Impact of resource allocation on offspring production in six species of leaf cutter bees (Megachilidae: Hymenoptera)

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Abstract

The present study was undertaken to assess the amount of food provisioned by the mother to produce viable male and female offspring in six species of leaf-cutter bees, namely *Megachile Lerma, Megachile cephalotes, Megachile stirostoma, Megachile lanata, Megachile disjunct* and *Megachile carbonara*. Our findings suggest that the quantity of pollen mass deposited in the brood cell was related to the sex of the bee, with male cells receiving significantly lower pollen mass compared to females in all six species studied. There was a positive correlation (r = 0.70) between the quantity of pollen provisioned per cell with the body mass of the male and female adult bees in all six species.

Keywords: resource allocation, maternal investment, leaf cutter bees

Introduction

Members of the Megachilidae are much diverse, living in solitary and made nests in pre-existing cavities in the ground, wood, stems, or even arboreal termite nests. They typically use nest material like cut leaves, petals, resin and mud to line their cells and partitioning (Krombein, 1967) [5] and nest material preferences will vary from species to species.

The megachilids are commonly called Leaf cutter bees (LCB) are an excellent subject to address questions of sex allocation. Maternal investment in solitary bees is strongly influenced by the availability of resources and the condition of parent also can influence decision on sex investment (Trivers and Willard, 1973 [13]; Torchio and Tepedino, 1980 [12]). Most of the LCB, have female biased sex ratio (1:1.4) and produce female offspring in the interior cells and males in the exterior cells (Krombein, 1967 [5]; Hegde, 2016 [3]). The resources in space and time are critical for reproduction and influence parental decision on allocation of resources to sons and daughters (Sedinger and Raveling, 1986) [11]. Theoretically, a mother is expected to trade-off allocation to number and sex of offspring to maximize her lifetime reproductive success (Peterson and Roitberg, 2006a) [8]. However, information about the quantity of pollen required for a single brood cell to rear an offspring by leaf cutter bees is sparse (Peterson and Roitberg, 2006b) [9]. Generally, females were investing more resource to produce a daughter than the sons. Therefore, present study to know the quantity of resources provisioned in the cell to indicate the sex of the offspring.

Material and Methods

Experiments were carried out in Gandhi Krishi Vignana Kendra (GKVK) of University of Agricultural Sciences, Bangalore, Karnataka, India. The study area comes under the eastern dry Agro-climatic zone of Karnataka state and has diverse vegetation including field crops, horticultural crops, medicinal plants, and several species of garden plants, wild trees, shrubs and weeds that would be sources of nectar and pollen for bees.

Based on the LCB activity ten nesting sites were selected. Each site was provided with artificial nests made from *Ipomoea* reeds. These reeds were harvested from the nearby lake cut into 15 cm long pieces and then sun dried for a week, which helps in hardening and preventing nests from fungal development. After that pith was removed carefully and the reeds were made hollow, such reeds were placed in a plastic pipe to and hung in a roof at an angle to prevent rain from entering the nests. Immediately after bees occupying the nest's, freshly closed nests were brought to the laboratory and the nests were categorized based on the size and nesting material (leaf or resin or mud), kept separately in rearing cages to identify the species. Further, ten nests of each species were kept separately to determine adult emergence pattern and recorded the dry body mass of male and female adults of all the bee species.

After defining the species and their emergence pattern, a total of 31 newly constructed nests across the species were brought to the lab and cut open the all the cells to understand whether the quantity of pollen provisioned varied between species and the sex of the offspring. In all those cells in which the eggs had not hatched, the provisioned pollen mass was weighed, which contains a total of 102 cells.

Results

The female LCB constructed a linear nest with number of brood cells, where each cell is made by lining the cell walls of the nest cavity with leaf pieces or soil or resin and then provisioned this "cell" with a mixture of pollen and nectar (referred to below collectively as pollen), above which an egg was laid before sealing the cell. New cells are added in front of completed cell in succession. After completion of the nest, the mother closes the nest entrance by making a thick wall. All food is consumed by brood before going to emerging as an adult.

