

Research article

Social polymorphism in the sweat bee *Lasioglossum (Evylaeus) baleicum* (Cockerell) (Hymenoptera, Halictidae) in Hokkaido, northern Japan

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Summary. The life cycle and social behaviour of the sweat bee *Lasioglossum (Evylaeus) baleicum* (Cockerell) was investigated in two geographically separate populations in Hokkaido, northern Japan. Colonies were excavated throughout the brood rearing season from an aggregation in Nishioka forest park, Sapporo, and near Kawakita in eastern Hokkaido during 2000 and 2001. The Nishioka population produced two discrete broods during the year and was weakly eusocial; 57% of workers were mated and 28% exhibited some ovarian development, 12–16% of the first brood was male, and workers were on average 4.5% smaller than their respective queen. In contrast, the population at Kawakita was solitary, and produced a single brood per year with an unbiased sex ratio. In addition however, there were some solitary colonies in the Nishioka population and evidence of a partial second brood in some colonies at Kawakita, suggesting differences between the populations are not fixed and that this species is truly socially polymorphic. *L. (E.) baleicum* is a member of the *fulvicorne* species group, which includes other examples of social polymorphic species as well as solitary and eusocial species, though this is the only species of this group so far known to exhibit a solitary/non-delayed eusocial polymorphism. Recent studies suggest that social polymorphism has both genetic and environmental influences, raising questions as to the relative import of each.

Key words: Halictidae, social polymorphism, *Lasioglossum*, life cycle.

Introduction

Halictine bees are considered useful for the investigation of hypotheses regarding the origins of eusociality because they exhibit a wide range of social behaviours that vary both inter- and intraspecifically (review in Packer, 1997; Wcislo and

Danforth, 1997). Eusociality has arisen three times in halictid bees, with up to twelve reversions to solitary behaviour and sociality can exhibit a wide diversity within closely related species (Packer, 1991, 1997; Danforth, 2002). Eusociality is predominantly facultative (except at least in *Lasioglossum (Evylaeus) malachurum* Richards, 2000; Paxton et al., 2002) and may occur as delayed eusociality (where matrilineal associations arise after a period of overwintering, usually in singly-brooded populations) or non-delayed eusociality (where mother-daughter associations arise in the same year), and communal and semisocial species are known (Packer, 1993; Kukuk and Sage, 1994; Danforth, 2002). Some otherwise eusocial species are restricted to solitary behaviour at high altitudes (e.g.: *Halictus rubicundus*, Eickwort et al., 1996; *Lasioglossum (Evylaeus) calceatum*, Sakagami and Munakata, 1972) or latitudes (*L. (E.) apristum*, Miyanaga et al., 1999). Social behaviour may also exhibit variation within a population, at a given time (*Augochlorella striata* Packer, 1990) or over time (*H. rubicundus*, Yanega, 1989; *H. ligatus*, Richards and Packer, 1995).

Recently, the growing database of biological information and modern molecular techniques have permitted increasingly extensive phylogenetic analyses that have challenged the view that eusociality is an evolutionary end-point, and indicated that reversions to solitary behaviour and/or social polymorphism may be more common than previously thought (Wcislo and Danforth, 1997; Danforth, 2002). However, while such analyses are certainly heuristic in terms of identifying areas of evolutionary interest (Packer, 1997), the use of phylogenetics to map the pattern of social evolution can be complicated by a high degree of interspecific social variation, the often cryptic presence of intraspecific social polymorphism, and the possibility of frequent evolutionary reversals (Packer, 1997; Wcislo and Danforth, 1997). While some species are almost certainly obligately solitary, it remains unclear in many other cases whether the observed behaviour at a given locality and time is representative of the species as

a whole (Wcislo, 1997; Wcislo and Danforth, 1997). Furthermore, if species are socially polymorphic (i.e. differ in social behaviour between populations), it is often unclear whether these differences are environmentally mediated or genetically fixed. Analyses of socially polymorphic species are thus of particular interest, in terms of clarifying the pervasiveness of this trait and its status in evolutionary terms, to elucidate the relative import of environmental and genetic influences on the evolution and maintenance of social behaviour, and to investigate the polarity of behavioural change from which it is derived. Only detailed field and lab studies of individual species can debunk any verisimilitude that may reside in social classifications based on less comprehensive analyses, and potentially reveal behaviours that may otherwise be rare or cryptic in nature.

