

# Low relatedness and frequent inter-nest movements in a eusocial sweat bee

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**Abstract** Halictid bees are good systems for studying the evolution and maintenance of eusociality, because they form small societies where females have multiple behavioural options (stay or leave, reproduce or help). Here, we investigate colony organization, inter-nest movements and patterns of reproduction in *Halictus scabiosae*, a species where foundresses rear a first brood of females that often behave as helpers to rear a second brood. Using non-destructive sampling and microsatellite genotyping, we monitored the genotypic composition of a sample of colonies over the entire reproductive season, which allowed us to reconstruct sibships and infer parentage within and across colonies. We detected that foundresses and females from the first brood often moved to foreign colonies. Moreover, foundresses were frequently replaced. At least 5 % of the females from the first brood reproduced. Eight of the ten cases of reproduction by first brood females occurred in foreign colonies. Because of extensive bee movements, many colonies contained offspring from unrelated individuals. The average genetic relatedness among bees sampled from the same colony was moderate ( $0.33 \pm 0.02$ ). The relatedness of the second brood to their colony foundresses and first brood females was only 0.14 and 0.21, respectively. The labile colony membership decreases the intra-colony relatedness and thus the inclusive fitness of helpers, but the

behavioural flexibility of these bees may allow them to cope with variable environmental constraints.

**Keywords** Social evolution · Helping behaviour · Eusociality · Drifting · Halictid bees

## Introduction

The hallmark of eusociality is the reproductive division of labour, which means that some society members forfeit direct reproduction to help rearing the offspring of others. A caste of non-reproductive helpers can evolve by kin selection (Hamilton 1964; Bourke 2011). There is indeed phylogenetic evidence that eusociality originally evolved in simple mother–offspring associations, that is, in groups of highly related individuals (Hughes et al. 2008). However, eusocial insects often have complex colony structures. In many ant, bee and wasp species, multiple breeders per nest and movements of individuals among nests tend to decrease the relatedness among nestmates, and thus the inclusive fitness of helpers, which raises questions on the maintenance of eusociality (e.g. Chapuisat and Keller 1999; Queller et al. 2000; Paxton et al. 2002; Richards et al. 2003).

Facultatively eusocial bee and wasp species are ideal model systems to study the evolution and maintenance of eusociality, because the females have retained a great flexibility in their behavioural and reproductive options (Crespi and Yanega 1995; Schwarz et al. 2007). Helpers in these species can combine helping and direct reproduction, depending on constraints and opportunities (Field et al. 2006; Yagi and Hasegawa 2012). In halictid bees, helpers may work to increase colony survival and productivity (Brand and Chapuisat 2014), obtain some reproductive share (Richards et al. 1995), leave to found a colony

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independently (Rehan et al. 2013), or drift to foreign colonies late in the season (Ulrich et al. 2009). In allodapine bees and paper wasps, subordinates are often waiting to inherit the nest (Leadbeater et al. 2011; Schwarz et al. 2011).

Whether an individual stays or leaves, and helps or reproduces, will depend on the ecological and social factors that influence the pay-offs of alternative strategies (e.g. Keller and Chapuisat 1999). Helping is favoured when the benefits of help weighted by relatedness are greater than its costs, the latter amounting to the direct fitness obtained if the individual leaves the colony to breed independently (Hamilton 1964). The pay-offs of alternative strategies are likely to vary with colony size. In small groups of bees and wasps, dominance hierarchies may lead to reproductive division of labour (West-Eberhard 1967; Turillazzi and West-Eberhard 1996), the impact of helpers is larger than in bigger groups (e.g. Schwarz 1988; Cronin and Schwarz 1997; Brand and Chapuisat 2014) and helpers have a higher chance to replace the dominant breeder (Field and Cant 2009; Schwarz et al. 2011). Moreover, other group members may influence the options of the focal individual. In particular, the reproducers or helpers can coerce other individuals into a helper role (Michener and Brothers 1974; Rattiéks and Wenseleers 2008). For example, in halictid bees the foundress may limit the food resources of her daughters, thereby reducing their chances of independent reproduction (Alexander 1974; Charnov 1978; Kapheim et al. 2011; Brand and Chapuisat 2012, 2014).

