

# Evidence for geographic variation in colony social organization in an obligately social sweat bee, *Lasioglossum malachurum* Kirby (Hymenoptera; Halictidae)

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**Abstract:** The expression of altruism and colony eusociality are both a matter of degree in social sweat bees. Even in obligately social species, variation in these traits may be observed across a species' range. *Lasioglossum (Evylaeus) malachurum* (Kirby) is an obligately eusocial sweat bee found across Europe. In western Europe, *L. malachurum* exhibits north–south clines of increasing colony size associated with the production of more worker broods, and worker production of males, but societies conform to the model of a classically eusocial hymenopteran insect. A population of *L. malachurum* studied from 1994 to 1998 at Agios Nikolaos Monemvasias in southern Greece exhibits a startlingly different type of social structure. Dissections of female bees collected while foraging on flowers or from excavations of nests showed that the majority of mid- to late-summer workers are mated and (or) have developing ovaries, indicating that some workers are highly reproductive. Nest excavations indicated that in many or most colonies, the queen has disappeared by midsummer, before ovipositing the final, reproductive brood. In orphan nests, workers become the major reproductives, which suggests that males and gynes in the final brood are the offspring of workers. The very long breeding season in southern Greece may explain why colonies often outlive their queen. The result is the expression of a multivoltine colony cycle and a behavioural switch from eusocial to semisocial colony organization.

**Résumé :** L'expression de l'altruisme et de l'eusocialité est une question de degré chez les halictes sociaux. Même dans l'espèce obligatoirement sociale, on peut observer la variation de ces traits à travers un intervalle de espèces. *Lasioglossum (Evylaeus) malachurum* (Kirby) est un halicte eusocial obligatoire trouvé partout en Europe. En Europe de l'ouest, *L. malachurum* suit des gradients nord–sud où la taille des colonies augmente par augmentation de la production de couvées d'ouvrières et par reproduction des abeilles ouvrières mâles, mais les sociétés se conforment au modèle d'un insecte hyménoptère eusocial dans son sens classique. Une population de *L. malachurum* étudiée de 1994 à 1998 à Agios Nikolaos Monemvasias dans le sud de la Grèce a un type de structure sociale radicalement différent. La dissection de femelles butineuses récoltées sur les fleurs ou obtenues par excavation des nids indique que la majorité des ouvrières de mi-été ou de fin d'été sont déjà accouplées et (ou) ont des ovaires en développement, ce qui prouve que certaines ouvrières sont de bons reproducteurs. L'excavation de nids a démontré que dans plusieurs colonies ou dans la plupart, les reines sont disparues au milieu de l'été, avant la ponte de la couvée reproductrice finale. Dans les nids orphelins, les ouvrières deviennent les principaux reproducteurs, ce qui indique que les mâles et les gynes issus de la dernière couvée sont la progéniture d'ouvrières. La très longue saison de reproduction dans le sud de la Grèce peut expliquer pourquoi les colonies survivent souvent à leurs reines. On assiste alors à l'expression d'un cycle multivoltin et à un changement du comportement de la colonie qui passe d'une organisation eusociale à une organisation semisociale.

[Traduit par la Rédaction]

## Introduction

One of the main goals of social insect biology is to discover the evolutionary processes by which solitarily breeding, nonsocial insects give rise to cooperatively breeding ones, and why cooperatively breeding insects sometimes revert to the solitary mode. Detailed comparisons of species exhibiting variation in social organization of the colony, in the strength of altruistic behaviour, and in different patterns of reproductive skew are designed to elucidate the environmental conditions that favour solitary or cooperative breeding

among adults in different ecological situations (Wcislo 1997). This approach is especially valuable for studying halictine sweat bees, since even obligately social species may exhibit marked plasticity in social behaviour.

Sweat bee breeding behaviour can be described in terms of three broad categories: solitary, obligately social, and facultatively social (Richards 1994; Packer 1997). In solitary nests, foundresses raise their brood alone and the cycle is repeated by each generation. In obligately social sweat bees, there is always some cooperation among adult female nestmates in raising the reproductive brood. In eusocial species, the colony cycle includes at least two phases of brood production, with females of the early brood (workers) helping to raise offspring of the final, or reproductive, brood. Facultatively social species, also referred to as socially poly-morphic (Richards 1994; Packer 1997), include both solitary

Received October 8, 1999. Accepted March 23, 2000.