Most halictine species remain unstudied behaviourally or defined by limited data, and new information can alter the interpretation of evolutionary patterns (e.g. Packer, 1991, 1997). Thus, further fleshing out of the database of biological information is highly desirable. The subgenus *Evylaeus* contains examples of solitary, eusocial and socially polymorphic species (Packer, 1997; Wcislo and Danforth, 1997), making it a worthy topic of further focus. Phylogenetic evidence indicates a eusocial ancestor for *Evylaeus* with multiple reversions to solitary behaviour (Packer, 1991; Danforth, 2002), though there remains a paucity of data on most species. Here, we provide the first detailed analysis of the life cycle and social behaviour of *L. (E.) baleicum* (Cockerell), a member of the *fulvicorne* species group (Sakagami et al., 1994; O. Tadauchi, pers. com.), and present evidence for social polymorphism both within and between two populations of this species.

Materials and methods

Two aggregations of *Lasioglossum (Evylaeus) baleicum* were studied in Hokkaido, Japan during 2000 and 2001, at a campsite in Nishioka forest park, in southern Sapporo (150 m, 141°35'E, 43°00'N) and on the side of a minor road near Kawakita town, eastern Hokkaido (alt. 280 m, 144°55'E, 43°42'N; hereafter termed Nishioka and Kawakita sites, respectively). Identification of specimens was confirmed by O. Tadauchi (Kyushu University), and a preliminary comparison of 475 bp of *Ef-1 α* nuclear DNA, that indicated sequence fragments were identical. Colonies at Nishioka occupied a narrow (approx. 2 m high and 15 m long) earth bank inclined at approximately 30 degrees, bordering a small campsite in a large forest park consisting predominantly of White Birch (*Betula platyphylla japonica*), Oak (*Quercus mongolica*) and Willow (*Salix* sp.). The soil was light clay, which was generally moist and almost completely free of rocks and roots. Throughout the season, the site was almost always shaded because of the northern aspect of the bank and adjacent tree line. The Kawakita aggregation was similarly surrounded by extensive White Birch and Oak forest. Nests were located in a small (approximately 4 m high and 6 m across) bank of soil composition similar to that at Nishioka, but differing in having a less shaded southerly aspect. Although both sites were at least superficially similar with respect to floral and soil characteristics, the climate of eastern Hokkaido (Kawakita) is considerably colder than that of Sapporo (Fig. 1). Temperatures during the study years were not considerably different from historical averages. Temperatures are cooler year-round in Kawakita and, in particular, are approximately five degrees colder in Kawakita than in Nishioka in late spring and early summer.

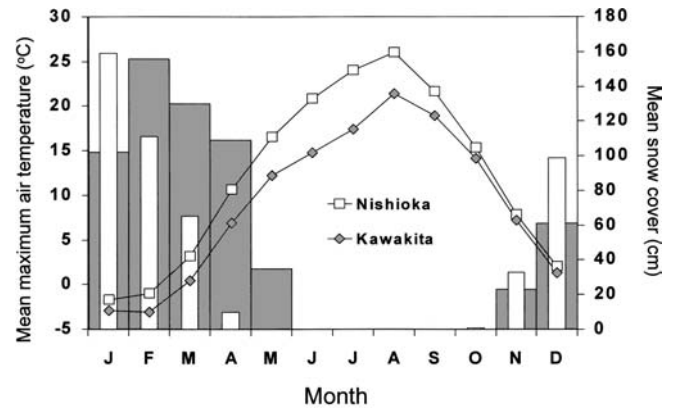


Figure 1. Mean monthly temperature (lines) and snow cover (bars) throughout the year at Nishioka (white) and Kawakita (shaded). Data are compiled from historical climate records from weather stations at Sapporo (Nishioka) and Kawakita town (Kawakita), respectively

Furthermore, snow cover at Kawakita is protracted, likely delaying the initiation of bee activity in spring.

Nests were excavated at irregular intervals during 2000 and 2001 at both localities (see Fig. 2); data for Nishioka are more extensive for 2001 when more frequent excavations were possible, whereas data are limited for both years for Kawakita as the site was not discovered until the summer of 2000, comprised fewer nests, and had limited access in spring because of snow. Excavations were performed early in the morning or when nests were closed during inactive periods when it was likely all occupants were inside. The surface soil was scraped away gently to reveal nest burrows, which were then excavated by carefully following tunnels. The depth to the deepest part of the nest and the middle of cell clusters was recorded. All adults and brood were removed and placed in Kahle's solution for later dissection. Dissections were performed to determine the reproductive condition of females; ovarian development was recorded as the mean length of the three largest oocytes and insemination status was inferred from the opacity of spermathecae. Mandibular wear was scored from 1 (no wear) to 5 (worn past base of preapical tooth; Sakagami and Hayashida, 1958). Wing wear was measured as the sum of the number of nicks on both wings; totally worn wing margins were scored as having a wing wear of 10. Overwintered and newly eclosed females could be distinguished based on wing and mandibular condition and colouration. Voucher specimens of *L. (E.) baleicum* collected during this study have been lodged in the Hokkaido University Museum.

