by intracolony interactions (Crozier and Pamilo 1996; Bourke 2011). Eusocial species feature a female-biased brood sex ratio due to the fact that female offspring typically develop into sterile or subfertile workers (Wilson 1971; Michener 1974; Schwarz et al. 2007). It is also thought that sex ratio investment in eusocial Hymenoptera is female biased if workers control investment, because workers are more closely related to female than to male siblings (Trivers and Hare 1976). The social roles of individual females in primitive and advanced eusocial species are strongly influenced by nutritional cues during development (Wilson 1971; Michener 1974). It is thus thought that maternal investment, which involves the carefully controlled provisioning of each offspring, likely played an important role in the evolution of sociality (Alexander 1974; Craig 1983), because for subfertile individuals, it can be beneficial to adopt a worker role (West-Eberhard 1975). Dominance hierarchies in social insects are frequently determined by body size; during social interactions, it is normally the smaller individual which assumes a subordinate position (Smith et al. 2009). In temperate species, however, small body size may also reduce an individual's capacity to survive the lengthy winter season (O'Donnell 1998). Temperate *Ceratina* small carpenter bees are normally solitary, but a handful of species are known to also produce a particularly small daughter in the first brood cell position: *C. calcarata* (Johnson 1988; Rehan and Richards 2010a), *Ceratina dupla* (Vickruck 2010), *Ceratina flavipes* (Maeta et al. 1992; Sakagami and Maeta 1977), *Ceratina japonica* (Sakagami and Maeta 1984), and *Ceratina okinawa* (Maeta and Sakagami 1995).

Provisioning behavior in many species of *Ceratina* is atypical among the subsocial and solitary bees, as they perform both mass and progressive provisioning (Sakagami and Maeta 1977; Lewis and Richards 2017). During brood establishment, female *Ceratina* undertake mass provisioning, as may be considered typical of mothers of many bee species (Michener 2007). Later in the season, however, *Ceratina* begin foraging again, progressively provisioning their mature offspring by pollen and probably nectar before the end of the blooming season (Sakagami and Maeta 1977; Lewis and Richards 2017). It is unknown whether this two-period provisioning behavior is universal to *Ceratina*, though it has been documented in temperate species around the globe: *C. japonica*, *C. flavipes* (Sakagami and Maeta 1977), *C. calcarata* (Lewis and Richards 2017), and *C. cucurbitina* (Mikát et al. 2016). Progressive provisioning of mature offspring has also been observed in the closely related genus *Xylocopa* (Richards and Course 2015), but is otherwise uncommon in insects (Wilson 1971; Tallamy and Wood 1986). It is currently thought the second round of feeding helps to ensure that offspring survive a protracted overwintering period before establishing new nests the following spring (Lewis and Richards 2017). Though late-season progressive provisioning in *Ceratina* is normally performed by the mother, this task may also be undertaken by the small, eldest daughter (Sakagami and Maeta 1977; Rehan et al. 2014; Lewis and Richards 2017). It is hypothesized that mothers underfeed their eldest daughter to constrain her development and induce a worker-like role (Maeta et al. 1992; Rehan and Richards 2010a; Lawson et al. 2016); as is seen in the brood manipulation of some primitively eusocial Hymenoptera (Alexander 1974; Kapheim et al. 2011).

The aims of this study are threefold. First, we quantify the foraging and nesting behavior of the North American small carpenter bee species, *C. calcarata*. Second, we describe the prolonged maternal care and worker production in this species. Third, we characterize the role dwarf eldest daughters to serve as alloparental workers and an insurance mechanism in the event of maternal mortality to assure the survival of siblings.

Methods

Study species

The small carpenter bee *C. calcarata* (Robertson 1900) belongs to the family Apidae and subfamily Xylocopinae. This species is broadly distributed across the eastern region of the USA and Canada (Rehan and Sheffield 2011; Shell and Rehan 2016). Once a female establishes her nest within the pithy core of a broken twig, she forages on a wide range of flowering plants (Lawson et al. 2016; McFrederick and Rehan 2016). Active brood nests are always solitary, with only one provisioning female (Rehan and Richards 2010b). Females have two phases of foraging (Lewis and Richards 2017), which are separated by period in which mother guard fully provisioned nest with larvae and pupae (Rehan and Richards 2010b). This species is univoltine and females produce only one nest in their lifetime (Rehan and Richards 2010b; Vickruck et al. 2011). Young individuals of both sexes overwinter then mate and establish new nests in spring (Rehan and Richards 2010b).