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and social populations, or even solitary and social colonies within a single population. Facultative eusociality has been observed in *Lasioglossum calceatum* Scopoli (Sakagami and Munakata 1972), *Halictus rubicundus* Christ (Eickwort et al. 1996), and *Augochlorella striata* Provancher (Packer 1990), all of which exhibit at least a partial reversion to solitary colony cycles in regions with a short growing season. The phylogenetic positions of these socially polymorphic species imply a reversion to solitary behaviour in those populations in which it is expressed.

Somewhat disconcertingly, recent investigations have tended to show that there is far more intraspecific variation in sweat bee social behaviour than was previously predicted, even in obligately social species. For instance, *Halictus ligatus* Say exhibits marked geographic variation in important social parameters such as the incidence of multifemale nest-founding, overall colony size, queen-worker size dimorphism, and worker reproductivity (Kirkton 1968; Litte 1977; Michener and Bennett 1977; Packer 1986). In this bee, the strength of eusocial colony organization is clearly associated with environmental factors: harsher weather conditions result in stronger eusociality and milder conditions in weaker eusociality (Richards et al. 1995), but never in the complete loss of sociality.

A classically kin-selected, eusocial sweat bee species is one in which a mother queen monopolizes oviposition, and is assisted to raise her reproductive brood by altruistic daughter workers that neither mate nor develop eggs (Eickwort 1985). As in other eusocial Hymenoptera, this definition of the classical eusocial worker is often stretched to include those that produce male offspring (e.g., Trivers and Hare 1976). *Lasioglossum (Evyllaesus) malachurum* (Kirby) is often regarded as the exemplar of a classically eusocial sweat bee. All known populations are eusocial but demographic variation is known to exist. In northern Europe, only one worker brood is produced before the reproductive brood, while in more southerly populations, two or three worker broods may be produced (G. Knerer, unpublished data, cited in Packer and Knerer 1985). Since successive worker broods are both more numerous and larger in body size (Knerer 1973), colonies in southern Europe reach much larger sizes and probably produce more reproductives by the end of the breeding season. In some southern populations, many workers exhibit developing ovaries, although few are mated (Knerer 1992), which implies the existence of a north-south cline of increasing worker reproduction of males. These observations present no challenge to the definition of a eusocial worker.

In 1998 I found two nesting aggregations of *L. malachurum* near the village of Agios Nikolaos Monemvasias (ANM) in the southeastern corner of the Peloponnesos near the southeastern tip of mainland Greece. Based on Knerer's observations in southern France and in Spain, I predicted that in Greece, *L. malachurum* would exhibit a strongly eusocial colony structure in which queens monopolize oviposition of the reproductive brood and there is little or no evidence of worker reproduction. If workers were found to lay eggs, their reproduction would be limited to the production of males. These predictions were soon overturned by the surprising discovery that many midsummer workers were mated and had well-developed ovaries, suggesting widespread worker reproduction of both female and male offspring. Previously this

phenomenon has only been observed in *H. ligatus* (Richards et al. 1995). As it turns out, in southern Greece, as elsewhere, *L. malachurum* is social, but worker behaviour and colony social organization appear to be dramatically different from that of *L. malachurum* elsewhere in Europe.

## Methods

### Study site

The study area is centred on ANM and has a typical Mediterranean landscape dominated by scrub and olive groves. Winters are cool and rainy, while summers are long, hot, and very dry. ANM itself is a small village situated in an area of intense agricultural development for olive groves. The soils in the area are predominantly red clay and sandy yellow soil; these are quite soft in spring but harden to a rocklike consistency in summer. In spring and early summer, wildflowers, especially yellow Compositae, are very abundant, and some persist throughout the summer.

Bees were observed and collected at various times of the spring and summer in 1989, 1994, 1996, 1997, and 1998. In 1998, several nesting aggregations of *L. malachurum* were discovered within 2 km of ANM. I originally planned to map large sweat bee nesting aggregations by surveying a 1-km transect grid centred on ANM, but by 1998, a huge increase in bulldozer activity (cutting new olive terraces out of the mountainsides) had already destroyed several previously noted bee nesting sites. I therefore limited my survey to an inspection of the shoulders of dirt paths and roads around the village. Nests of *L. malachurum* were identified by a small mound of excavated soil surrounding a round central entrance, and their location was recorded with a hand-held Global Positioning System (GPS) unit. For consistency, all locations were recorded with reference to my house in the centre of ANM.