In the facultatively eusocial sweat bee *Halictus scabiosae*, the foundresses raise a first brood composed mostly of females that help to rear a second brood of females and males (Brand and Chapuisat 2012, 2014). Due to their small size and low fat reserves, the first brood females are probably unable to found their own colony or to overwinter (Brand and Chapuisat 2012). Occasional cases of co-founding by multiple females (=pleometrosis), evictions of subordinates, nest usurpation and drifting of second brood females late in the season have been documented (Knerer and Plateaux-Quénu 1967; Gogala 1991; Ulrich et al. 2009). Together, these previous studies indicate that this system is flexible, which calls for a more detailed investigation of how quantitative variations in helping, dispersal and reproduction affect the social and genetic organization of the group.

Here, we investigate the behavioural options of females and their impact on social organization in *H. scabiosae*. We aim to better understand how female behaviour and colony genetic structure vary, as these factors are central to the evolution and maintenance of eusociality. We focus on three main questions. What is the degree of relatedness between females and the brood they rear? Do first brood females behave exclusively as non-reproductive helpers, or do they also get a share of reproduction? Do bees move between

nests? To answer these questions, we monitored a large number of nests over an entire breeding season. We used non-destructive sampling and microsatellite genotyping to document patterns of relatedness, reproduction and inter-nest movements in the foundresses, first and second brood cohorts.

## Materials and methods

### Life cycle and study population of *H. scabiosae*

*H. scabiosae* is a facultatively eusocial halictid bee forming annual colonies. In spring, overwintered females establish underground nests—each nest has its own entrance, and will constitute a separate colony. Foundresses usually breed alone, but joint colony founding (=pleometrosis) is quite common in some populations. For example, 31 % of the nests had multiple foundresses near Lausanne in the south-west of Switzerland (Ulrich et al. 2009). The foundresses lay eggs in individual cells stocked with provisions of pollen and nectar (mass-provisioning, Brand and Chapuisat 2012). A first brood (B1) consisting primarily of small-sized females, with about 5 % of males, emerges from the nests in June and July (Ulrich et al. 2009; Brand and Chapuisat 2012, 2014). Females from the first brood are able to mate and reproduce, but most of them remain unmated and tend to stay in their natal colony to help raise a second brood (B2) of females and males (Batra 1966; Ulrich et al. 2009; Brand and Chapuisat 2012, 2014). B1 females excavate new cells, forage to provision the offspring and occasionally defend the colony against predators, parasites or intraspecific usurpers. The females and males from the second brood emerge from the nests in August and September. After mating, the B2 females either disperse or stay in their natal nest (Ulrich et al. 2009), and after overwintering they become the next generation of foundresses in the following spring (Ulrich et al. 2009; Brand and Chapuisat 2012).

Our study site is a dry, south-exposed embankment located in Adlikon, near Zürich, in northern Switzerland (Brand and Chapuisat 2012, 2014). This site is densely populated with more than 1000 nests over an area of ca. 30 × 10 m. However, many of these nests are short-lived and do not produce any offspring, while the successful nests produce only few B2 females or males (Brand and Chapuisat 2014).