Nest establishment and relocation

Nest collections and behavioral observations were performed at the University of New Hampshire in Durham, New Hampshire, USA. In April of 2016, habitable stems were created from raspberry (*Rubus idaeus*) by cutting dry stalks, attaching each to a 40-cm-long bamboo rod, and using this rod to stake the structure in the ground at two fields near this location. *Ceratina* nest establishment was regularly monitored at both farms by visually inspecting the stems at 2-day intervals between May 8 and June 27, and then during weekly intervals between June 27 and July 22. Nest founding was determined by the observation of a small (~ 4 mm), round hole and loose pith in the exposed core of the dead broken stems. Each founded nest was marked with flagging tape and assigned a unique ID, and the date of establishment was recorded.

For observing foraging behavior, we relocated and aggregated nests from original sites to plots with 30 nests. It is known that relocation of nests does not distort female behavior (Lewis and Richards 2017). Relocation was performed in early morning (until 7:00) to ensure that all individuals were inside the nest. We performed primary establishment of foraging plots on May 31; however, we added some later-founded nests after this date to our plots. Therefore, we observed in total 129 nests through the season, however, only some of them (31) for whole season (Table S1).

Nest observations

To begin each observation day, we enclosed each observed nest entrance with a small transparent plastic cup, which prevented bees from departing or returning without first being recorded. When a bee left the nest, she entered the cup and the time was recorded, the cup was then opened to allow the individual to continue foraging. The cup was then placed back over the entrance, such that when the bee returned, she was unable to go inside and therefore she flew around the twig containing her nest. The individual's time of return was recorded and the cup was removed, allowing her to re-enter the nest. On some occasions, an individual returned after only a very brief departure (2–10 s). These observations were removed from the dataset as they were considered highly unlikely to be foraging flights.

From late July onwards, the maturing offspring started to emerge and become active foragers, raising the possibility of multiple bees foraging from a single nest. We thus began recording the age and sex of foraging individuals, and giving each a unique paint mark on the thorax and abdomen. Age was assessed according to wing wear and complexion—mothers have darker wings and extensive wing wear by this point in the season, while the wings of young adults are clear and undamaged (Rehan and Richards 2010b).

We collected behavioral data from approximately 60 nests during each observation day with an average of 10 observation days per nest (range 1–20). Two people (MM and CF) observed the nests together; therefore, each observed 30 nests. Foraging observations were performed 3 or 4 days per week pending suitable conditions. A different set of 60 nests was observed each day, and no nest was observed for two consecutive days. Observations were performed only on sunny or partly cloudy days, as bees are largely inactive during overcast or rainy periods. Nest observations began at 8:00 each day, before females started foraging activity. Observations normally ended at 16:00. Not all bees returned by 16:00; however, in late afternoon, foraging activity strongly decreased between 15:00 and 16:00 with very little foraging activity (7.5% of all departures at this period). Observations were terminated in the event of unexpected rain or overcast skies (usually between 14:00 and 15:45). Length of each foraging trip (difference between time of departure and time of arrival), length of handling time (difference between time of arrival and next departure), and number of foraging flights per day for all mothers and any foraging daughters in each nest were recorded.

Nest dissections

We removed a minimum of 10 randomly selected nests for dissection each week from June 16 to September 15. Additional nests were taken directly from the field at the peak of full brood nest activity (July 20–August 2). Nests were collected before 7:30 or after 19:00 and entrances were sealed with masking tape to ensure that all occupants were present during nest assessments. Nests were briefly stored in a cold room to pacify adult bees and prevent destruction of nest structure; nests were then split longitudinally with a pocketknife to record developmental stage according to contents (Rehan and Richards 2010b). Newly founded nests contained only a clean pith tunnel without cells, provisions, or partitions; actively brooding nests contained provisions and an egg in the last closed cell; full brood nests contained larvae and pupae but no newly laid eggs; full-mature brood nests contained newly eclosed adults alongside larvae or pupae; and mature brood nests contained only mature bees. Only full brood nests ($N = 100$) were used for analyses of maternal investment, as these nests represented the entirety of any mother's reproductive efforts.

