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Phenology and social behaviour of the endemic Sable Island Sweat Bee, *Lasioglossum sablense*

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Abstract. *Lasioglossum (Dialictus) sablense* Gibbs, 2010 (Hymenoptera: Halictidae) is endemic to Sable Island, an isolated sandbar located about 160 km east of Nova Scotia, Canada. *Lasioglossum sablense* is currently listed as Threatened due to its restricted geographic distribution, and promoting its conservation requires detailed information about nesting phenology, behaviour, and other life history details. We combined measurements of body size, wear, and ovarian status from adult females collected from flowers in 2016 and 2017 with measurements and behavioural observations of foragers collected at the Sable Island Station in 2019 and 2022, to compile a preliminary description of flight phenology and social behaviour. Like many members of its genus, *L. sablense* exhibited a diphasic life history. Phase 1 began when large, fertilized adult females emerged from hibernation, began nest and brood cell construction, and foraged to provision Brood 1, which comprised both daughters and sons. Most nests initiated during Phase 1 reactivated during Phase 2, with adult Brood 1 daughters foraging to provision Brood 2. Observations of bees at nest entrances demonstrated that some reactivated nests contained multiple adult females. Phase 1 foragers were larger, less worn, and had marginally higher levels of ovarian development than Phase 2 foragers. Five large females collected during Phase 2 had high levels of wear, suggesting they were long-lived Phase 1 foundresses that resumed foraging during Phase 2. Taken together, these observations suggest a mix of univoltine (single generation) and bivoltine (two generation) life histories, as well as a mix of solitary and social behaviour in *L. sablense*.

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INTRODUCTION

Sable Island is a partially vegetated sandbar that sits in the Atlantic Ocean about 160 km east of the Nova Scotia mainland in eastern North America. Approximately 40 km long, with a maximum width of 1.3 km, and comprising a total area of 2,700 ha (~27 sq km), the island's dimensions vary as its shoreline is subjected to seasonal and long-term changes in patterns of sand erosion and deposition (Eamer *et al.*, 2022). Geologically, Sable Island is an emergent sandbar that became clear of ice as glaciers retreated after the Last Glacial Maximum, about 12,000 to 13,000 years ago (Stea *et al.*, 1998). Although the island is described as having an impoverished flora and fauna, a number of endemic and geographically restricted plants and animals have been recorded (Howden *et al.*, 1970; Catling *et al.*, 1984, 2009; Lucas & Brunelle, 2016). Five species of bees (Hymenoptera, Anthophila) are found on the island, including two, closely related sweat bee species, *Lasioglossum (Dialictus) sablense* Gibbs (Halictidae), the endemic Sable Island Sweat Bee, and *L. (D.) novascotiae* (Mitchell), the Nova Scotia Sweat Bee, which despite its name has a wide range across Canada and eastern North America (Gibbs, 2010). In 2014, *L. sablense* was assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada due to its restricted geographic distribution (COSEWIC, 2014), and in 2018 it was listed under the Species at Risk Act (SARA; Parks Canada 2020); it was also listed as Threatened under the Nova Scotia Endangered Species Act in 2017 (https://nslegislature.ca/legc/bills/57th_1st/3rd_read/b065.htm).

In this paper we provide the first formal study of reproductive phenology and social behaviour of *L. sablense* (Fig. 1), combining behavioural observations of bees at their nests in 2019 and 2022, with social trait information (body size and reproductive status) from adult female bees collected in 2016 and 2017, prior to SARA listing. The objective of this study was to fill major gaps in knowledge about the species' reproductive biology, which will enhance monitoring and management of this protected species. In addition, phenological and behavioural data can be used in comparative studies of social evolution in the subgenus *L. (Dialictus)*, a group in which sociality is clearly an evolutionarily labile trait (Breed, 1976; Wcislo *et al.*, 1993; Awde & Richards, 2018; Corbin *et al.*, 2021).

MATERIAL AND METHODS

Field Sites

There has been a continuous human presence on Sable Island since 1801, and the Sable Island Station was built in 1943. Roughly 50% of the island's land surface is vegetated, and about 185 plant species occur in distinctive vegetation communities comprised of herbs and low shrubs (Colville *et al.*, 2016). Approximately 20% of plant species are introductions and grow mainly where human activities and structures provide suitable habitat.