### Bee sampling

In May and June 2009, we marked 974 nests of *H. scabiosae* with numbered nails and flags, and recorded their positions using a global positioning system (Leica GPS1200, horizontal and vertical accuracy of 10 and 20 mm,

respectively). For the microsatellite analysis, we non-destructively sampled 471 bees from 76 nests: 44 foundresses, 196 B1 females, 8 B1 males, 199 B2 females, 18 B2 males, plus 6 males (1 B1 and 5 B2) that turned out to be diploid (Online Resource 1, Table S1). We captured the bees with net traps placed on the nest entrance on non-rainy days, as described previously (Brand and Chapuisat 2012, 2014). We obtained a partial sample of the bees from each nest, because some bees might have stayed in the nest or managed to escape. In addition, we also sampled eight foundresses while they were foraging out of their nest in early spring. In prospect of the microsatellite genotyping, we sampled the tip (about 2 mm) of the tarsus from one hind leg of each captured bee, and stored it in 99 % ethanol for later analysis. We then released each bee near its nest hole. This sampling procedure appeared to have minimal impact on the bees. First, a similar removal of the terminal part of one tarsus had no effect on the survival and foraging efficiency of bumblebees (Holehouse et al. 2003). Second, in a pilot study in 2008, we found that *H. scabiosae* colonies that had been sampled for microsatellite analysis as described above ( $n = 46$ ) did not differ significantly from control, non-manipulated colonies ( $n = 153$ ) in terms of colony productivity (=number of B2 individuals produced per colony;  $F_{1,199} = 0.018$ ,  $P = 0.89$ ) and colony survival (=proportion of colonies that produced B2 individuals;  $F_{1,199} = 0.025$ ,  $P = 0.88$ ; see Brand and Chapuisat 2014 for details).

We trapped overwintered females (foundresses) between May 6th and June 4th, and marked them with individual colour codes using quick-drying honeybee marking paints (Apicolori, Bienen-Meier Künten). We sampled B1 offspring between June 25th and August 24th and B2 offspring between August 11th and September 8th. We marked each captured offspring with one dot of paint, to avoid double counting. Within each colony, the two broods do not temporarily overlap, and we could easily distinguish B2 from B1 females based on previous marking, head width (Brand and Chapuisat 2012), wing wear and mandibular wear (Mueller and Wolflueller 1993). The rate of colony failure was estimated as the proportion of colonies that disappeared and/or did not produce B2 offspring.

### DNA extraction and microsatellite analysis

We extracted DNA from each sample of bee tarsus by proteinase K digestion followed by phenol–chloroform purification and ethanol precipitation (Hoy 2003). We resuspended the DNA in 50  $\mu$ l ddH<sub>2</sub>O. We amplified 11 microsatellite loci in three multiplex PCRs using the protocol described by Ulrich et al. (2009) with minor modifications in the PCR cycle [15 min at 95 °C, 35  $\times$  (30 s at 94 °C, 90 s at Ta 58/60 °C, 60 s at 72 °C),

30 min at 60 °C], PCR mix (4  $\mu$ l DNA template, 2.5  $\mu$ l Qiagen multiplex PCR mastermix, 0.5  $\mu$ l of multiplex primers, 1  $\mu$ l ddH<sub>2</sub>O) and thermocycler (T1, Biometra, Goettingen, Germany). We mixed amplification products of the second and third multiplex PCR in 1:1 proportion, and analysed them separately from products of the first multiplex PCR, on an ABI Prism 3100 Genetic Analyzer (see Ulrich et al. 2009). Alleles were scored with Genemapper<sup>®</sup> software v 4.0. The 11 microsatellites had from six to 25 alleles per locus, with an average of 13.7 alleles per locus and a mean expected heterozygosity of 0.69 (Online Resource 1, Table S2). Together, these markers are powerful to infer parentage. When we use the equations in Soro et al. (2009), the population-wide probability of non-detection of a second fathering male ( $d_p$ , i.e. the probability that two males share the same genotype at all loci) is  $5 \times 10^{-7}$ , and the probability of non-detection of an additional matriline among a set of putative daughters ( $d_m$ ) ranges from  $3 \times 10^{-7}$  to 0.025.

One B1 male and five B2 males were diploid. These six diploid males were included in the pedigree analyses because they give useful information on inter-nest movements, but they were excluded from relatedness calculations. Similarly, the eight foundresses sampled while foraging were included in the pedigree analysis, but they were excluded from nestmate relatedness calculations, as they had not been assigned to nests.