Nests in two aggregations beside dirt roads were individually marked in order to count them and to observe foragers at the nest entrances. The two aggregations are referred to as MALA1, a loose aggregation of 42 nests in a dirt road on a hillside above ANM, and MALA2, a dense aggregation of about 250 nests in a valley below the village. The edges of aggregation MALA2 were defined by a roadbed and retaining wall, so nest density was measured by direct count. It was not possible to define the borders of aggregation MALA1, so nest density was measured in terms of nearest neighbour distance by measuring the straight-line distance from each nest entrance to the entrance of its nearest neighbour, using a metre stick. In July 1999, I was unable to relocate either aggregation, and it is likely that both were destroyed by road grading during the spring.

### Nest excavations

In June 1998, four nests with living occupants were fully excavated and two were partially excavated at aggregation MALA2. Two more nests contained no living brood or adults at the time of excavation. Excavations were halted when it was discovered that this aggregation was located above an irrigation pipe, with nests extending below the pipe. Nests were excavated after white powder was blown down the entrance in order to visualize the tunnels. Fully excavated nests were dug to a depth of about 5 cm below the last brood cell or end of the tunnel (whichever was deeper) to ensure that no sections had been missed. All nest occupants were collected and stored in ethanol.

### Dissections and measurements

Bees were collected while foraging on flowers, when entering or departing from individually marked nests (1998 only), or during nest excavations. Most bees were stored in 70–90% ethanol or in Kahle's solution, but a few were pinned.



**Table 1.** Contents of nests excavated at site MALA2 in June 1998.

Nest No.	Date excavated	Nest contents	Female head width (mean $\pm$ 1 SD, mm)
104	22 June	1 ♀ adult 1 ♀ <i>Sphcodes</i> sp. adult	2.05 ( $n = 1$ )
101	23 June	5 ♀ pupae 16 ♀ adults 5 filled-in brood cells	2.21 $\pm$ 0.07 ( $n = 3$ ) 2.17 $\pm$ 0.04 ( $n = 14$ )
103	26 June	1 ♀ pupa 4 ♀ adults 6 filled-in brood cells	2.09 ( $n = 1$ )
105	29 June	14 ♀ adults 4 ♂ <i>Sphcodes</i> sp. adults	2.16 $\pm$ 0.06 ( $n = 14$ )
102 (partial)	23 June	3 ♀ pupae 3 ♀ adults 1 ♂ adult	2.11 $\pm$ 0.05 ( $n = 3$ )
107 (partial)	29 June	2 ♀ adults 1 ♂ adult	

**Note:** All the females were worker-sized individuals. The parasites found in nests 104 and 105 were probably *Sphcodes monilicornis*.

by mid-July, the reproductive brood (possibly preceded by a fourth worker brood) was still to be produced.

Short observations (1 h per day) on open nests in aggregation MALA1 on 27 May ( $n = 7$  nests), 28 May ( $n = 4$ ), and 8 June ( $n = 6$ ) 1998 revealed that they contained a minimum of 0–4 foragers, and most nests had a guard at the entrance. Thus, nests appeared to contain approximately 1–5 active workers at this time. On 8 June, only 5 of the 42 nests had active foragers, 1 nest had a female in the entrance but no foragers were seen, 1 nest had been taken over by ants, and the remaining 33 nests were closed. Guards occasionally repelled returning resident foragers, but these would often gain entrance to the nest when another forager arrived and was admitted. I also observed adult females flying in zigzag patterns a few centimetres above the ground, stopping at intervals to inspect the terrain. Some of these bees were evidently lost, because they were carrying pollen and eventually entered nests, but a few may have been searching for nests to join. Guards at entrances prevented such attempts, but no fights were ever seen.

In the fourth week of June 1998, four nests with living occupants were completely excavated and two were partially excavated at site MALA2 (Table 1). Nests contained adults and pupae but no larvae. No queens were found. While it is possible that they might have been missed in the partially excavated nests, in the fully excavated nests an effort was made to excavate to at least 5 cm below the end of the nest, so most likely the queens were dead. The vast majority of nest occupants were female: only 2 males, both adult, were found. Nest parasites, probably *Sphcodes monilicornis* Kirby, were found in two of the six nests excavated and may have been an important cause of mortality.