Results

Nest architecture

Nest architecture was the same at both localities and somewhat typical of many *Evylaeus* species. Nests consisted of a single unbranched burrow that was usually vertical, but occasionally slanted or curved, and were usually closed out of foraging times. Brood were reared in individual, horizontally aligned cells arranged in a stacked cluster that was separated from the surrounding soil by a narrow space, and supported by several earthen struts. Brood clusters occupied a central position within the burrow axis, and clusters were generally positioned approximately midway or toward the lower portion of the burrow (see Packer et al., 1989a for dia-

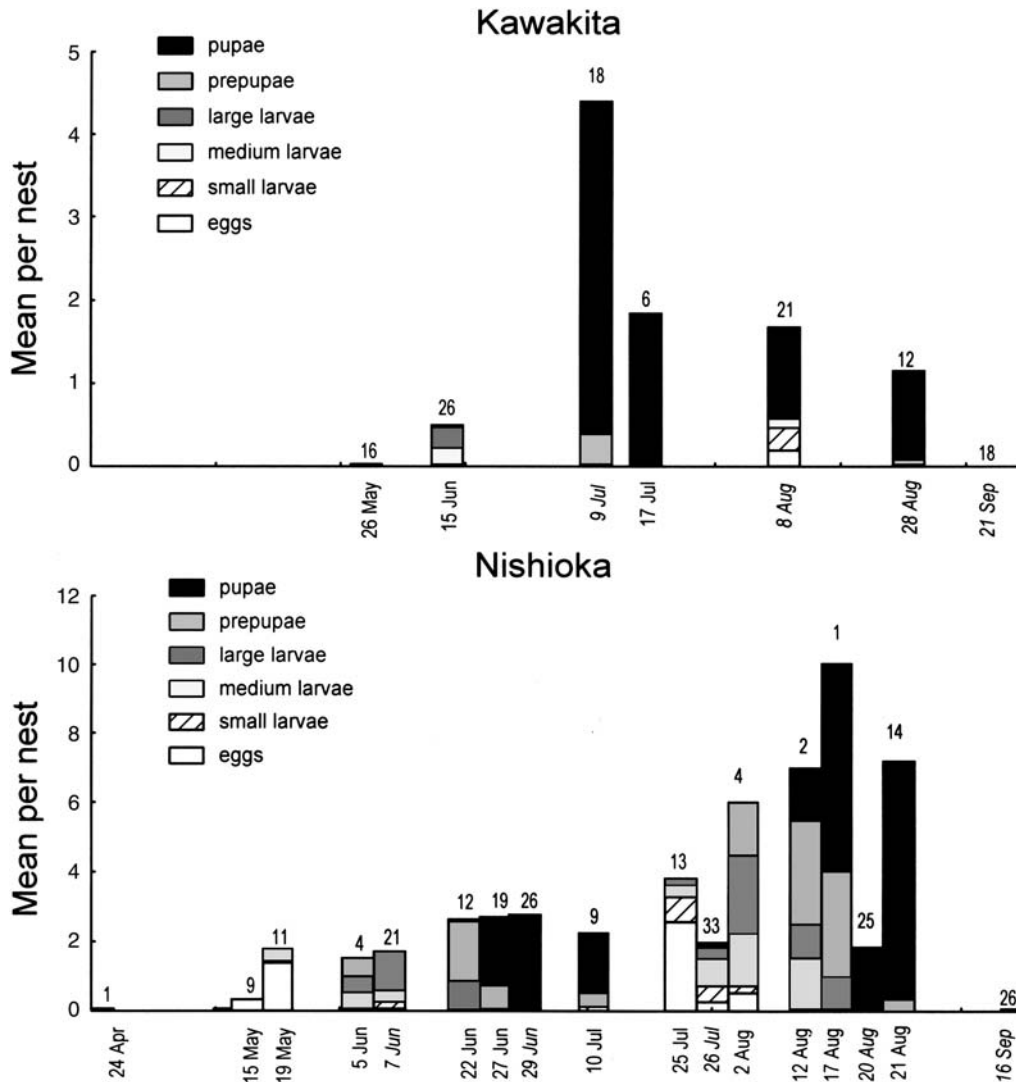


Figure 2. Colony phenology revealed by bar graphs of mean number of each brood stage per nest at Kawakita (above) and Nishioka (below), and for both years (2001 sample dates are italicised), indicating two discrete brood rearing periods at Nishioka. Sample size (number of nests excavated) is indicated above each bar