Four areas have been identified in the grounds of the Sable Island Station as critical nesting habitat for *L. sablense* (Parks Canada 2020; map at https://wildlife-species.az.ec.gc.ca/species-risk-registry/virtual_sara/files//plans/RsAp-HalictaSableSweatBee-v00-2020Mar-Eng1.pdf page 17). All four areas have been subject to concentrated human activity for decades, including daily foot and vehicle traffic and staging of equipment and cargo. These activities have contributed to soil compaction and the maintenance of sparse vegetation cover at the four sites. The nest observations reported here are from

the largest of the four nesting areas (Fig. 2), which is at slightly higher elevation than most other areas of the station and about 10–15 m from a stand of *Rosa rugosa* Thunb. (Rosaceae). *Rosa rugosa* appears to be an important forage species for *Lasioglossum* on the island, with as many as ten bees at a time feeding on one flower, especially early in the season (Z. Lucas, unpub. obs.). Despite concerted efforts to search apparently suitable nesting habitat in various locations across the Island from 2019 to 2024, only scattered single nests and no additional nesting aggregations have been located in other locations on Sable Island (D. Kehler, unpub. obs.).



Figures 1–2. Specimens and nests of *Lasioglossum sablense*. **1.** Female (left) and male (right) specimens immobilized by sponges in glass vials, allowing for closer examination. Photo credit: Frederica Jacks. **2.** Nesting aggregation near the Alternate Power Unit (APU) building at the Parks Canada Station, with nest entrances marked by coloured flags, showing the extent of the aggregation (approximately 8 m). Nests were also marked with flat metal washers, which are not visible in this photo. Note that most nests were found in the well trodden path between buildings. Photo credit: Miriam Richards

Specimen Collections

All *L. sablense* specimens used for dissections were collected in 2016 and 2017, prior to recognition of the species' status under SARA in 2018. Two *L. sablense* specimens were collected near the APU building at the Sable Island Station on 1 and 2 June 2016, using a yellow bowl trap placed on the ground and filled with water and a drop of dishwashing detergent. Another 97 specimens were collected by targeted netting during surveys of forage plant species for *Lasioglossum* (both *L. sablense* and *L. novascotiae*) on 2 June 2016, 2 to 4 August 2016, and 1 to 6 August 2017. Plant species surveyed were *Vaccinium macrocarpon* Aiton (Ericaceae), *Rosa virginiana* Mill (Rosaceae), *Sibbaldiopsis tridentata* Aiton (Rydb.) (Rosaceae), *Achillea millefolium* L. (Asteraceae), *Scorzoneroides autumnalis* (L.) Moench, and *Leucanthemum vulgare* Lam. (Asteraceae), at seven locations from the Sable Island Station (43.9329, -60.0074) eastward to 43.9483, -59.8187. Bees foraging on flowers were collected into vials of 70% EtOH and within 24 h were placed in glass vials with fresh 70% EtOH for storage, then sent to the Nova Scotia Museum of Natural History for identification.

Lasioglossum sablense and *L. novascotiae* can be reliably distinguished from each other morphologically by the density of punctures on the mesoscutum (Gibbs, 2010), a trait that is clearly visible when live specimens are immobilized (Fig. 1). On an ongoing basis, we regularly confirmed the accuracy of field identifications by bringing a subset of immobilized specimens into the lab for identification using a microscope under higher magnification.

Observations of Bees at Nests

An aggregation comprising at least 95 nests was discovered along a footpath between the Alternate Power Unit (APU) building and the garage at the Sable Island Station on 3 July 2019 (Fig. 2). The nesting aggregation covered a sandy area roughly 2 m wide and 10 m long, and most nests were found along the edges of the packed footpath. From 3 to 9 July 2019, nests were identified when a female was observed departing from or arriving at the entrance. Additional observations were carried out at nests near the APU building between 8 and 15 August 2022, using similar methods.

Nest entrances were marked with short flags or with flat steel washers to which a piece of tape was attached with the nest number (Fig. 2). The washers were usually set down after a forager entered the nest, to avoid confusing females, which often did orientation flights around the nest entrance on their next foraging flight. Although some nests had temporary tumuli, these were easily obliterated by wind or rain after nest entrances were closed at the end of the day, so the number of nest entrances was likely underestimated. Occasionally, two nest entrances were found within a few millimetres of each other, and these were assumed to represent separate nests, rather than one nest with two entrances.