### Nestmate relatedness and pedigree relationships

We estimated the life-for-life coefficient of genetic relatedness among nestmates ( $r$ ) using the algorithm of Queller and Goodnight (1989), as implemented in the computer program Relatedness 5.0.8. We measured the relatedness of the recipient to the actor. Allele frequencies in the background population were estimated weighing nests equally. Standard errors and 95 % confidence intervals were obtained by jackknifing over loci (Queller and Goodnight 1989).

To document patterns of reproduction and movements between nests, we inferred close pedigree relationships among all sampled bees. We used the maximum likelihood approach implemented in the computer program COLONY 2.0, which sorts individuals belonging to an “offspring sample” into most probable sibships (=full-sib groups), and infers parentage to potential parents (Jones and Wang 2010). We included all genotypes of B1 females ( $n = 196$ ), B2 females ( $n = 199$ ) and diploid males ( $n = 6$ ) in the “offspring sample”. We included all genotypes of foundresses ( $n = 52$ ) and B1 females ( $n = 196$ ) in the sample of candidate mothers. COLONY accounts for genotyping errors such as allelic dropout, scoring errors and mutations (Jones and Wang 2010). We explored various rates of errors

for allelic dropout (5 %; frequency of blank individuals; square root of frequency of blank individuals), as well as for other genotyping errors (2; 5; 8 %; Wang 2004). These variations in error rates had negligible impact on the inferred sibships (see Wang 2004 for a similar analysis of ant data). We report results with the frequency of blank individuals for allelic dropout and a frequency of 5 % for other genotyping errors. We attributed the B1 and B2 haploid males ( $n = 8$  and 18, respectively) to sibships with the version 1.2 of the program COLONY, which handles haploid genotypes. Except for the relatedness and pedigree analyses described above, all statistical analyses were carried out in R 2.10.1 (R Development Core Team 2011).

## Results

### Relatedness among colony members

Out of the 974 nests that we marked in May and June, 354 (36.3 %) produced females or males in the first brood (B1), and 204 (20.9 %) produced females or males in the second brood (B2). In the subsample of 76 nests where we sampled bees with net traps, the colonies produced on average  $2.58 \pm 2.16$  (SD) B1 females,  $0.12 \pm 0.36$  B1 males,  $2.62 \pm 3.56$  B2 females and  $0.30 \pm 0.73$  B2 males (Online Resource 1, Table S1). We detected pleometrotic foundress associations in ten of these nests (13.2 %; Online Resource 1, Table S1). These are conservative estimates, as some bees were not captured.

The population-wide estimate of the average relatedness among bees sampled from the same colonies was  $0.33 \pm 0.02$  (mean  $\pm$  SE; 95 % confidence interval [0.29; 0.37]). Within and across categories of nestmates (foundresses, B1 females, B1 males, B2 females, B2 males), the relatedness ranged from  $0.05 \pm 0.07$  to  $0.45 \pm 0.02$  (Table 1). These moderate average values indicate that multiple matrilineal frequently coexist in the same nest, which may be due to polygyny, foundress replacement, egg dumping, or drifting of worker adults.

Co-foundresses sampled from the same nest in spring were not significantly related: their relatedness estimate was close to zero, and the 95 % confidence interval overlapped with zero (Table 1). The foundresses that we captured in spring were moderately related to the females and males later produced in the same nest (Table 1). Overall, the relatedness of the second brood (males and females) to their colony foundresses was  $0.14 \pm 0.04$  (95 % CI [0.04; 0.24]).