Table 1. Nest depths and cell depths during provisioning of the first and second brood for Nishioka and the first and only brood at Kawakita. The number of nests is indicated in parenthesis and differs for nest length and cell depth as some measures were ambiguous or absent and were not included

Site and Brood number	Year	Nest depth (mm) mean ± SE	Cell depth (mm) mean ± SE
Nishioka 1 st brood	2000	76.8 ± 28.3 (33)	28.7 ± 6.3 (24)
	2001	59.4 ± 20.0 (33)	25.7 ± 9.1 (30)
Nishoka 2 nd brood	2000	121.6 ± 32.9 (29)	46.1 ± 19.4 (18)
	2001	75.0 ± 20.7 (21)	48.3 ± 15.3 (21)
Kawakita	2000	58.9 ± 5.81 (13)	30.6 ± 2.0 (18)
	2001	44.59 ± 6.77 (32)	51.1 ± 4.3 (14)

grams of similar nests of *L. (E.) comagenense*). Nest depths are summarised in Table 1, for during the provisioning of first and second broods at Nishioka and for the first and only brood (see below) at Kawakita. Data indicate variation in nest depths between years and sites but exhibit no distinct trends.

Life cycle and sociality at Kawakita

At Kawakita, nests were initiated in late May or early June after the snow melt (see Fig. 1). Nests generally contained a single female during spring, but one colony excavated on 15 June 2001 contained two females, both of which had some mandibular wear, but little or no ovarian development. There was no evidence of extended survivorship (females living longer than one year) at Kawakita, though data are limited as the site was not accessible early in the season. Brood census data for all collections are summarised in Figure 2, which indicates a period of brood laying in early June, followed by pupation in July, with the first adults eclosing before August 8. A crude estimate of egg to adult time of approximately 32–75 days can be made based on the collection data, from the laying of the first brood between 26 May and 15 June sample to the first presence of new adults between 17 July and 8 August. Figure 2 also suggests a second period of egg laying in the 8 August sample. However, only 10 of 18 nests contained brood, and only 4 of these nests contained young brood (non-pupae), with a further 3 nests each containing a single pollen ball. All colonies with small brood or pollen balls contained evidence of a previous brood in the form of refilled or empty brood cells. In addition, only 7 colonies contained females with some ovarian development (defined here as mean ovary size of > 0.1 mm); 2 of these had small brood and 2 contained a pollen ball. Thus, 11 of 21 colonies contained no evidence of a second brood (in the form of young brood, pollen balls or females with developed ovaries), suggesting the majority are singly brooded. Because of the late stage of the season and the immature stage of even the most developed brood (a medium larva), it is unclear whether any colonies could have successfully reared a second brood before winter. Furthermore, during the mid-summer of 2001 (July 17) there was no evidence for any ovarian development or brood laying.

In the August 8 colonies with some evidence of a second brood ($n = 10$), 9 colonies contained 2 females and a single nest had 4 females. Of these colonies, 7 contained only new unworn females with undeveloped ovaries; one of these had eggs and a small larva, and a second had a pollen ball, while the remaining 5 had no brood. These data indicate at least one example of potential sib provisioning in a subsequently orphaned colony. The colony with 4 females contained one old female with developed ovaries and 3 newly eclosed females but no brood. Of the remaining 2 colonies, one contained an old female with developed ovaries and a newly eclosed female and some brood (a small and medium larva and some pollen balls), whereas the final nest contained an old female with undeveloped ovaries, a new female with

enlarged ovaries and a pollen ball. These data reveal a potential for eusociality in a small number of nests, though once again it is unclear how functional this would be given probable time constraints on rearing this brood. The frequency distribution of mean brood per nest for 2000 and 2001 is shown in Figure 3. The brood was significantly larger in 2000 (using Log of total brood per nest: $t_{26} = 2.78$, $P = 0.01$). The mean numerical sex ratio (proportion of male brood in nests where all brood could be sexed) of the Kawakita first brood is shown in Figure 4, which indicates that sex ratio differs between years, but is unbiased in the larger sample in 2000 (single sample t-test with test value of 0.5: $t_{12} = 0.24$, $P = 0.812$) and does not have the high female bias typical of worker broods in eusocial populations.