We observed the nesting activity of six species of leaf cutter bees of the genus *Megachile viz*., *M. lerma* (Cameron, 1908), *M. lanata* (Fabricius, 1775), *M. disjuncta* (Fabricius, 1781), *M. cephalotes* (Smith, 1853), *M. stirostoma* (Cameron, 1913), and *M. carbonaria* (Smith, 1853) were encountered. They constructed nests in preformed cavities using various materials like leaves, mud, resin *etc* (Fig 1 and Table 1). The material used for cell construction was found to be species specific. *M. lerma* and *M. carbonaria* used leaves, *M. lanata* used soil, *M. disjuncta* used both soil and resin, while *M. cephalotes* and *M. stirostoma* used resins.

Fig 1: Leaf cutter bee species and their nesting structures

Table 1: Body length, nesting sites and nesting materials of the selected bee species

Bee species	Body length (mm)	Natural Nesting Sites	Nesting material	Nest width (mm)
Megachile lerma	7-10	Hollow stems, cracks and holes in building	Leaf	<0.8
Megachile lanata	11-15	Hollow stems, dead bored wood, cracks and holes in building	Soil	0.8-10
Maegachile disjuncta	8-15	Hollow stems, dead bored wood, cracks and holes in building	Resin, soil	0.8-10
Megachile cephalotes	8-12	Hollow stems, dead bored wood, cracks and holes in building	Resin, soil	0.8-10
Megachile stirostoma	10-15	Hollow stems, dead bored wood, cracks and holes in building	Resin, soil	0.8-10
Megachile carbonaria	12-14	Cracks and holes in building	Leaf	>13

The quantity of pollen required to rear a single larva varied with body size of the bee species. Out of six species *M. lerma* needed least quantity of food (131 ♂ and 174 ♀ mg) followed by *M. cephalotes* (129♂ and 187♀ mg), *M. stirostoma* (142♂ and 243♀ mg), *M. lanata* (190♂ and 252♀ mg), *M. disjuncta* (170♂ and 322♀ mg) and *M. carbonaria* (512♂ and 846♀ mg) (Fig. 2). There was a positive correlation ($r = 0.70$) between the quantity of pollen provisioned per cell with the dry weight of the bee emerged from it. The linear regression indicated ($Y = 9.90X - 92.80$; $P<0.01$; $F = 101.20$, $t = 10.06$; $R^2 = 0.49$) that 49 percent variation in the pollen weight is explained by dry body mass of bee, hence it is a major ecological factor driving in sex allocation (Table 2; Fig. 3) and significantly contributing for the changes in the dependent variable.

