Insect. Soc. (2013) 60:389–392
DOI 10.1007/s00040-013-0304-8

Insectes Sociaux

RESEARCH ARTICLE

Colony disturbance and solitary nest initiation by workers in the obligately eusocial sweat bee, *Halictus ligatus*

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Received: 11 April 2013 / Revised: 3 June 2013 / Accepted: 4 June 2013 / Published online: 20 June 2013

Abstract Sweat bees are one of the most socially polymorphic lineages on the planet. In obligately eusocial species, newly enclosed females may become either queens or workers, depending on the environmental and social circumstances of the nest into which they emerge. In socially polymorphic species, females also have the option of nesting solitarily, founding a nest and raising future reproductives alone, without the help of other adult females. *Halictus ligatus* is a widespread Nearctic, ground-nesting sweat bee. It has been particularly well studied in Ontario, where detailed studies have described it as obligately eusocial. Here we report evidence that the flexibility of female *H. ligatus* actually extends to expressing behaviour more typical of socially polymorphic species, those in which some individuals reproduce solitarily. In a population in southern Ontario, black wasps (*Astata* sp.) emerged from the soil beneath the nesting aggregation and proceeded to excavate their own nesting tunnels, dislocating many *H. ligatus* nest entrances. Young workers whose natal nests were destroyed by the wasp activity constructed new nests, so under very specific circumstances, it is possible for potential altruists to nest solitarily.

Keywords Aberrant behaviour · Social polymorphism · Facultatively social · Worker polyphenism · Queen mortality · Worker reproduction

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Introduction

Sweat bees (Hymenoptera: Halictidae) are arguably the most socially polymorphic lineage on the planet (Michener, 1974). The social variability evident at the colony level reflects the behavioural flexibility of individual females. In obligately eusocial sweat bee species, newly enclosed females may become either queens or workers, depending on the environmental and social circumstances of the nest into which they emerge (Michener, 1974). In socially polymorphic species, females also have the option of nesting solitarily, founding a nest and raising future reproductives alone, without the help of other adult females (Schwarz et al., 2007).

Halictus ligatus is a widespread Nearctic, ground-nesting sweat bee. It has been particularly well studied in Ontario, where detailed studies have described it as obligately eusocial (Packer, 1986; Richards and Packer, 1995). This is because colonies are founded by overwintered gynes that typically produce a brood of workers, which in turn help their mother raise the reproductive brood. Solitary nesting has never been observed, although a queen that loses all her worker brood may eventually resume foraging to provision the reproductive brood herself (Richards and Packer, 1995). Many workers mate and have developed ovaries, laying eggs even in queen-right nests (Richards et al., 1995), and when a queen dies, a recently enclosed worker may become a replacement queen whose behaviour thereafter is indistinguishable from that of the foundress queen. Workers that emerge into empty nests can overwinter and become nest foundresses the following spring (Richards and Packer, 1994). Gynes also may be able to switch castes. When overwintered gynes encounter each other in spring, they may remain together as nest co-foundresses, with one becoming the dominant foundress, while others become

subordinates (Richards and Packer, 1998). This distinction in the behaviour of spring foundresses is analogous to that of summer queens and workers. Thus, there is considerable evidence that adult females can switch between the queen and worker caste roles that define obligate eusociality (Schwarz et al., 2007). Here, we report that the flexibility of female *H. ligatus* actually extends to expressing behaviour more typical of socially polymorphic species, those in which some individuals reproduce solitarily. When workers were orphaned by the soil-excavating activities of *Astata* wasps, they excavated new nests, effectively becoming mid-summer foundresses.

Methods

In late May 2006, we surveyed a sweat bee nesting aggregation on the campus of Brock University in St. Catharines, Ontario, Canada (W 79 14′ 57″ N 43 07′ 11″), marking all visible nest entrances with roofing nails. Nest excavation and bee dissection methods are detailed in Richards et al. (2010). Head width (HW) is a strong predictor of body size in sweat bees and was measured from the dorsal view as the greatest distance across the compound eyes. Wing wear (WW) is a useful proxy for age and foraging activity in bees and was ranked by the number of nicks and tears in the apical margin of the forewing; pristine wing margins, with no nicks and tears received a score of zero, and wings with the apical margin completely obliterated received a score of five. Reproductive status was estimated based on dissection of the metasoma. Ovarian development was assigned by scoring the four largest oocytes with fractional scores of ¼, ½, ¾, or 1, indicating their size relative to a fully developed oocyte. These scores were then summed to make a total ovarian development score (TOD). Females with undeveloped or only thickened ovaries, but no visible oocytes were assigned ovarian development scores of 0 or 0.1, respectively.