The relatedness among nestmate females from the same brood was  $0.43 \pm 0.02$  and  $0.45 \pm 0.02$  for B1 females and B2 females, respectively (Table 1). These values are significantly lower than the relatedness expected for full sisters (the 95 % confidence intervals do not encompass 0.75,

Table 1), which indicates that a proportion of the nests contain multiple sibships. The relatedness of the B2 females to the B1 females from the same nest was  $0.20 \pm 0.04$ , a value significantly lower than the relatedness among nestmate females belonging to the same brood (non-overlapping confidence intervals, Table 1). The fact that the between-brood relatedness is significantly lower than the within-brood relatedness indicates that B1 and B2 females from the same nests often have different mothers (e.g. Chapuisat et al. 2004). The average relatedness of males to nestmate females was not significantly different from the one expected for brothers, or for a mix of unrelated males and sons (the confidence intervals encompass 0.25, Table 1). Overall, the relatedness of the second brood (males and females) to the first brood females in their colony (the potential helpers) was  $0.21 \pm 0.04$  (95 % CI [0.12, 0.29]).

### Pedigree relationships and partitioning of reproduction

By sorting the bee genotypes with the computer program COLONY, we obtained 134 full-sib groups (=sibships). In one nest, two sibships were likely maternal half-sibs of a doubly mated foundress. We did not identify any other clear case of multiple mating, which indicates that females generally mate once.

Each of the 134 sibships consisted of one to 20 females and males from the B1 and B2 cohorts (mean  $\pm$  SD  $3.2 \pm 3.6$ ). For 36 of these sibships, an inferred maternal genotype matched the one of a sampled foundress (26 cases) or B1 female (10 cases), respectively. Hence, half of the 52 genotyped foundresses and 5.1 % of the 196 genotyped B1 females had offspring within our sample of B1 and B2 individuals. The foundresses had on average  $2.35 \pm 1.26$  B1 and  $2.04 \pm 4.05$  B2 offspring, whereas reproducing B1 females had on average  $2.40 \pm 2.50$  B2 offspring. These are conservative estimates, as we did not capture all bees.

We further investigated the partitioning of reproduction in nests from which we had sampled multiple nestmates (Online Resource 1, Table S1). In line with the low relatedness estimates, 66.7 % of these nests (46 out of 69) contained more than one sibship, indicating polygyny, foundress replacement, egg dumping, or drifting of worker adults. For example, in one of these nests the foundress produced two B1 females and one B2 female, and one of these B1 females produced two B2 females and a male. The remaining 23 nests (33.3 %) contained a single sibship, consistent with monogyny. On average, in each nest, we detected  $1.74 \pm 1.03$  and  $1.86 \pm 1.01$  sibships in the first and second brood, respectively, and  $2.58 \pm 1.54$  sibships when considering both broods together. The rate of colony failure was significantly higher for nests with one sibship than for nests with multiple sibships ( $\chi^2 = 13.47$ ,  $P < 0.001$ ).

**Table 1** Average relatedness among nestmates,  $\pm$ standard errors, with 95 % confidence intervals in square brackets

Actor	Recipient				
	Foundresses	B1 females	B1 males	B2 females	B2 males
Foundresses	0.05 $\pm$ 0.07 [−0.11; 0.20] N = 10	0.15 $\pm$ 0.04 [0.07; 0.23] N = 29	0.24 $\pm$ 0.05 [0.13; 0.35] N = 6	0.14 $\pm$ 0.05 [0.03; 0.25] N = 16	0.16 $\pm$ 0.06 [0.04; 0.28] N = 6
B1 females	–	0.43 $\pm$ 0.02 [0.39; 0.47] N = 47	0.15 $\pm$ 0.07 [0.01; 0.30] N = 5	0.20 $\pm$ 0.04 [0.12; 0.29] N = 40	0.28 $\pm$ 0.05 [0.18; 0.38] N = 11
B2 females	–	–	–	0.45 $\pm$ 0.02 [0.40; 0.50] N = 37	0.25 $\pm$ 0.03 [0.19; 0.32] N = 11

N indicates the number of nests—the calculation is based on nests that had multiple nestmates in the relevant class (see Online Resource 1, Table S1 for numbers of individuals)