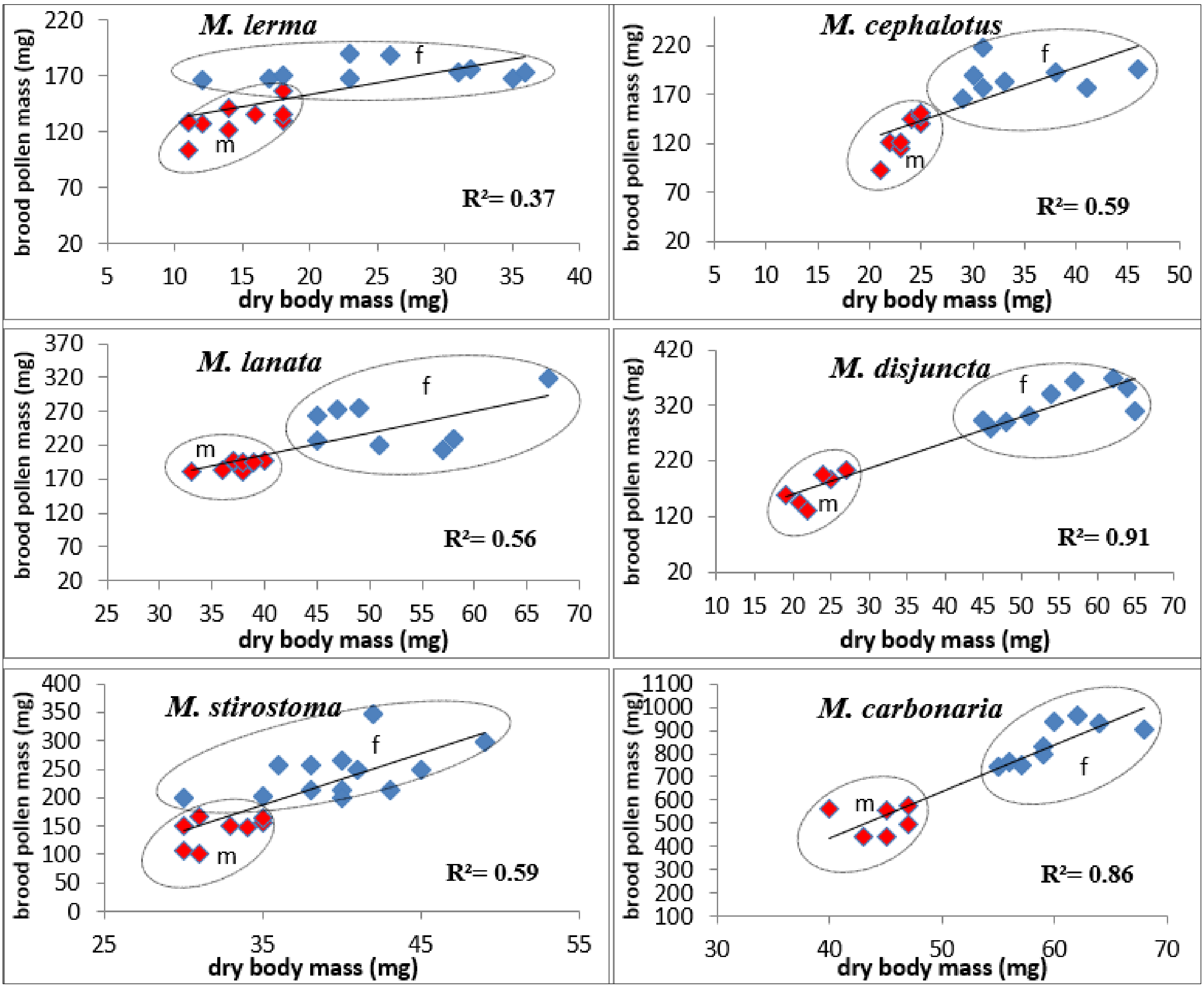

Fig 2: Relationship between the average brood cell pollen mass and the average dry body mass of the six *Megachile* species (m-male, f-female)

Table 2: Average food provision per brood and dry body mass of the six *Megachile* species

Bee species	Average food provision per brood cell				Average dry body mass					
					Males			Females		
	[mg]	sd	N	n	[mg]	sd	n	[mg]	Sd	n
Megachile lerma	152.40	22.19		20						
Male	131.78	13.72	5	10	14.3	3.0	10	25.3	8.1	10
Female	174.00	08.74		10						
Megachile cephalotes	158.37	35.41		16						
Male	129.50	20.25	5	8	23.3	1.6	6	36.5	9.5	10
Female	187.25	15.65		8						
Megachile stirostoma	205.09	72.14		21						
Male	142.88	25.63	6	08	34.0	3.0	3	40.3	5.4	9
Female	243.38	43.49		13						
Megachile lanata	223.40	41.57		15						
Male	190.14	7.80	5	7	37.0	6.2	10	48.	10.0	10
Female	252.50	36.48		8						
Maegachile disjuncta	261.46	83.05		15						
Male	170.33	29.23	4	6	22.0	3.8	10	53.6	8.0	10
Female	322.22	33.98		9						
Megachile carbonaria	712.93	185.86		15						
Male	512.33	61.96	6	6	42.1	6.3	7	61.2	8.7	7
Female	846.67	88.03		9						

In six species characterized by a distinct sex dimorphism in size, the average food provision per brood cell is given separately for males and females. sd= standard deviation; N= number of nets; n=number of brood cells and number of specimens weighed, respectively.