Results

On 5 July at around 10.00 h, black wasps (*Astata* sp.) began to emerge from the soil beneath the nesting aggregation and proceeded to excavate their own nesting tunnels, dislocating many *H. ligatus* nest entrances. On 6 July, the wasps were again active by 10.00 h and were observed excavating nest openings approximately 2 cm in diameter, resulting in further disruption and destruction of *H. ligatus* nests. Throughout the day, wasps were observed returning to their nests with large prey (green stink bugs, *Chinavia halaris*). Wasp nest construction and foraging activity continued until late August, with 2–20 wasps being observed whenever we were excavating bee nests. By mid-July, dozens of *H. ligatus* nests (or at least the sections visible to us) had been destroyed by the wasps, and on 14 July, many *H. ligatus* females were observed hovering over the soil searching for nest entrances.

Between 7 July and 8 August 2006, we excavated 23 *H. ligatus* nests (Table 1). Four of these were distinctive because the burrows were very shallow (Fig. 1B), the only adult present was a worker, and there were no or very few brood that were very young. Nest 245 (excavated 19 July) was 13 cm deep and contained no brood cells. The adult bee was medium-sized (head width (HW) 2.85 mm) with no

Table 1 Nesting biology of *Halictus ligatus* nests excavated in July, 2006

Variable	Type of nest			Comparison of nest types ($df = 2$)
	Queen present ($n = 10$)	Orphaned ($n = 7$)	New ($n = 4$)	
Nest depth	30.7 cm	30.6 cm	19.2 cm	$H = 8.31$, $p = 0.02$
No. workers	3.1 (range 0–7)	2.9 (0–5)	1	$H = 6.33$, $p = 0.04$
No. brood	12.9 (range 0–30)	12.2 (1–20)	0.8 (0–2)	$H = 7.39$, $p = 0.02$
Queen traits				
HW	3.2 mm (SD 0.3)	3.0 (dead queen)	–	–
WW	2.0 (range 1–5)	–	–	–
MW	4.6 (range 4–5)	–	–	–
TOD	1.5 (SD 0.7)	–	–	–
Worker traits				
HW	2.8 mm (SD 0.2)	2.71 (0.1)	2.8 (0.1)	$H = 3.19$, $p = 0.20$
WW	0.7 (range 0–5)	0.2 (0–1)	0.2 (0–1)	$H = 3.49$, $p = 0.17$
MW	2.2 (range 0–5)	2.2 (0–5)	3.2 (2–5)	$H = 2.01$, $p = 0.37$
TOD	0.6 (SD 0.3)	0.8 (0.5)	1.2 (0.7)	$H = 2.73$, $p = 0.26$

HW head width, *WW* wing wear, *MW* mandibular wear, *TOD* total ovarian development

Kruskal–Wallis one-way analysis of variance tests performed in RStudio (v.0.97.248)

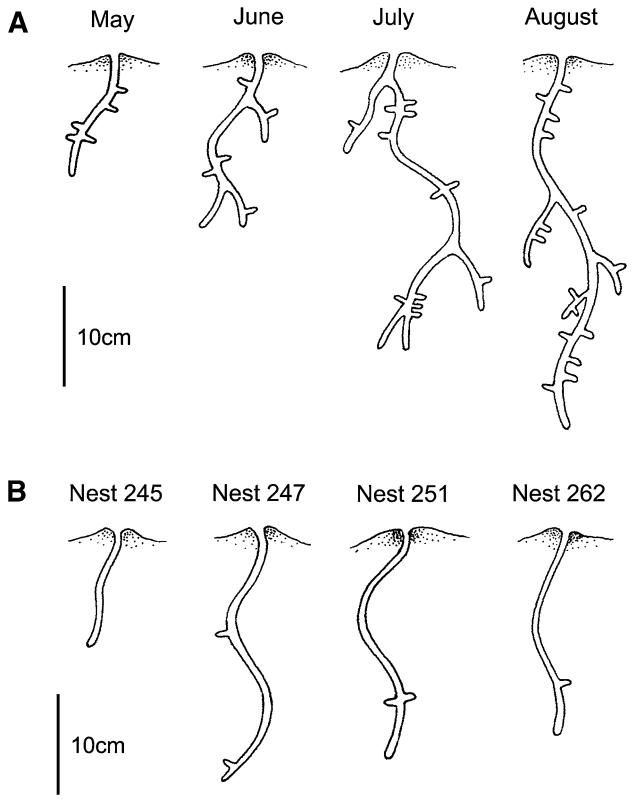

Fig. 1 Nest architecture of *Halictus ligatus* colonies in St. Catharines, Ontario. **a** Average nest depths and number of brood cells. **b** Newly founded nests by orphaned 'worker' bees in July–August, 2006

wing wear (WW), and had a mandibular wear (MW) score of 2. She was mated and had one ¼ developed oocyte. Nest 247 (excavated 19 July) was 21 cm deep and contained one empty brood cell and one brood cell with a provision mass and egg. The adult occupant was small (HW 2.8 mm), had no wing wear and some mandibular wear (MW 3), was mated, and had considerable ovarian development (one ¾ oocyte and two ¼ oocytes). Nest 251 (excavated 25 July) was 15 cm deep and contained two closed brood cells, each with a provision mass and egg. The female was small (HW 2.75 mm), had low wing wear (WW 1), heavy mandibular wear (MW 5), was mated and had one fully developed oocyte indicating that she was ready to lay an egg. Nest 262 (excavated 8 August) was 21 cm deep and contained a round (male) pollen ball and egg. The small female (HW 2.75 mm) had no wing wear (WW 0) and moderate mandibular wear (MW 3). She was mated and had one ¾ oocyte, indicating she was probably within a day of laying an egg.