Life cycle and sociality at Nishioka

The relatively early snow melt at Nishioka (see Fig. 1) permitted nest founding in late April or early May. Spring colonies contained a single female ($n = 103$), indicating that the majority of colonies were singly founded. There was one exception to this: a single nest from the 2001 sample (June 22) contained 2 females, both of which had moderate wing and mandibular wear, some ovarian development and were inseminated, suggesting a communal or quasisocial assemblage (i.e. females from a single generation, with no reproductive skew and with or without alloparental care respectively). Two females excavated from separate nests on May 19, 2001, possessed the maximum degree of mandibular wear, high wing wear, well developed ovaries and were inseminated, suggesting they were probably second year queens. No other females at this time showed such signs of previous activity.

Figure 2 illustrates the mean number of various brood per nest for each excavation in 2000 and 2001, indicating two distinct periods of brood production. The first began in May, with pupation in late June and adult eclosion in July, and the second began in mid to late July with pupation and adult eclosion in late August. In 2001, the first adults eclosed between the 19–24 July samples for the first brood and August 24 (reared in the lab) for the second brood. Thus, based on the nest census data, an estimate of egg to adult time can be inferred as approximately 65–70 days for the first brood and 36 days for the second brood.

During the laying of the second brood (July 26 in 2000, July 25 and August 2 in 2001), 24 nests contained a single female (total number of nests = 50), 5 of which contained no brood. In seven cases the worn female had undeveloped ovaries (including 3 with no brood suggesting they were singly brooded). The remaining single female colonies all contained a mated queen with enlarged ovaries. There were 26 multifemale colonies, most containing 2 females, though four contained 3 females and 1 contained 7 females. Queens (overwintered females) and workers (newly eclosed females) could be distinguished by colouration and condition of the wings and mandibles. Two of 50 colonies contained 2 queens, both had a single worker, and 4 colonies contained no queen

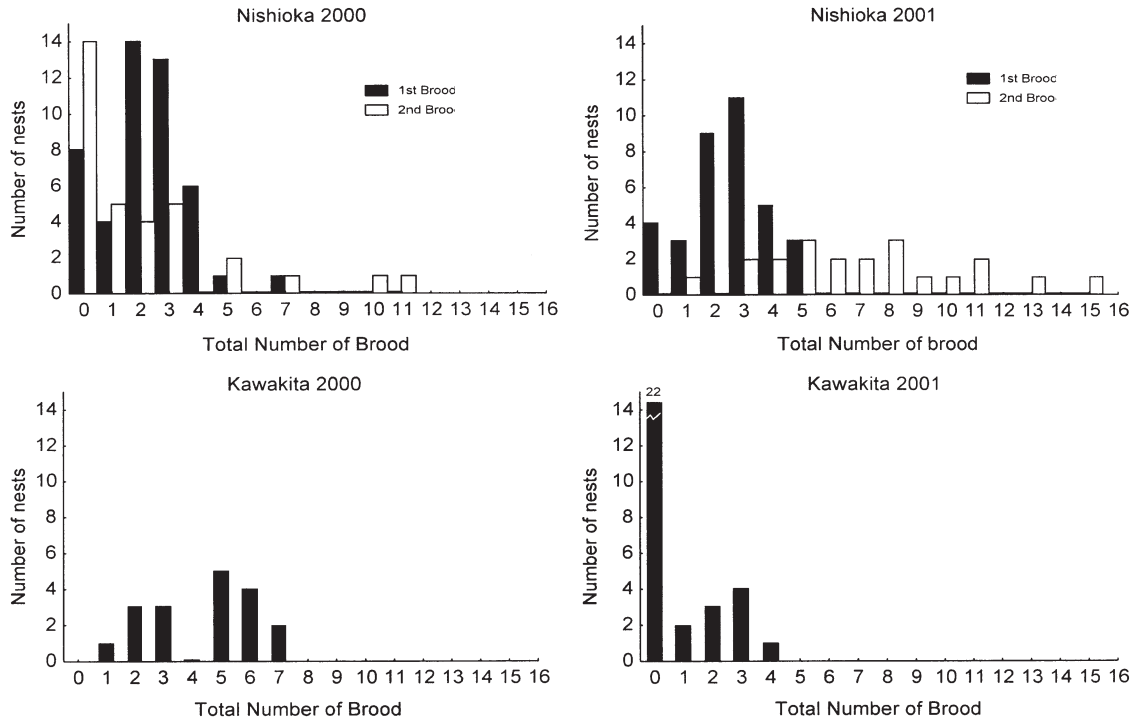


Figure 3. Histogram of number of brood per nest for the spring brood (shaded bars) and summer brood (white bars). Sample dates included are; for Nishioka spring brood: 7 and 29 June 2000, and 5, 22 and 27 June 2001; summer brood: 26 July 2000 and 2, 12, 17 and 21 August 2001; Kawakita spring brood: 9 July 2000 and 15 June and 17 July 2001)