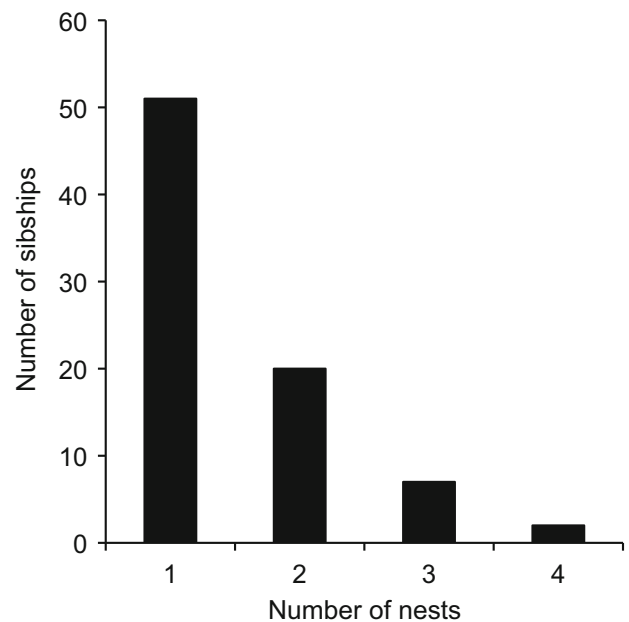
**Inter-nest movements**

We detected that the foundresses and/or their offspring frequently moved between nests. Many of the foundresses had offspring in other nests than the ones in which we captured them for the first time. Such cases of nest switching occurred for 12 (46 %) of the 26 foundresses that matched a sibship in our sample of B1 and B2 individuals. The situations were diverse, as the B1, B2 or both broods were distributed in foreign nests (Online Resource 1, Table S3). Similarly, eight of the ten B1 females that reproduced (i.e. were mothers of some of the B2 individuals we sampled) had offspring in another nest than the one in which they were first captured. The average distance between the nest of origin of a foundress or B1 female and the nest in which it had offspring was  $9.7 \pm 10.6$  m and  $10.6 \pm 8.6$  m for foundresses and B1 females, respectively.

Further evidence of inter-nest movements is provided by the fact that sibships were often distributed in multiple nests (Fig. 1; Online Resource 1, Fig. S1, Table S4). Specifically, 29 sibships were sampled in more than one nest, which amounts to 36.3 % of all sibships with more than one individual. Across the entire sample, sibships occupied  $1.30 \pm 0.64$  nests on average (range 1–4 nests). The mean distance between nests containing split sibships was  $12.7 \pm 15.3$  m.

**Discussion**

We used non-destructive sampling coupled with microsatellite analysis to monitor the genotypic composition of colonies of the halictid bee *H. scabiosae* over the entire reproductive season. We found that colony composition was labile, and that bees frequently moved between colonies. First, foundresses commonly switched to other empty or occupied nests during the nest-founding phase. Moreover, some of their offspring also switched nests, so that overall 46 % of the foundresses had offspring in other



**Fig. 1** Distribution of sibships across nests. The number of sibships (with two or more full-sib) detected in one to four nests is indicated. See Online Resource 1, Table S4 for details

nests than the ones in which we captured them for the first time. Second, two thirds of the nests from which we had sampled multiple bees contained two or more sibships. Finally, more than a third of all sibships with more than one individual were distributed in multiple nests. Such full-sib groups distributed in multiple nests attest that either the mother or the offspring have moved between nests (e.g. Packer 1986; Ulrich et al. 2009; Peso and Richards 2011).

Why do bees frequently move to other nests? Some movements may result from recognition errors. The repeated capture of bees might also have contributed to increase inter-nest movements. However, frequent drifting was also detected in a previous study of *H. scabiosae* where females were removed upon capture (Ulrich et al. 2009). Our

extensive nest survey further shows that many bees abandoned their nests early in the season, and that almost two-thirds of the founded nests did not produce any offspring. In halictid bees and paper wasps, foundresses from failed or usurped nests, as well as evicted co-foundresses, are likely to drift to other nests (Knerer and Plateaux-Quénu 1967; Gogala 1991; Nonacs and Reeve 1993; Zobel and Paxton 2007).