Discussion

Most likely, these four unusual nests were new nests constructed by young workers whose natal nests were destroyed by the wasp activity. When their nests were lost, it seems that workers recapitulated the behaviours normally expressed by gynes when they awaken from hibernation in spring and establish new nests. Thus, newly eclosed workers are not constrained to summer worker behaviour, but are behaviourally totipotent, capable of expressing any of the behaviours typical of adult females under the right circumstances, including spring queen-like behaviours. Interestingly, circumstantial evidence indicates that this behavioural flexibility extends even to old queens. Nest 235 (excavated 18 July) contained a medium-sized female who by her level of wear was probably a queen (HW 2.8, WW 3, MW 5). However, her nest was only 14 cm deep and showed no evidence that it had ever contained any brood cells. Very likely, this queen was also renesting following the destruction of her former nest. It is also possible that this queen was reentering hibernation for the second winter. Although summer nest founding has never previously been observed in *H. ligatus*, it has been observed in other primitively eusocial sweat bees. The difference between facultative and obligate eusociality may lie in the frequency with which "solitary" nest-founding occurs and in the circumstances that elicit it. Costa and Fitzgerald (1996) and Wcislo (1997) review semantic debates over social insect terminology, and the problem of variation within taxa. In *Augochlorella aurata* (Mueller, 1996) and *Lasioglossum duplex* (Sakagami, 1977), "worker" nest-founding is relatively common and in the latter species, may be associated with early queen mortality (Yagi and Hasegawa, 2012). Detailed studies of *H. ligatus* have only detected the phenomenon under the peculiar circumstances of midsummer nest destruction that we observed here in 2006.

Acknowledgments Special thanks to Karmi Oxman for the illustrations in Fig. 1. This work was supported by NSERC scholarships to SMR and NSERC Discovery grants to MHR.

References

Costa J.T. and Fitzgerald T.D. 1996. Developments in social terminology: semantic battles in a conceptual war. *Trends Ecol. Evol.* **11**: 285–289

Michener C.D. 1974. *Social Behaviour of the Bees*. Belknap Press, Cambridge MA

Mueller U.G. 1996. Life history and social evolution of the primitively eusocial bee *Augochlorella striata* (Hymenoptera: Halictidae). *J. Kansas Entomol. Soc.* **69**: 116–138

Packer L. 1986. Multiple foundress associations in a temperate population of *Halictus ligatus*. *Can. J. Zool.* **64**: 2325–2332

Richards M.H. and Packer L. 1994. Trophic aspects of caste determination in a primitively eusocial sweat bee. *Behav. Ecol. Sociobiol.* **34**: 385–391

Richards M.H. and Packer L. 1995. Annual variation in survival and reproduction of the primitively eusocial sweat bee *Halictus ligatus* (Hymenoptera: Halictidae). *Can. J. Zool.* **73**: 933–941

Richards M.H. and Packer L. 1998. Demography and relatedness in multiple foundress nests of the social sweat bee, *Halictus ligatus*. *Insect. Soc.* **45**: 97–109

Richards M.H., Packer L. and Seger J. 1995. Unexpected patterns of parentage and relatedness in a primitively eusocial bee. *Nature* **373**: 239–241

Richards M.H., Vickruck J. and Rehan S.M. 2010. Colony social organization of *Halictus confusus* in southern Ontario, with comments on the sociality in the subgenus *H. (Seladonia). J. Hymenopt. Res.* **19**: 144–158

Sakagami S.F. 1977. Seasonal change of nest survival and related aspects in an aggregation of *Lasioglossum duplex* (Dalla Torre), a eusocial halictine bee (Hymenoptera: Halictidae). *Res. Popul. Ecol.* **19**: 69–86

Schwarz M.P., Richards M.H. and Danforth B.N. 2007. Changing paradigms in insect social evolution: insights from halictine and allodapine bees. *Annu. Rev. Entomol*. **52:** 127–150

Wcislo W.T. 1997. Are behavioural classifications blinders to studying natural variation? In: *The Evolution of Social Behaviour in Insects and Arachnids* (Choe J.C. and Crespi B.J., Eds), Cambridge University Press. pp 8–13

Yagi N. and Hasegawa E. 2012. A halictid bee with sympatric solitary and eusocial nests offers evidence for Hamilton's rule. *Nat. Commun.* **3**: 939