For each nest, we recorded the number and developmental stage of all offspring. Each mother was then measured for head width using a Nikon SMZ800 dissecting scope with mounted Unitron 15854 LED light. Head width was measured as the maximum transectional length between the outer edges of compound eyes viewed face-on. Head width is a reliable proxy of body mass in this species (Rehan and Richards 2010b). We also determined the sex and measured the head width of each juvenile adult offspring. Any offspring collected in egg, larval, or pupal stages were reared to adulthood in lab and assessed for sex and head width upon eclosion. Though some offspring died before eclosing, sex and head width (size) was determined from pupae. We assumed that pupal head width is the same as the head width of resulting adults.

Data analyses

All statistical analyses were performed using R (R Development Core Team 2011). Differences in the observed sex ratio from the expectation from 1:1 were tested by chi square tests. Sexual dimorphism was tested by Wilcoxon rank sum test, because the size distribution of males and females was significantly different from normal (as determined by Shapiro-Wilk tests). Linear mixed models were employed to test factors influencing the length of foraging trips and handling time, with repeated measures on the same nests. Dependent variables were log transformed before analysis. Nest identity and date of observation were included as random factors.

Results

Sex and size of offspring

Of the 761 offspring collected from full brood nests, 401 were male and 360 were female. Although sex ratio was slightly male-biased (53% male), it was not significantly different from the expectation of an equal 1:1 sex ratio (Chi = 2.2089, df = 1, $p = 0.14$). Sex ratio was highly variable between nests. Individual offspring sex was significantly associated with brood cell position. The sex of offspring in the first brood cell was significantly female biased, with males occupying the first brood cell in only 24% (21/86) of nests (Chi square test, $N = 86$, $X^2 = 22.512$, df = 1, $p = 0.00002$). In other brood cells, the sex ratio was not significantly different from 1:1 except for the fourth brood cell position, in which there was a significant male bias (Table S2).

There was a notable difference in body size between male and female offspring as measured by head width: female body size (mean ± SD, 1.99 ± 0.12 mm, $N = 360$) was significantly larger than male body size (1.79 ± 0.09 mm, $N = 401$; Wilcoxon test, $N = 761$, df = 1, W = 114,830, $p < 0.000001$). The mean head width of female offspring in first brood cell position was 1.88 ± 0.10 mm ($N = 65$) and the mean head width of males in first brood cell was 1.70 ± 0.10 mm ($N = 21$). The mean head width for offspring in other cell position than first was 2.02 ± 0.12 mm for females ($N = 295$) and 1.79 ± 0.09 mm for males ($N = 380$). Female offspring in first brood cells were significantly smaller than the average for females in other brood cells from the same nest (Paired t test, $N = 65$, $t = 7.8961$, $p < 0.00001$). The difference in body size between first brood cell males and their male siblings, by comparison, was not significant (Paired t test, $N = 21$, $t = 0.62083$, $p = 0.5425$).

Phenology of foraging behavior

During the cell-provisioning period (May 8 to June 27), mothers were usually active in a high proportion of nests (average 80%; Fig. 1). The highest proportion of active nests was observed in mid-June (June 20), when 100% of the nests were active. During the summer foraging break period (June 28 to July 26), only a small proportion of the nests demonstrated any foraging activity (average 12% of nests). The proportion of nests with actively foraging mothers increased sharply from the end of July through early August, but steadily decreased from August 3 through the end of the season (Fig. 1). In an average day of the mature offspring feeding period, 47% of nests had mother foraging activity. In comparison with mothers, daughters foraged in only 11% of the nests on average in same period. Peak daughter activity was observed on September 1, when offspring were observed foraging in 29% of nests. Young adult bees began leaving their natal nests