### Body size

The distribution of female body sizes in terms of head width and wing length is shown in Fig. 2. Since only one foundress was found, a statistical comparison of queen and worker body sizes is not worthwhile, but queens are proba-

bly much larger than workers (Figs. 1 and 2). One unusually small individual was found in mid-May 1997 ("S" in Fig. 2). In 1998, the year for which data are most complete, the body size of workers increased from May to June (Fig. 1; ANOVA for HW:  $F_{[1,76]} = 15.37$ ,  $p < 0.0002$ ). However, when temporal variation was accounted for, mean body size did not vary significantly among five 1998 nests from which at least 2 females were available for comparison (partial regression,  $F_{[5]} = 0.69$ , ns).

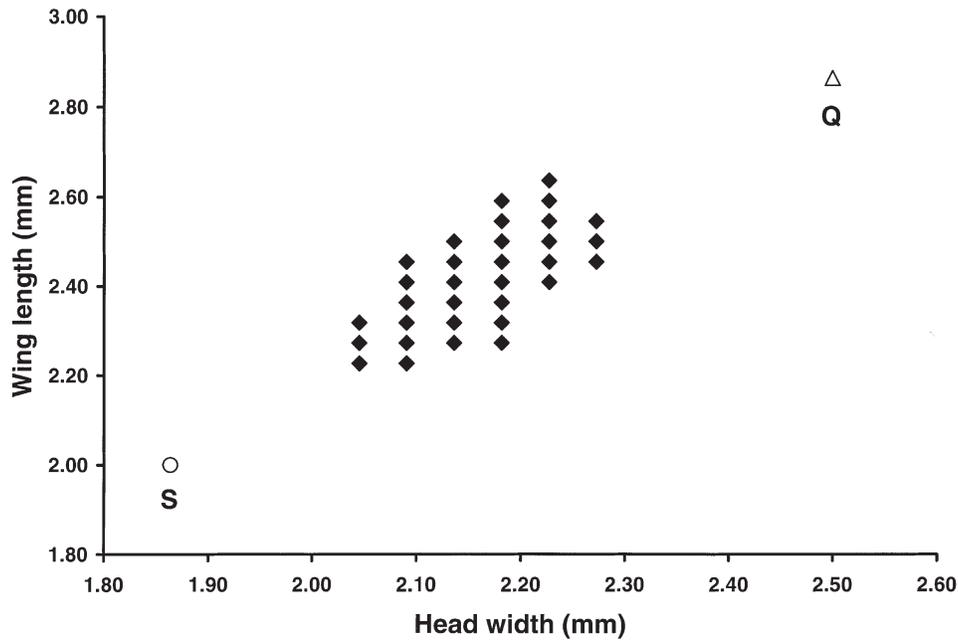
### Social organization

The physical wear and tear exhibited by adult females as a result of nest-maintenance activities such as digging was assessed in terms of mandibular wear. Most workers exhibited some degree of wear (Fig. 3), and those that were not worn were probably mostly young. Degree of mandibular wear was not correlated with worker head width (Pearson's  $\rho = 0.12971$ ,  $df = 88$ , ns).

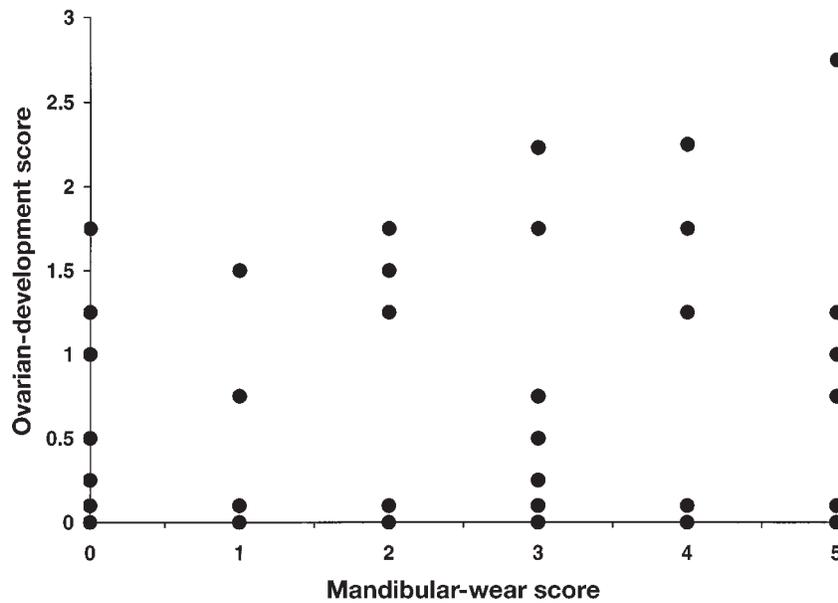
Many workers were reproductive, judging by their advanced state of ovarian development (Figs. 3 and 4). Ovarian development was significantly correlated with mandibular wear (Fig. 3; Pearson's  $\rho = 0.2443$ ,  $df = 88$ ,  $p = 0.0218$ ) but not with head width ( $\rho = 0.03743$ ,  $df = 89$ , ns). Only about half of workers showed no ovarian development or had only slightly thickened ovaries, and only about one-third of workers were unmated. Mated workers were no more likely to have developed ovaries than unmated workers ( $\chi^2 = 0.002$ ,  $df = 1$ , ns). Although only 1 male was discovered during nest excavations, a few were found on flowers, so males were available for workers to mate with.