To identify which of the two *Lasioglossum* species were the subject of our observations in 2019, we caught 10 females nesting across the main aggregation and examined them briefly with a 10x eyepiece micrometer before releasing them; all 10 were identified as *L. sablense*. In 2019, we found females of *L. novascotiae* nesting in the vicinity, in small patches of sandy soil near other buildings 40 to 100 m away from the main aggregation, but not in the main sweat bee nesting aggregation near the APU or in three other small nesting aggregations in the vicinity. In 2022, bees from six nests were caught and individually marked for observations at nest entrances; two were

identified as *L. sablense* and four as *L. novascotiae*, suggesting that by 2022, the APU aggregation comprised nests of both species.

Phenology and Behavioural Observations

Female bees were observed at nest entrances during short observation periods (30 min to 4 h) on 3 to 10 July, 22 July, and 5 to 9 August in 2019, and on 8, 10, 12, 14 and 15 August in 2022. Observations of females at nest entrances were aimed mainly at determining whether single or multiple females were resident or foraging. In 2022, 13 adult females were caught (six at nest entrances and seven flying around the aggregation), then individually marked on the thorax with enamel paint to facilitate behavioural observations at nest entrances. We recorded behaviours typically observed in nest-based studies of sweat bee sociality (*e.g.*, Awde & Richards, 2018; Packer, 1992, Wcislo *et al.*, 1993): whether nest entrances were open or closed, departures of adult females from their nests (including orientation flights), arrivals of adult females at nest entrances with or without pollen loads, searching behaviour by adult females, and nest digging. In 2019 we also conducted short visual surveys (15 to 30 min) of sweat bees foraging on flowers growing within the station precincts on 27 June, 16 July, 22 July, and 9 August. Also in 2022, on 6 days between 8 to 15 August, we netted bees foraging on flowers within the station precinct, confirmed that they were *L. sablense*, and then measured head width, wing wear, and mandibular wear, before release.

Female Traits Related to Sociality

In total, 97 female specimens were netted from flowers in 2016 and 2017. For these specimens, we measured head width, mandibular wear and wing wear, as these can be measured without damaging specimens. We dissected and measured wing length for only a subset of these specimens ($n = 30$) because *L. sablense* specimens can no longer be collected without permits. In selecting females for dissection, we prioritized those with higher wing wear scores, as these were most likely to have been engaged in brood provisioning activities; measurement and dissection methods follow Corbin *et al.* (2021). Briefly, head width (HW) was measured as the widest distance across the head, including the compound eyes, in millimetres. To measure costal vein length (CVL), we detached the wings, taped them to paper with clear tape to hold them flat, and then measured the length of the costal vein in millimetres. Wing wear and mandibular wear were each measured on a scale from 0 (no wear) to 5 (very worn), and then summed to create a total wear score (TW) for each specimen. Females were dissected and their ovarian status was evaluated in two ways. First, the sizes of all developing oocytes relative to a fully developed egg ready to lay (1/4, 1/2, 3/4, and 1) were summed to create a volumetric ovarian development score (OD). Second, we scored females according to the fractional size of their largest developing oocyte; those with at least one 1/2-developed oocyte were classified as 'fecund' (Breed, 1976). The heads of three specimens were detached during transport so could not be positively associated with the dissected abdomens.

Data Analysis

All statistical analyses were run in R, version 4.4.1, running under R-Studio. For comparisons between Phase 1 and 2 females, we used one-way ANOVA to compare size and ovarian development scores, Kruskal-Wallis tests to compare total wear scores, and a Fisher exact test to compare the proportions of fecund females. To investigate the influence of body size on wear or on ovarian scores (represented as Y) during

Phases 1 and 2, we used the *lm* function and linear models of the form $Y \sim \text{size} + \text{phase} + \text{size} * \text{phase}$.

RESULTS

Phenology and Behaviour Outside the Nest

Observations at nest entrances in 2019 suggested two successive periods of brood provisioning activity. From 5 to 7 July 2019, more than half of nest entrances were open at least once during the day (Table 1). By 9 July and again on 22 July, fewer than 15% of marked nests were open, suggesting that the first brood-provisioning phase had finished, with foundresses remaining in their burrows until the emergence of their first workers. Throughout the month of July, we only ever observed a single female in each nest. In early July, we also observed females engaged in the low, sinuous flight patterns characteristic of searching behaviour, in which females fly back and forth close to the ground, occasionally landing and crawling about on the sand and under vegetation, inspecting the surface. These females likely were nest foundresses looking for suitable nest excavation sites. Supporting this interpretation, there were several instances in which we marked and observed a single nest entrance, but subsequently found two separate nest entrances at the same spot.