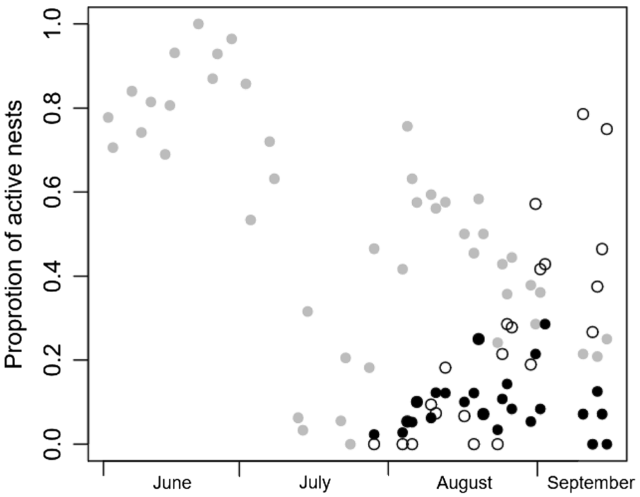

Fig. 1 Season changes in proportion of active nests. Each point represents the daily proportion of nests with foraging activity. Gray symbol–mother, black closed symbols–daughter, black open symbols–leaving young females

without returning at the start of the mature offspring feeding period (July 27), and the proportion of nests abandoned by offspring strongly increased after August 30. Observed offspring nest abandonment reached a peak on September 9, when at least one offspring left 79% of the nests.

During the mature offspring feeding period (July 27–September 1), there was extensive variability in pattern of foraging activity between individual nests. From nests observed for this entire period ($N = 52$), the mother was active at least once in 81% (42/52) of nests, daughters were active in 29% (15/52), and two nests (4%) exhibited foraging behavior by daughters only. In 15% of the nests (8/52), instead of foraging activity, only nest abandonment events were observed during the mature brood feeding period.

Foraging activity of mothers

The highest average maternal foraging activity was observed during the cell-provisioning period (6.12 trips per day; Fig. 2). At this stage, the most active nests had more than 20 foraging trips per day, with the highest recorded number of 35 trips in 1 day. During the summer break period, by contrast, most nests were inactive and those which foraged made few trips per day (0.23 on average, Table 1). Frequency of foraging trips increased again during the mature offspring feeding period, with an average of 1.73 maternal foraging trips per day. Excluding nests without any foraging behavior, the average number of daily foraging trips was 3.54 for active nests. The highest recorded frequency of foraging trips was 15 during this second provisioning period. During the nest abandonment period, the foraging frequency decreased again, sinking to an average of 0.44 foraging trips per day.

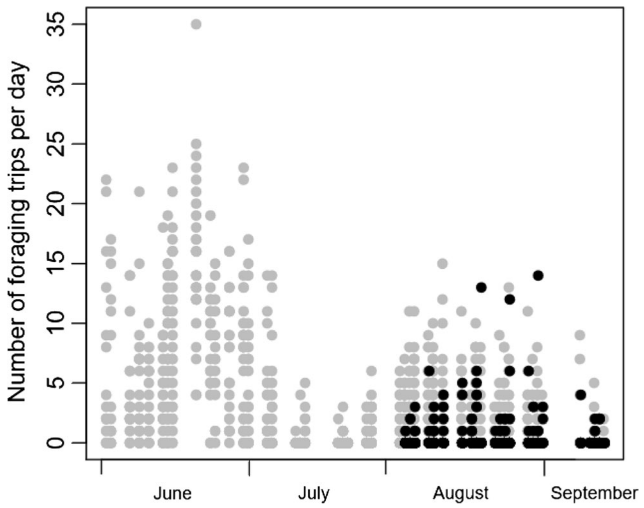

Fig. 2 Number of foraging trips per day for observed mothers (gray) and daughters (black)