Dissections revealed that 4 females found in nest excavations were extremely fat; that is, their abdomens were almost completely filled with fat body. Fat bees also had meconium in the lower gut, 2 had incompletely hardened wings, and none showed any mandibular or wing wear, so they were assumed to be newly eclosed. Remarkably, 2 of these young females were mated (perhaps implying that they occasionally mate in the natal nest) and 1 had thickening ovaries. No

**Fig. 2.** Body-size distribution of female *L. malachurum*. The majority of individuals were workers ( $n = 74$ ). “Q” is a foundress from Melissa. The species identity of the unusually small individual “S” was confirmed by Laurence Packer (personal communication).



**Fig. 3.** Ovarian development and mandibular wear in workers collected in 1998. Ovarian development is calculated as summed fractions of developing oocytes. Mandibular wear ranges from 0 (no wear) to 5 (very worn). For an explanation of the ovarian-development score see the text.



foraging workers were fat, and no females with meconium in the lower gut were skinny.

**Discussion**

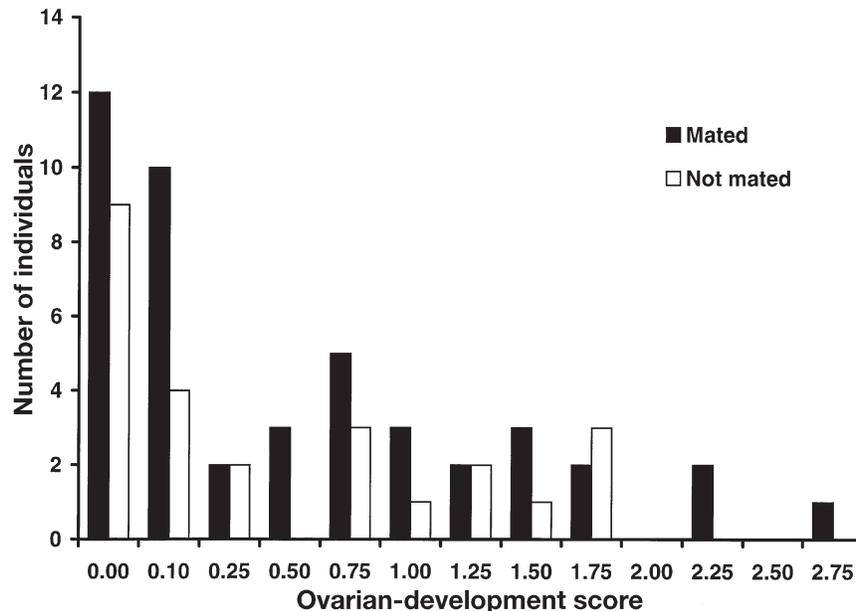
**Social variation in *L. malachurum***

*Lasioglossum malachurum* has often been considered the model of a strongly eusocial sweat bee, with large queens that monopolize oviposition and small, altruistic, usually sterile workers. Intraspecific social variation was thought to be limited to demographic differences in the number and size of

broods produced each summer. Now it appears that there may be profound differences in colony social organization across the species’ range. And even though *L. malachurum* is obligately social, it is difficult to strictly apply the term eusocial to the southern Greek population, where workers may very well be responsible for most reproductive brood oviposition.