Later in the season, drifting to foreign nests may serve to reduce competition for nest inheritance among related females, by decreasing the number of related females hibernating in the same nest (Ulrich et al. 2009). In the current study, we found ten cases where a sibship had at least two members per nest in two or more nests (Online Resource 1, Table S4). Such cases suggest that the mother has moved to other nests, either temporarily (egg dumping, e.g. Packer 1986) or permanently. Joint drifting of multiple full-sibs to the same nest is less likely, given the high number of nests in the population and large mean distance between nests containing split sibships. In many other cases, a single member of a sibship was sampled in a foreign nest, which could be due to the drifting of the mother or the adult offspring. Co-foundresses sampled in the same nest in spring were not significantly related, which further indicates that many bees move among nests and do not stay with sisters in their natal nest.

The colony organization was highly variable, with occasional cases of pleometrosis, polygyny, foundress replacement and egg dumping. The presence of multiple lineages in the same nests coupled with extensive inter-nest movements of the foundresses, B1 and B2 females resulted in low average degrees of relatedness among colony members. In particular, the relatedness of B2 females and males to foundresses was only 0.14, on average. Hence, foundresses are far from monopolizing reproduction in the nests where they were first captured. The relatedness of B2 females and males to B1 females was also moderate, with an estimate of 0.21 on average, which further indicates that bees often move to foreign nests. Low intra-colony relatedness should typically be associated with lower incentive for helping and higher competition to get a share of reproduction (Ratnieks et al. 2006).

The presence of multiple females cooperating or multiple sibships in the same nest is likely to increase colony survival and productivity. In this study population of *H. scabiosae*, colonies with a single sibship had a higher failure rate than colonies with multiple sibships. This is a common pattern in wasps and bees, which might be due to a better division of labour or a better ability to cope with predation, nest usurpation or parasitism in colonies with multiple reproductive females (Tibbetts and Reeve 2003; Smith et al. 2007; Rehan et al. 2011; Yagi and Hasegawa 2012). The possibility of nest reuse and delayed reproduction by subordinates may also contribute to favour nest sharing by multiple females,

particularly when constraints on independent nesting are high (Schwarz et al. 2011; Rehan et al. 2014).

The majority (about 95 %) of the females from the first brood behaved as helpers and did not reproduce. We detected that about 5 % of the B1 females had B2 offspring. Eight of the ten cases of reproduction by first brood females occurred in foreign colonies. By drifting, B1 females may avoid being coerced by the dominant foundress (Michener and Brothers 1974; Hogendoorn and Schwarz 1998), or may decrease local competition with relatives (Ulrich et al. 2009). In other social insect species, workers that drift to foreign colonies often show higher rates of reproduction than workers staying in their natal colony (Paxton et al. 2002; Lopez-Vaamonde et al. 2004; Yagi and Hasegawa 2012; Blacher et al. 2013).

To sum up, *H. scabiosae* forms small societies with labile colony membership, high failure rates and extensive bee movements among colonies. The colonies have low productivity, and due to frequent drifting to foreign nests, the B2 brood is only moderately related to the foundresses and B1 females that reared it. The vast majority of the B1 females behave as helpers, which may be in part due to high rates of colony failure and constraints associated with their small body size (Brand and Chapuisat 2012). Most, if not all, of the colonies become eusocial as the season progresses (e.g. 87 % of the colonies had B1 females in our partial sample, most of them helping to rear the B2 brood; Online Resource 1, Table S1). The low relatedness coupled with low productivity is surprising for a eusocial species, because it is associated with low inclusive fitness. However, in *H. scabiosae* helping is occasionally combined with direct reproduction, and may be partly enforced (Brand and Chapuisat 2012). Moreover, the great behavioural flexibility and labile colony organization of these bees might allow them to adapt to changing conditions and to cope with variable environmental constraints.

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