The duration of foraging trips was also highly variable, and fluctuated over the course of the season (median 16.88 min, range 0.18–306.8 min). Though most trips were only a few minutes long, there was a highly significant difference between trip duration during the cell-provisioning and mature-offspring feeding periods (mixed linear model, chi = 108.42, df = 1, $p < 0.000001$), with a difference of 23.17 min between periods (95% CI: 16.91–30.62 min). Though fewer in number, foraging trips made during the mature-offspring feeding period generally lasted longer than in the cell-provisioning period (Fig. 3, Table 2). Length of handling time was highly variable (median 11.47 min, range 0.4–279.88 min), but usually lasted only a few minutes. The length of handling time was significantly shorter in the cell-provisioning period than in the mature offspring feeding period (mixed linear model, chi = 11.883, df = 1, $p = 0.00057$), with a difference of 6.11 min (95% CI: 2.45–10.70 min).

Taken together, the number of foraging trips is higher in the cell-provisioning period; however, the length of foraging trips is longer in the mature offspring feeding period. Therefore, this puts into question: in which period do mothers spend more time outside of the nest? Active mothers spent on average 159.0 min per day outside of their nests across the entire active season (range 1.83–597.25 min). In the cell-provisioning period, mothers spent 149.1 min outside the nest on average (median 145.10 min, range 2.61–429.93 min). During the mature-offspring feeding period, however, mothers spent significantly more time outside the nest than during the cell-provisioning period (mean 179.1 min, median 174.96 min, range 5.30–597.25 min; mixed linear model, chi = 4.65, df = 1, $p = 0.0309$), with a difference of 36.55 min (95% CI: 2.81–80.78 min).

Maternal nest orphanage rates also increased throughout the course of the season. Incidence of orphaned nests strongly increased in the first half of August, and more than half of the

Table 1 Number of foraging trips per day of mother and daughter

Observed female	Period	All observational days included			Only days with activity included		
		N	Mean	SD	*N*	Mean	SD
Mother	Cell provisioning	405	6.09	6.12	325	7.59	5.94
	Summer break	185	0.23	0.72	23	1.83	1.15
	Offspring feeding	615	1.73	2.50	300	3.54	2.53
	Leaving	89	0.44	1.44	12	3.25	2.56
	Total	1294	2.79	4.49	660	5.47	4.99
Daughter	Offspring feeding	615	0.26	1.20	56	2.89	2.87
	Leaving	89	0.13	0.57	6	2.00	1.10
	Total	704	0.13	0.85	62	2.81	2.76