but had 2 workers. The mean number of workers per nest during provisioning of the second brood was 1.7 ± 0.2 ($n = 26$; mode = 1), which was markedly lower than the number of potential workers from the first brood (approximately 2.4 in both years, based on the number of female pupae). This may suggest mortality or dispersal of some first brood females. Figure 5 summarises the relationship between ovary size and head width for queens and workers in multifemale nests, indicating substantial overlap in morphology and reproductive capability. Workers were inseminated in 56.5% of cases where status could be determined ($n = 23$), with ovaries on average 35.8% (range: 6–126%) the size of those of the respective queen, and 28% of workers had some ovarian development (> 0.1 mm). The ovary size of workers was not statistically related to insemination status ($t_{21} = -0.65$, $P = 0.52$) or head width (Pearson correlation: $r = 0.18$, $P = 0.24$, $n = 44$), but was significantly smaller than queens overall ($U = 153.5$, $z = -5.25$, $P < 0.001$). Workers were on average 4.5% smaller than their respective queen ($n = 22$ colonies), and were significantly smaller than queens overall ($t_{67} = -3.55$, $P = 0.001$).

Figure 3 summarises the number of brood per nest for each year and brood. The second brood was significantly larger than the first in 2001 (Mann-Whitney $U = 72$, $z = -4.8$, $P < 0.001$), whereas they did not differ in 2000. However, the size of the 2000 second brood is likely an underestimate as eggs were probably still being laid, and the second brood in 2001 was significantly larger than in 2000 ($t_{38} = -3.51$, $P = 0.001$), whereas the first brood did not differ between years

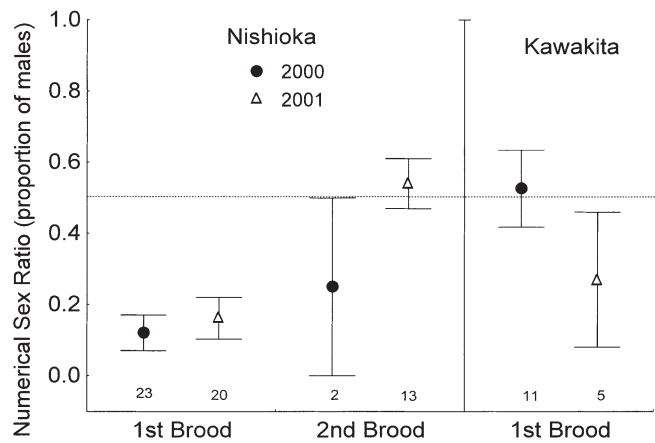


Figure 4. Mean sex ratio (proportion of males) \pm standard error for colonies containing only sexable brood (pupae), indicating female biased spring brood at Nishioka but not at Kawakita. Samples for each brood are the same as listed for Figure 3

($t_{66} = -0.66$, $P = 0.51$). The large proportion of colonies that contained no brood during the 2000 second brood provisioning phase (42%; Fig. 3) may further indicate that not all colonies produced a second brood. Furthermore, only three colonies without brood in 2000 ($n = 14$) contained a female with some ovarian development. In contrast, all 2001 colonies contained some brood during the second brood provisioning phase. Nine nests (42%) excavated on 26 July 2000

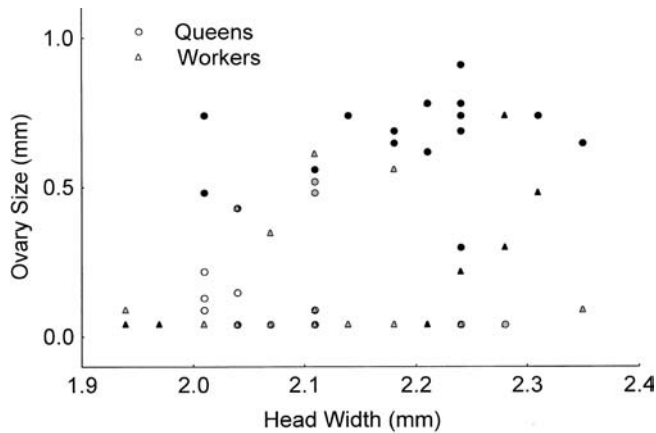


Figure 5. Scattergram of headwidth (mm) versus mean ovary size (mm) for queens and workers in multifemale nests from Nishioka from 25 July 2001, 26 July 2000 and 2 August 2001. Circles indicate queens and triangles indicate workers. Insemination status is designated by black (inseminated), white (uninseminated) or grey (unknown)