The critical difference in colony social organization in southern Greece, compared with other *L. malachurum* populations, including Mediterranean populations, is that so many reproductive workers are mated, making them capable of

**Fig. 4.** Ovarian development and matedness in workers collected in 1998. Only unmated workers with an ovarian-development score of 0 fit the strictest definition of classical altruists.



producing diploid eggs. Observations by G. Knerer (Packer and Knerer 1985; Knerer 1992) hint at a north–south cline of increasing worker production of males but not females. In the Isle of Wight in England, *L. malachurum* colonies produce only a single worker brood each year, and about 3% of workers have developed ovaries. In the Dordogne in southern France and Estepona in southern Spain, Knerer observed 2–3 worker broods each year; 30% of workers had developed ovaries. According to Knerer’s earlier analyses (Packer and Knerer 1985), fewer than 1% of these workers were mated, but later analyses (Knerer 1992) indicated that up to 10% of workers were mated. In a population near Paris, Knerer observed that 3 of 31 workers were mated when caught on 30 July; these must have been second-brood workers. At Gardanne, near Marseilles in southern France, he observed that no second-brood workers were mated, but 3 of 47 third-brood workers were mated, indicating that the proportion of mated workers rose throughout the summer. Unfortunately, although Knerer observed *L. malachurum* in central Greece (Knerer 1992), he gave no indication of the reproductive status of workers in that area.

Evidence of mating and ovarian development do not show conclusively that *L. malachurum* workers reproduce, but it is hardly surprising that they would do so when so many nests are orphaned before the final brood is produced. Differences in queens’ life-spans at northern and southern latitudes may be a crucial factor explaining social variation across Europe. Although further studies are required to confirm this, nest excavations at ANM indicate that most queens probably die by the time the third worker brood emerges in mid-June, which is about 3–4 months after nest-founding, and one of the main causes of queen mortality may be predation by *Sphcodes* sp. At more northerly latitudes, the same average life-span would guarantee that most queens would survive to the time of reproductive-brood oviposition. In Greece, if queens often do not live long enough to lay the reproductive-brood eggs, then they must be laid by workers or the colony

will produce no reproductives. At ANM, many midsummer *L. malachurum* workers are mated and have developing ovaries, and so are capable of producing both the males and the gynes of the reproductive brood. Thus, in many nests, the gynes and males of the final brood are likely to be the offspring of workers, and sweat bee colonies pass from a eusocial to a semisocial stage (sensu Michener 1974). Worker reproduction of gynes has been inferred in *H. ligatus*, where it increases under conditions such as early queen mortality (Richards and Packer 1995; Richards et al. 1995).

What environmental phenomena could underlie this north–south cline of increasing worker reproduction, decreasing strength of eusociality, and a decreasing queen–worker reproductive skew in *L. malachurum*? One important factor must be the length of the breeding season. In northern Europe, the relatively late spring and early fall allow colonies to produce only a single worker brood, and this in turn means that most queens probably survive to the time of reproductive-brood oviposition. In Mediterranean populations such as those in southern Greece, the very long breeding season allows for the production of three, or possibly even four, worker broods per year, but the breeding season seems to be much longer than the average life-span of queens. This means that many workers escape behavioural domination by the queen and gain extensive reproductive opportunities not usually available to workers in northern populations.

This pattern, in which the harshness of local environmental conditions and queen longevity have important effects on colony social organization, is strongly reminiscent of that observed in *H. ligatus* (Kirkton 1968; Litte 1977; Michener and Bennett 1977; Packer 1986). In both *H. ligatus* and *L. malachurum*, northern populations appear to be more strongly eusocial and southern populations are less eusocial (although tropical populations of *H. ligatus* may actually be *H. poeyi* Lepeletier (Carman and Packer 1996; Danforth et al. 1998), the pattern of decreasing eusociality in milder environments still holds for definite *H. ligatus*). In *H. ligatus*, variation in

the strength of eusocial colony organization has been observed even within a single population in southern Ontario, Canada, where cool wet weather leads to stronger eusociality and warmer weather leads to weaker eusociality (Richards and Packer 1995, 1996; Richards et al. 1995). It is very interesting that quite the opposite pattern is observed in the socially polymorphic species *H. rubicundus* and *L. calceatum*, which are truly solitary in the harsher conditions at high altitudes, where the growing season is very short, and eusocial in the milder conditions at low altitudes, where the summer is long enough for raising two broods (Sakagami and Munakata 1972; Eickwort et al. 1996). This implies that there are two distinct geographical patterns of social variation: obligately eusocial species are more strongly social under harsh conditions and facultatively eusocial species are less social.