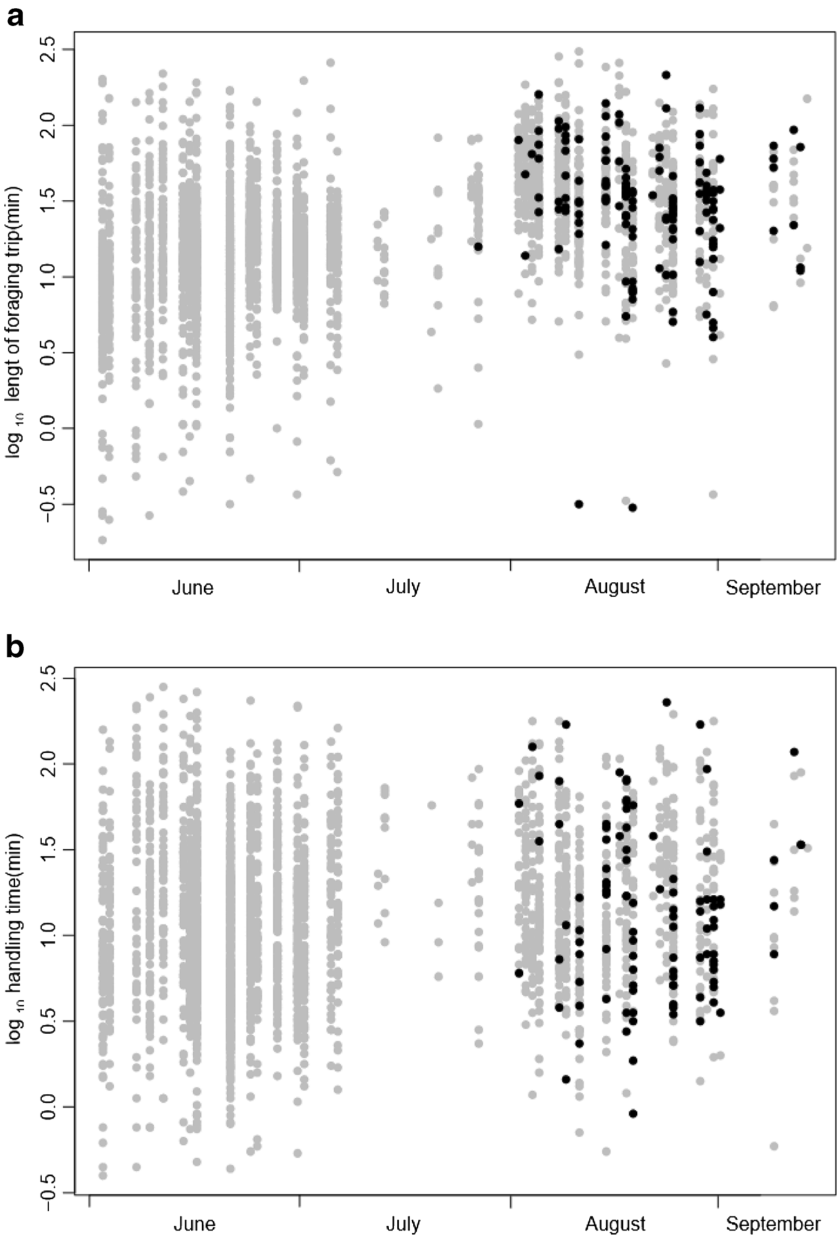

Fig. 3 Length of foraging trips (**a**) and length of handling time (**b**) throughout the season. Both length of foraging trips and handling time are in logarithmic scale; gray points–mother, black points–daughter

Table 2 Quantitative parameters of foraging flight duration and handling times between flights for *Ceratina calcarata*

Focal female	Period	Length of foraging trip (min)				Length of handling time between foraging trips (min)			
		N	Mean	SD	Median	*N*	Mean	SD	Median
Mother	Cell provisioning	2216	18.88	21.08	13.84	1962	19.83	28.31	10.28
	Summer break	37	24.31	20.52	17.27	20	35.78	24.28	28.46
	Mature feeding	885	45.74	35.76	37.42	687	25.34	27.63	15.32
	Leaving	22	40.45	30.82	38.83	16	25.62	26.44	17.15
	All periods	3160	26.61	28.75	16.88	2685	21.39	28.22	11.47
Daughter	Mature feeding	131	38.54	29.71	31.50	94	25.28	36.25	11.33
	Leaving	9	46.24	30.76	52.75	6	39.17	39.75	30.48
	All periods	140	39.03	29.72	31.53	100	26.12	36.41	12.57

remaining nests were orphaned by late August. By the end of the foraging season, in mid-September, nearly all (93%) nests were orphaned.

Foraging activity of dwarf daughters

A daughter was active in 29% of the nests (15/52) that we observed during the whole mature-offspring feeding period. In six of these nests, a dwarf daughter joined her active mother in foraging. In seven nests, the daughter's foraging began following the last day of her mother's foraging. Dwarf daughters were significantly more active, with more foraging trips per day, when operating alone than in those nests in which they were actively foraging with their mother (Poisson generalized linear mixed model, Chi = 5.2129, df = 1, $p = 0.02$). Two nests featured late-season foraging activity only by the daughter, with no contributions from the mother. In two other nests, we observed two different daughters foraging on separate days. In almost all cases, foraging daughters were the smallest female offspring in their nest.

Foraging daughters made an average of 0.26 trips per day during the entire mature-offspring feeding period. However, considering only those nests for which at least one foraging flight was made per day, this average increased to 2.89 trips per day (Table 2). The highest number of daughter foraging trips made on a single day was 14. During the nest abandonment period, there was a decrease of daughter foraging activity to just 0.11 trips per day (Table 1).