Table 1. Proportions of *Lasioglossum sablense* nests that were active during occasional surveys in 2019. Nests were recorded as active if the nest entrance was open or if a female was observed departing or arriving with pollen. The decline in activity from 9 to 22 July suggests a quiescent period between B1 and B2 provisioning phases.

Date	Nest entrances observed	Nests with activity (%)
5 July	67	50 (75)
6 July	24	16 (67)
7 July	20	11 (55)
9 July	21	3 (12)
22 July	68	10 (15)
5 August	57	26 (46)

On 5 August 2019, almost half of nests reactivated (reopened, see Table 1), and foragers were again observed departing and arriving at nest entrances. Some nests contained multiple females; for instance, at least three females entered nest 63 within the span of one minute on 5 August 2019. Three females were individually marked at one nest between 12 and 15 August 2022, two of them with high wear scores (TW = 9 for both) and one with a low wear score (TW = 2). At another nest, two different females were caught on 12 and 15 August 2022.

Visual surveys of bees on flowers around the Field Station on 27 June, 16 July, and 22 July 2019 indicated that all foragers were females, but on 9 August that year, males were also observed on flowers. Since male *Lasioglossum* do not overwinter, the males must have been newly eclosed, indicating that Brood 1 were reaching adulthood. Similarly, observations and netting of specimens on flowers from 8 to 15 August 2022 yielded both females and males. One male examined on 11 August 2022 had highly worn wings (WW = 5), suggesting considerable flight activity, whereas three other males caught the same day showed no wing wear (WW = 0) and likely were newly eclosed. All together, these observations suggest that Phase 2 of the colony cycle occurs

in early August following eclosion of Brood 1, nest reactivation, and renewed brood provisioning activity for Brood 2.

In a mix of marked *L. sablense* and *L. novascotiae* nests surveyed in August 2022, about 70% had either nest guards or foragers. In observations of four active nests confirmed to belong to *L. sablense* between 8 and 15 August 2022, there seemed to be no more than one female carrying pollen to each nest on any particular day, and the maximum number of pollen trips observed per day was only three. In one nest, for instance, at least three unmarked females entered the nest in quick succession, only one of them carrying pollen. In another nest, three females were individually marked, but only one was observed carrying pollen.

Female Traits Related to Sociality

Based on the two-brood phenology inferred above, we assumed that adult females observed or collected in June or July (Phase 1) were nest foundresses, while those collected or measured in August (Phase 2) were Brood 1 daughters. Based on comparisons among all 97 females collected in 2016 and 2017, Phase 1 females were significantly larger than those collected in Phase 2 (Fig. 3) but had similar wear scores (Table 2). The average difference in head width between Phase 1 and 2 females was 1.8%. Within the subset of 30 dissected females, Phase 1 females were also larger and more worn, but only the wear difference was significant (Table 2). Overall, we interpret these patterns as showing that Phase 1 females were on average slightly larger and more worn than Phase 2 females.