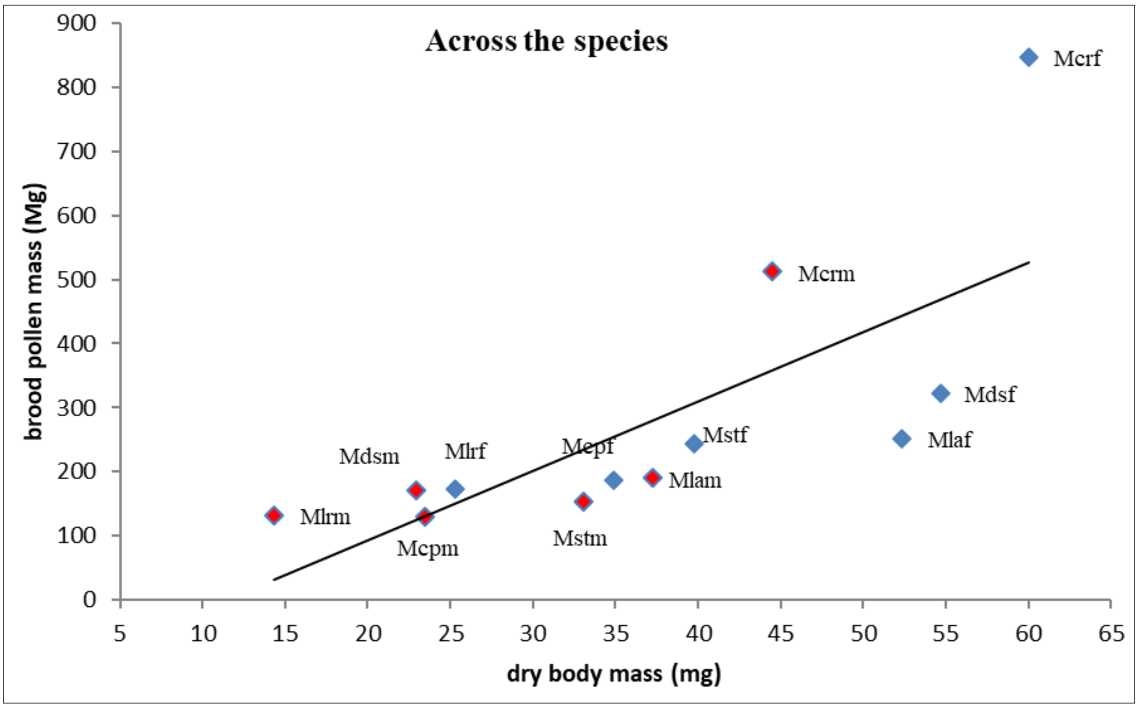

Fig 3: Relationship between the average brood cell pollen mass and the average dry body mass of the six *Megachile* species examined. Linear regression y= 9.90 x – 92. 80 (F= 101.20, t= 10.06, P= <0.01, R^2= 0.49). Mlrm, *M. lerma* (male); Mlrf, *M. lerma* (female); Mcpm, *M. cephalotus* (male); Mcpf, *M. cephalotus* (female); Mstm, *M. stirostoma* (male); Mstf, *M. stirostoma* (female); Mdsm, *M. disjuncta* (male); Mdsf, *M. disjuncta* (female); Mlam, *M. lanata* (male); Mlaf, *M. lanata* (female); Mcrm, *M. carbonaria* (male); Mcrf, *M. carbonaria* (female)