Notably, the foraging behavior of active daughters closely mirrored the foraging behavior of maternal foragers in the mature-offspring feeding period (Fig. 3). There was neither difference in length of foraging trips between mothers and daughters (mixed linear model, chi = 0.6309, df = 1, $p = 0.43$), nor was there any difference in the length of handling time between foraging mothers and daughters (mixed linear model, chi = 1.5856, df = 1, $p = 0.21$).

Discussion

Parental investment in the size and sex of offspring is under strong selection for assured fitness returns (Smith and Fretwell 1974). For example, many social insect mothers make an initial investment in small offspring to take on risky foraging behavior while they specialize on future reproduction (Trivers and Hare 1976). Solitary and facultatively social species provide an important baseline to understand the evolution of social complexity from natural variation in maternal care and foraging behavior (Sakagami and Maeta 1977; Schwarz et al. 2007). Here, we characterize the parental investment strategies of a subsocial small carpenter bee and reveal the potential adaptive significance of prolonged maternal care and worker production in this species. Mothers provide an initial investment that is extended by workers providing alloparental care to siblings. Maternal manipulation of dwarf eldest daughters serves as an insurance mechanism in the event of maternal mortality to assure the survival of siblings. Insurance-based mechanisms are key factors that can explain the origin and maintenance of sociality in small insect societies (Field et al. 2000; Shreeves et al. 2003).

Foraging behavior of dwarf daughters

Across all nests, the first brood cell was strongly female biased, and females in this position were generally smaller than other females. The existence of a dwarf eldest daughter has been repeatedly reported for *C. calcarata* across North America (Johnson 1988; Rehan and Richards 2010a; Rehan et al. 2014; Lawson et al. 2016; Lewis and Richards 2017) and in Japanese *Ceratina* species (Sakagami and Maeta 1977, 1984).

We observed a daughter foraging actively in about one quarter of the nests during the mature-offspring feeding period. In general, daughters foraged less frequently than mothers. However, unlike Lewis and Richards (2017), we occasionally observed daughters foraging at the same time as their mothers. As daughter foraging was more common when a mother was absent, we suppose that this behavior may represent a form of insurance in those cases where a mother dies before she is able to feed her mature offspring. The proportion of orphaned nests increased through the mature-offspring feeding period, with dissections indicating extremely high proportions of motherless nests (93%). As such, most mothers probably do not survive until the end of the foraging season in mid-September. The foraging behaviors of active daughters do not appear different from those of foraging mothers, with no significant difference in the duration of foraging trips or handling time between trips. Therefore, it seems foraging daughters may adopt an effective alloparental role, despite clear morphological differences between themselves and their mother, with the head width of mothers 13% larger than their dwarf daughters on average. Daughter foraging may thus be an adaptive solution to situations wherein the death of a mother, which may not be uncommon during the late-season feeding period, would otherwise lead to mature offspring having to undertake risky foraging in order to avoid starvation. When we dissected nests with foraging daughters (n = 8), the forager was the smallest daughter in all instances. Two nests featured two foraging daughters and these individuals were the first and second smallest of the brood. Lewis and Richards (2017) similarly found that foraging was performed by females which were smaller than most other females in nest. Female body size relative to her siblings can strongly influence her probability of assuming a forager role.

Adaptive significance of dwarf daughters

The existence of a dwarf eldest daughter may at first seem paradoxical: during her initial brood provisioning, a mother is presumably in her best physical condition and should therefore be expected to invest in larger offspring (Seidelmann 2006). Her decision to produce significantly smaller offspring instead of normal size offspring may have several explanations, such as foraging more in order to produce larger offspring could lead to higher mortality, or a limitation on the amount of carried food rather than mature oocytes in the early nesting stage (Maeta et al. 1992). However, lower nutritional quality of available pollen is not likely for this polylectic species (Lawson et al. 2016). Under such scenarios, the more beneficial decision might be to invest in the cheaper sex (i.e., male) rather than produce malnourished females (Trivers and Willard 1973; Frank 1987). The persistent production of small females thus suggests the existence of an adaptive social function.