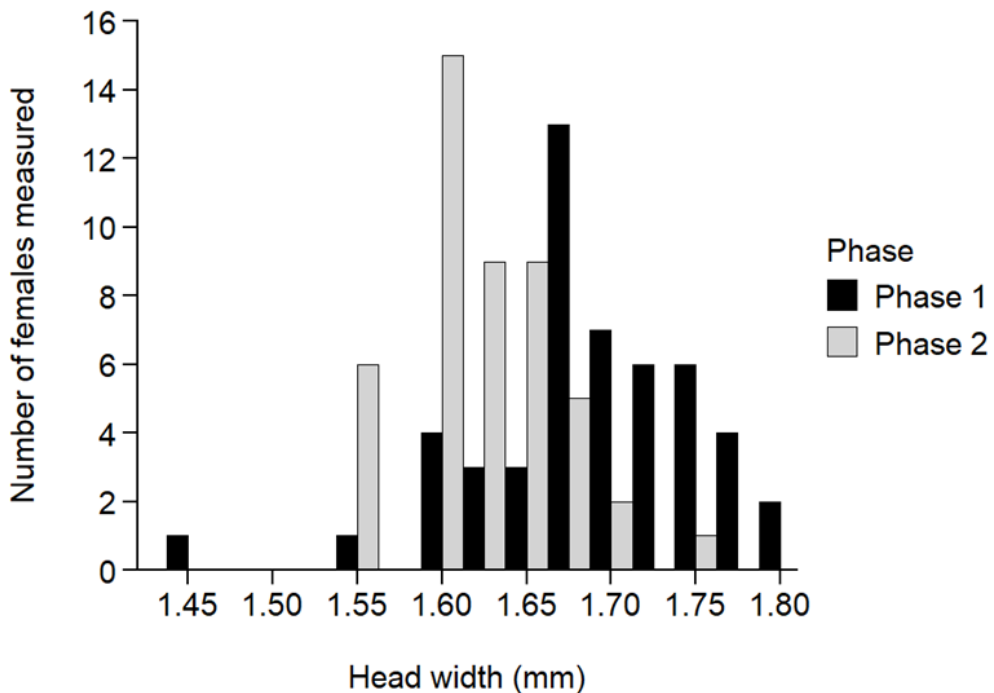


Figure 3. Head width distributions for all available females of *Lasioglossum sablense* collected during the first and second phases of the colony cycle in 2016 and 2017. Phase 1 females were significantly larger (see Table 2).

Table 2. Trait comparison for *Lasioglossum sablense* females collected in 2016 and 2017. Head width (mm) and total wear (TW) scores were measured in all females (Phase 1: $n = 50$, Phase 2: $n = 47$), whereas costal vein length (mm), ovarian development (OD) score, and fecundity were assessed in a subset of 30 dissected females (Phase 1: $n = 50$, Phase 2: $n = 15$). Comparison: Results from ANOVA tests unless otherwise indicated; K-W = Kruskal-Wallis test. Significant differences are indicated in boldface.

Trait	Dataset	Phase 1	Phase 2	Comparison
Head width (mean \pm s.d.)	all	1.70 \pm 0.07	1.63 \pm 0.05	$F=33.83$, $df=1,95$, $p = 8.08e-08$
	dissected	1.68 \pm 0.05	1.65 \pm 0.06	$F=1.83$, $df=1,28$, ns
Costal vein length (mean \pm s.d.)	dissected	1.90 \pm 0.06	1.88 \pm 0.08	$F=0.74$, $df=1,28$, ns
TW score (median, range)	all	2 (0–6)	3 (0–10)	K-Ws, $H=12.00$, $df=1$, ns
	dissected	3 (1–6)	4 (2–10)	K-W, $H=8.24$, $df=1$, $p = 0.004$
OD score (mean \pm s.d.)	dissected	0.98 \pm 0.44	0.67 \pm 0.46	$F=3.66$, $df=1,28$, $p = 0.066$
Proportion fecund	dissected	14 / 15 = 93%	11 / 15 = 73%	Fisher test, ns