contained no old female (mandibular wear < 3) and were presumably orphaned; 57% of orphaned nests contained brood, whereas 84% of nests containing a queen had brood, suggesting that orphaning may increase the likelihood that a second brood is not produced.

The numerical sex ratio (proportion of males) for colonies for which the sex of all brood could be determined is shown in Figure 4, which indicates that the first brood was strongly female biased in both years (single sample t-test with test value of 0.5: $t_{22} = -7.03$, $P < 0.001$ for 2000 and $t_{19} = -5.49$, $P < 0.001$ for 2001). Data for the second brood in 2000 are few, but the sex ratio in 2001 is clearly unbiased ($t_{12} = 0.55$, $P = 0.59$).

Discussion

The population of *Lasioglossum (Evyllaes) baleicum* at Nishioka in Hokkaido exhibits a two-brooded life cycle, a low level of queen-worker size dimorphism (4.5%), a moderate proportion of males in the first brood (12–16%), a small number of workers per nest (mode = 1), and considerable worker mating (57%) and ovarian development (36%); all consistent with a weak form of eusociality (Packer and Knerer, 1985). In contrast, the predominant single brood and unbiased sex ratio at Kawakita are characteristic of a solitary population. The infrequent sampling at Kawakita permits only a crude estimate of the egg to adult time at the eastern locality (32–75 days), which approximates at its maximum that of Nishioka (65–70 days), despite the lower temperatures at Kawakita, and the clear difference between development time of spring and summer broods at Nishioka. Hence, the limitation of the majority of colonies to a single brood at Kawakita would seem to be derived from the relatively late start and early finish to the season in eastern Hokkaido, and in particular from the delayed snow melt; a factor correlated with sociality in *H. rubicundus* (Soucy and Danforth, 2002).

However, in addition to the social variation between localities, there is some suggestion of social polymorphism within each site: some colonies at Nishioka in 2000 produced no second brood, and females did not have enlarged ovaries despite the continued presence of the queen in at least some nests; and some colonies at Kawakita contained evidence of a second brood and opportunities for sib rearing. The former suggests that singly brooded colonies at Nishioka were truly solitary rather than nests that had failed to achieve eusociality, and that solitary nests may be contemporaneous with eusocial colonies in this population. At Kawakita it is not clear if a second brood could be successfully reared in all years, but it would seem that females are probably capable of laying a second brood if conditions are favourable, and that opportunities for sib rearing do arise. In addition, the possibility of delayed eusociality at Kawakita cannot be ruled out; although some evidence for extended survivorship was found, our small sample sizes are far from conclusive. The variation in nest depths and brood success between years may be some indication of environmentally mediated variation in behaviour, though climate data did not indicate any marked difference in temperature between years of this study. Hence, *L. (E.) baleicum* would appear to be truly socially polymorphic, though lab experiments are needed to verify the behavioural potential of bees from each population in reversed environmental conditions.

Packer (1991) suggested that limited queen-worker size dimorphism and totipotency of workers in halictine bees may be important for colony survival of populations in environments where sufficient time for the provisioning of a second brood is not guaranteed. Many socially polymorphic species are characterised by these traits (Packer and Knerer, 1985; Wcislo, 1997; Wcislo and Danforth, 1997). The paucity of data on many species (Packer, 1997; Wcislo and Danforth, 1997) may belie the prevalence of social polymorphism, and more species may demonstrate a wider behavioural repertoire after detailed study. An enduring problem here is that social polymorphism is often difficult to discern, particularly with respect to delayed eusociality (Packer, 1997), and it is often difficult to divorce fixed (genetic) differences from true behavioural polymorphism (Wcislo and Danforth, 1997). Lab studies in controlled conditions and/or translocation experiments are a means to elucidate social polymorphic behaviour, and such studies are gradually gaining favour. Cronin (2001) demonstrated that translocation of two species of Australian allodapine bee between different habitats led to opportunities for the expression of different forms of social behaviour. In contrast, Maeta et al. (1993) showed that whereas eusociality was compatible with solitary behaviour in some species of *Ceratina*, non-delayed eusociality could not be induced in other closely related species without simulated diapause and treatment with a hormone analogue.