The proximate mechanism for producing a small first daughter is thought to be maternal manipulation of brood provisions (Lawson et al. 2016), as parental manipulation of offspring size is a well-known mechanism for hierarchical stratification of insect societies (Alexander 1974). Further, it may be an optimal investment strategy to produce a dedicated, small, forager-destined female, which costs less than her larger siblings. However, it remains to be determined what ultimate mechanism and possible fitness advantage induces the adoption of foraging and feeding behavior in these small daughters.

One possible explanation for foraging by the smallest daughters is their lower probability of winter survival. Population wide, average female body size is smaller before winter, which suggests a lower survivorship for smaller females in this species (Rehan and Richards 2010b). Foraging by small females also puts them at risk of dying from exhaustion or predation; and it is thus possible that a difference in average female body size before and after winter may be a consequence rather than cause of sibling feeding. If dwarf eldest daughters have low probability to surviving to become future reproductives, then it may be advantageous to help ensure their siblings' overwintering survival and fitness by assisting in feeding. Maeta et al. (1992) experimentally tested cold tolerance in *C. flavipes* and determined a relatively weak influence of body size on offspring survival in cold exposure for both males and females. However, reduced fat stores have been linked to reduced overwinter survivorship in bees and wasps (Strassmann et al. 1984; Toth et al. 2009; Durant et al. 2016, but see Richards and Packer 1996; Weissel et al. 2012). Therefore, it seems that the reduced body size of foraging daughters may already have a negative influence on winter survivorship, which is likely only exacerbated by her increased foraging activity and reduced fat stores.

Size-influenced dominance hierarchies are well documented in several primitive eusocial Hymenoptera (Hogendoorn and Velthuis 1999; Smith et al. 2009). Size-based hierarchies are not always present in *Ceratina* (Rehan et al. 2010), however, with some species demonstrating an atypical division of foraging behavior between a reproductively dominant female and a non-foraging, subordinate female (Rehan et al. 2010); though more common divisions of worker roles are observed as well (Sakagami and Maeta 1984; Maeta and Sakagami 1995). *C. calcarata* is a solitary nesting species in the brood cell provisioning phase (Rehan and Richards 2010b) with social ancestors (Rehan et al. 2012, 2013). As size-dependent aggression is known in *C. calcarata* (Rehan and Richards 2013; Withee and Rehan 2016), it is possible that foraging by small daughters in social nests may be derived from a more typical division of labor.

Daughter foraging occurs in only some nests (29%), and is thus apparently a facultative strategy. As we observed in two nests, foraging behavior may be adopted by at least two different daughters, and is thus not limited to only one female offspring. Also, as females from the first brood cell position were usually, but not always, the smallest female in the nest, eldest female offspring are probably not obligately required to feed their siblings. Production of a small female in the first brood cell may operate as insurance against brood loss in the not uncommon event that a mother dies before the end of the second feeding period.

Conclusion

Foraging behavior in *C. calcarata* is highly flexible and appears dependent on the needs of offspring in the nest. This behavioral plasticity thus appears advantageous to the mother, particularly when considering the small number of brood cells provisioned per day, and increasing likelihood of nest orphanage with seasonal progression. Mother and dwarf daughter foraging behavior during the mature-offspring feeding period is very similar, meaning daughters likely make highly effective alloparents in situations where their services are useful (usually in orphaned nests, but sometimes also in nests where mothers remain present). We propose that foraging by the dwarf daughter is primarily a form of insurance against late-season starvation in the case of maternal mortality. If produced, a dwarf female is usually present in the first brood cell of her nest, but the forager role is not limited to this female, and may be adopted by at least one other small female. It is possible that flexible foraging behavior in an ancestral species allowed for the formation of this unique type of parental care, which may adaptively combine maternal and sibling care to ensure the survival of young adults.

Acknowledgements We thank Wyatt Shell and member of the Rehan lab for comments and suggestions on this manuscript.

Compliance with ethical standards

Funding This work was supported by a mobility fund of Charles University of Prague and Integrative Animal Biology award no. SVV 260 434/2017 to MM. Additionally, this research was supported by NSF award no. 1456296 to SMR.

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