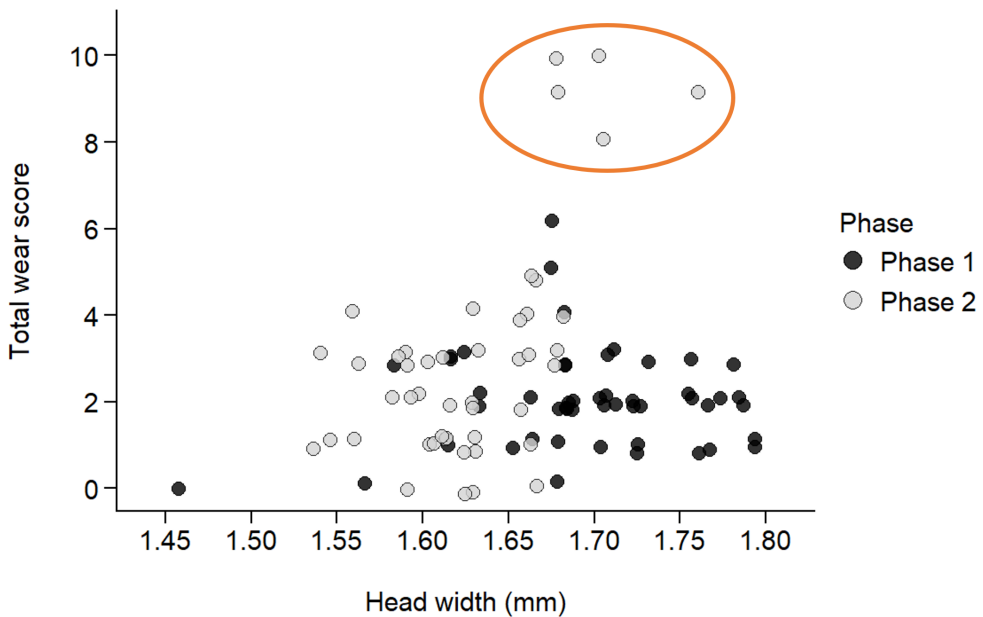


Figure 4. Relationship between head width (HW) and total wear score (TW) in all available *Lasioglossum sablense* females collected in 2016 and 2017. Phase 2, but not Phase 1 females, showed a significant association between these two variables, driven by five highly worn females collected in Phase 2 and indicated with a circle (see Supplemental Material, Table 1S for statistical analyses).

We analysed relationships between size (HW) and wear of foraging females collected in Phases 1 and 2 (Fig. 4). Wear scores tended to be higher in larger females (Table 1S). However, this result was driven by the very high wear scores of the five largest females collected during Phase 2, which likely were Phase 1 nest foundresses that began a second bout of foraging during Phase 2. When these were excluded from consideration, the significant association between size and wear disappeared, as did the difference in total wear between Phases 1 and 2 (Table 1S).

Comparison of ovarian development (OD) scores suggested that egg-laying capacity of Phase 1 females was marginally higher than that of Phase 2 females (Fig. 5), but the difference was only marginally significant ($p = 0.066$, Table 2). The majority of females were fecund (had at least one $\frac{1}{2}$ -developed oocyte) in both phases, with similar proportions (Table 2). Ovarian score was not significantly associated with body size, as measured by head width, but was marginally associated with costal vein length (Fig. 6, Table 2S).

There were four females with OD = 0 among the dissected specimens. One was collected in Phase 1 (6 June 2016), was relatively large (HW = 1.68 mm) and quite worn (TW = 6); the timing and her large size suggest that she was a moribund foundress. The other three were collected in Phase 2 (3 and 4 August 2016, and 1 August 2017), were smaller (HW = 1.66, 1.61, and 1.56, respectively) and had wear scores of TW = 4, 2, and 4, respectively). The timing of their capture and their relatively low wear scores suggest that they were workers.