Discussion

Megachile provide an excellent opportunity to study resource allocation, since quantity of food provided to the brood cell is likely to be strongly correlated with resulting offspring of either sex (Peterson and Roitberg, 2006b) [9]. Ecological conditions including availability of resource may also strongly influence sex allocation decisions (Koskela *et al.*, 2004) [4]. In LCBs, males are generally smaller than females; thus, we expect a smaller number of resources are used to produce a viable son than that needed to produce a daughter (Torchio and Tepedino 1980) [12]. However, females gain more benefits from being large because larger females produce more viable eggs and forage at a faster rate (Alcock 1979 [1], Cowan 1981 [2], Mangel *et al*., 1994 [6]). In this study we found that the larvae that are likely to develop into males were provided lower quantity of food compared to those larvae that developed into females. There was a strong correlation between dry body mass of bee and quantity of food provided to the brood. Overall, it is possible that the resource levels were different enough to result in changes to the number of resources allocated to each offspring. A look at the emergence pattern of bees shows that the cells that were constructed first, almost always produced females and cells that were constructed last, yielded males (Hegde, 2016) [3]. Probably it is the cell size that influences the queen to fertilize or not to fertilize each egg. Besides, bees that construct cells in series in reeds, the female can place male-producing eggs in cells near the entrance, from which the resultant adults could escape without disturbing the slower developing females. Since, males were smaller in size, its larvae required lesser provision and took shorter time to complete development thus leading to protandry.

Michener (2007) [7] Supported this study by showing female store sperm cells in the spermatheca, during the oviposition she can control the sex of each egg by delivering or not delivering sperm cells as the egg passes through the oviduct. Because of this arrangement, the female could able to regulate the sex of the offspring by placing female-producing eggs with more provisions compare to males' eggs provision. Also factors like parasitism, predation and abiotic factor could be a possible reason for producing or constructing female offspring cells in anterior position followed by male offspring cells in the posterior end or towards nest entrance. Because during my study I was observed that nest was frequently attacked by parasite (*Melittobia* sp., Cuckoo wasp, Chalcids and Bee fly or Bombyliidae) and predator (Some beetle sp.). Further work is needed to understand the fitness of the sons or daughters by altering the quantity of provision artificially and also learn how it is altered with changing ecological conditions like resource availability, predation pressure and nesting sites, needs to be looked into.

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References

1. Alcock J. The relation between female body size and provisioning behavior in the bee *Centris pallida* Fox (Hymenoptera: Anthophoridae). Journal of the Kansas Entomological Society, 1979; 52:623-632.
2. Cowan DP. Parental investment in two solitary wasps *Ancistrocerus adiabatus* and *Euodynerus foraminatus* (Eumenidae: Hymenoptera). Behavioral Ecology and Sociobiology, 1981; 9:95-102.

3. Hegde S. Nesting sites, nesting biology and trap nesting of leaf cutter bees (Hymenoptera:megachilidae). M.Sc. Thesis UAS GKVK Bengaluru, 2016, p52.
4. Koskela E, Huitu O, Koivula M, Korpimaki E, Mappes T. Sex-biased maternal investment in voles: importance of environmental conditions. Proceedings of the Royal Society of London, 2004; 271:1385-1391.
5. Krombein KV. Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Institution Press, Washington, DC, 1967, p576.
6. Mangel M, Rosenheim JA, Adler FR. Clutch size, offspring performance and intergenerational fitness. Behavioral Ecology, 1994; 5:412-417.
7. Michener CD. The bees of the world second edition, chapter 4. Development and Reproduction. The Johns Hopkins University Press Baltimore, 2007; 6:11.
8. Peterson JH, Roitberg BD. Impact of resource levels on sex ratio and resource allocation in the solitary bee, *Megachile rotundata.* Environment Entomology, 2006a; 35(5):1404-1410.
9. Peterson JH, Roitberg BD. Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee, *Megachile rotundata*. Behaviour Ecology Sociobiology, 2006b; 59:589–596. doi 10.1007/s00265-005-0085-9.
10. Richards KW. Ovarian development in the alfalfa leafcutter bee, *Megachile rotundata.* J. Apic. Res. 1994; 33:199-203.
11. Sedinger JS, Raveling DG. The timing of nesting of Canada Geese in relation to the quality and availability of their food plants. Journal of Animal Ecology, 1986; 55:1083-1102.
12. Torchio PF, Tepedino VJ. Sex ratio, body size and seasonality on a solitary bee, *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). Evolution, 1980; 34:993-1003.
13. Trivers RL, Willard DE. Natural selection of parental ability to vary the sex ratio of offspring. Science, 1973; 179:90-91.