Given the observed differences in colony social structure, the fitness consequences of altruism and non-altruism for workers are likely to be quite different in northern and southern *L. malachurum* populations. It is likely that across *L. malachurum*'s range, colonies are established by single foundresses. Thus, in northern populations, where queens monopolize oviposition, the inclusive fitness payoff of strongly altruistic behaviour is predicted to be very high, because workers will usually be raising full sisters and either brothers or a mixture of sons, nephews, and brothers. Furthermore, the fitness costs of worker egg-laying are probably also high: northern queens are likely more effective than southern queens at controlling worker behaviour because they will have fewer workers to contend with (e.g., Kukuk and May 1991). This means that northern workers may have less opportunity to lay eggs, and could incur significant interference or even damage should they attempt to. In southern populations, the fitness benefits of altruism may be significantly lower, especially for late workers, because altruistic workers will often be raising nieces and nephews. Moreover, the costs of egg laying may be lower, owing to less interference from the queen. Enhanced opportunities for raising daughters and sons also mean a decline in the relative benefits of helping versus reproducing. Even from the perspective of the queen, given that her life-span may be short, a better strategy may very well be for southern workers to take over reproductive brood oviposition in an expanding nest rather than for queens to monopolize oviposition of a small reproductive brood earlier in the summer.

### Reproductive castes in socially labile sweat bees

In *L. malachurum* nesting at ANM, as in *H. ligatus* nesting near Toronto (Richards et al. 1995), it is clear that some workers are reproductives in the full sense of the word: they produce eggs that develop into males or gynes, and potentially have very high rates of reproduction. Demographically, reproductive workers fill the same role as summer females of a bivoltine, solitary species, because they produce the foundress's grandchildren. Reproductive workers are still clearly members of the worker caste: they are much smaller than queens, are not produced in the final brood, are unlikely to have abundant fat bodies, are unlikely to hibernate through the winter, and have opportunities for providing help to nestmates. The term gyne is then reserved for females that do overwinter preparatory to becoming foundresses the following spring; that is, females that overwinter before reproduc-

ing. These females tend to be large and have abundant fat stores (Richards and Packer 1994).

Although there are important exceptions to these general descriptions of castes in social sweat bees, these exceptions are interpretable in the social context of particular species. Knerer (1992) noted the occasional existence of worker-sized *L. malachurum* queens in southern Spain, and interpreted this as evidence that gyne eggs were occasionally mistakenly laid on male-destined pollen masses. However, some newly emerged worker-sized females at ANM had abundant fat bodies (see above), so another possibility is that sometimes *L. malachurum* workers overwinter and become foundresses, as has been observed in *H. rubicundus* (Yanega 1989). In *H. ligatus*, small females destined to become workers do not have fat stores, although large females destined to become gynes do (Richards and Packer 1994), but occasionally *H. ligatus* workers overwinter and become foundresses the following spring. Nevertheless, hibernation does not define a foundress: in the perennial, strongly eusocial species *L. marginatum* Brullé, both workers and gynes hibernate (Plateaux-Quénu 1960), while *H. ligatus* gynes can become subordinates in multifoundress nest associations, essentially becoming overwintered workers (Richards and Packer 1994, 1998).

The extreme plasticity of caste-associated behaviour in social sweat bees is sometimes regarded as a problem because it makes strict distinctions between the queen and worker castes difficult to use, except in very strongly social species (Crespi and Yanega 1995; Sherman et al. 1995). And yet defining strict distinctions between reproductive castes is really secondary to the main issue in social insect biology, which is to determine the evolutionary and ecological factors that correlate with the expression of altruism by individuals. It is the degree to which altruism is expressed that defines colony social organization, therefore both altruism and eusociality are continuous variables that will always resist strict, qualitative definitions. An approach that is more helpful than forcing definitions onto labile behaviour and colony social expression is to describe different types of colony social organization in terms of critical variables that summarize the expression and consequences of helpful versus selfish behaviour in colonies. This will be particularly important in species such as *L. malachurum*, in which summer females exhibit a continuum of behaviour, from classic altruism to partial altruism combined with selfishness to being as selfish as queens and even benefiting from the cooperative behaviour of their more altruistic nestmates.

### Acknowledgements

I am most grateful to Eric von Wettberg and Dimitri Skandalis for field assistance under hot, trying conditions; to Laurence Packer for his patience during species identifications, to Michael Engel, Laurence Packer, Laura Wyman, and two anonymous reviewers for their comments on the manuscript; and especially for the generosity of the National Geographic Society, which provided funding for this study.

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