Intraspecific social polymorphism in halictines, commonly manifested as a solitary/eusocial polymorphism, is often ascribed to interpopulation differences in environmental influences, such as climate induced limitation on the number of broods in a season. Climatic differences may be derived from altitudinal (e.g.: *L. (E.) calceatum* and *L. (E.) rubicun-*

du; Sakagami and Munakata, 1972; Eickwort et al., 1996) or geographic (e.g.: *L. (E.) apristum*, *L. (E.) comagenense* and *L. (E.) fratellum*) differences between populations of a given species. Multiple social forms may also be present concurrently (*Augochlorella striata*; Packer, 1990), or occur in different seasons (eg: *Halictus (Halictus) rubicundus*; Yanega, 1989; *H. (H.) ligatus*; Richards and Packer, 1995) in the same population. Furthermore, lab studies (Miyanaga et al., 1998, 2000) have demonstrated that *Lasioglossum (Lasioglossum) mutillum* and *L. (L.) scitulum*, usually considered solitary, may exhibit social behaviour in an artificial environment, indicating a retention of plasticity that may not frequently be expressed, and thus observed, in nature. Other species listed as socially polymorphic include *Halictus (Seladonia) confusus*, *H. (S.) tumulorum*, *L. (E.) fratellum*, *L. (Dialictus) problematicum*, *H. (H.) sexcinctus* and *L. (E.) boreale* (see Packer, 1997 and Danforth, 2002 and references therein).

Solitary behaviour might in many cases be facultative, which could explain numerous apparently secondarily solitary species (Packer, 1991; Danforth et al., 2003). Nonetheless, some secondarily solitary species are almost certainly obligately so, and solitary behaviour in behaviourally polymorphic species can be viewed as a bet-hedging strategy (Danforth et al., 2003). Danforth et al. (2003) conclude that the pattern of social evolution inferred in a phylogenetic analysis of *Lasioglossum* species differed significantly from random, suggesting that sociality in the genus has a phylogenetic component despite significant evidence for the impact of environmental cues on the expression of social behaviour. Some studies have indicated that there is some genetic component to the expression of social behaviour; (Plateaux-Quénu et al., 2000; though genetic and phylogenetic analyses suggest these populations may represent separate species; Packer and Taylor, 1997; Danforth et al., 2003). Soucy and Danforth (2002), report that eusocial and solitary populations of *L. (E.) rubicundus* in North America belonged to different lineages, as determined by phylogenetic analyses of mitochondrial DNA. However, sociality was also correlated with at least one environmental variable, indicating some interaction between genetic and environmental factors in influencing the behaviour expressed, and supporting the concept of 'causal mosaics' (Crespi, 1996) as semi-cryptic determining mechanisms of sociality.

L. (E.) baleicum is a member of the *fulvicorne* group of carinate *Evyllaesus* (Sakagami et al., 1994; Danforth pers. comm.), other members of which exhibit a variety of social forms including solitary behaviour (*L. (E.) quebecensis*; Packer and Knerer, 1985), eusociality (*L. (E.) subtropicum*; Sakagami et al., 1994), and social polymorphism (*L. (E.) comagenense*, *L. (E.) fratellum*; Packer et al., 1989b; Batra, 1990; Heide, 1992; Field, 1996). However, whereas other socially polymorphic species of this group may exhibit eusociality only as delayed eusociality (i.e. where matrilineal associations arise after a period of overwintering), *L. (E.) baleicum* is the only member known to exhibit a social polymorphism incorporating solitary behaviour and non-delayed eusociality (where matrilineal associations arise during the same season), as seen in some other *Evyllaesus* (e.g.: *L. (E.)*

calceatum; Sakagami and Munakata, 1972; *L. (E.) apristum*; Miyanaga et al., 1999). Most species of this group occupy high latitude regions and/or a large altitudinal range, that presumably prohibit a two brooded life cycle at the cooler extreme of the range; the only known sub-tropical species, *L. (E.) subtropicum*, is eusocial in southern-most Japan and is closely allied with *L. (E.) baleicum* (Sakagami et al., 1994). The Nishioka and Kawakita populations of *L. (E.) baleicum* in Hokkaido appear to lie on separate sides of a borderline with respect to the capacity to support eusociality, such that both populations contain some colonies that exhibit behaviour characteristic of the other population.

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