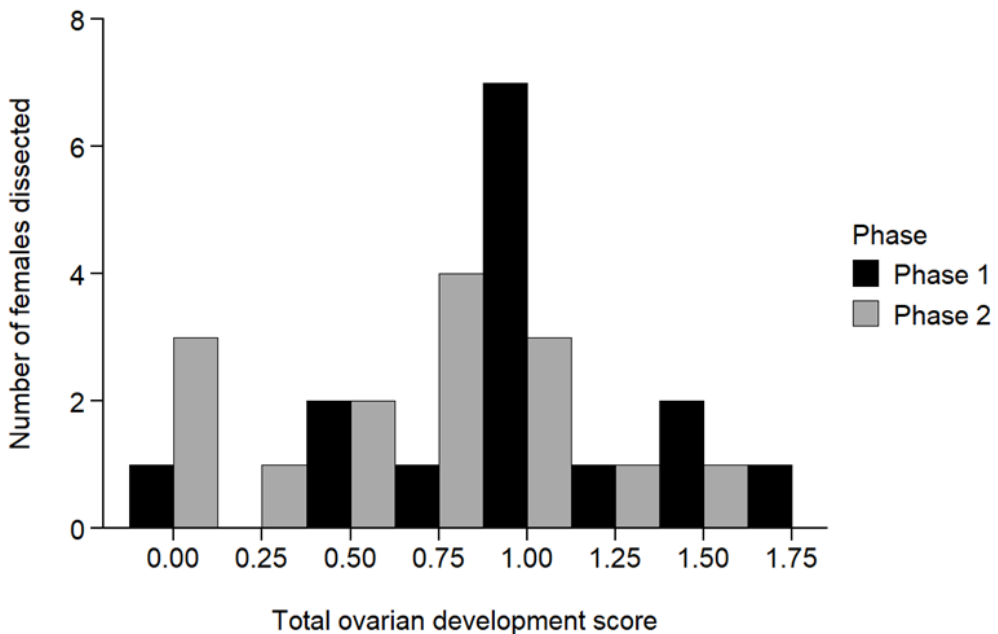
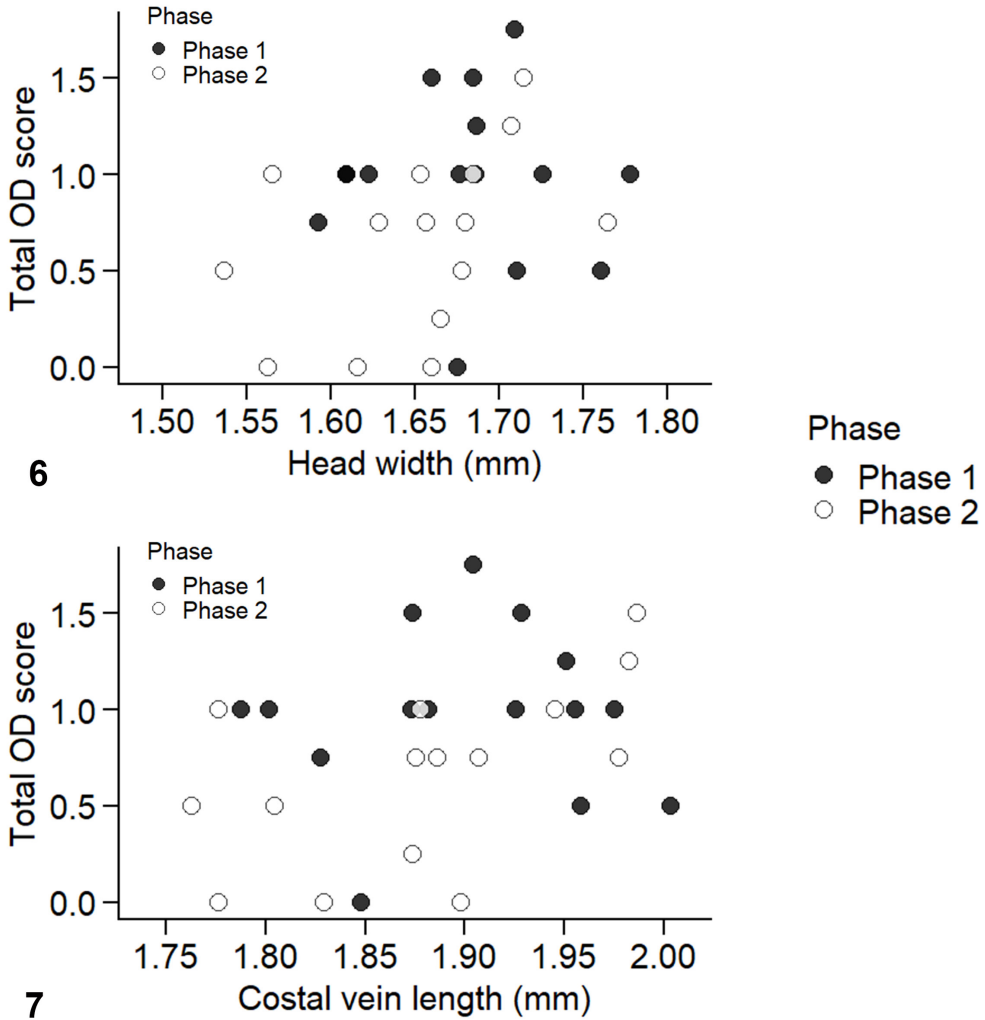


Figure 5. Comparison of ovarian development scores (OD) for *Lasioglossum sablense* females collected in 2016 and 2017. Phase 1 females tended to have higher OD scores than Phase 2 females (see Table 2).



Figures 6–7. Variation in ovarian development scores (OD) relative to body size and phenology for dissected females of *Lasioglossum sablense* ($n = 30$) collected in 2016 and 2017 (see Supplemental Material, Table 2S for statistical analyses). **6.** OD scores according to head width. **7.** OD scores according to costal vein length. Points are horizontally jittered to show overlapping values.

DISCUSSION

Based on the preliminary data presented here, we suggest the following summary of *L. sablense* phenology and social behaviour. Foundresses begin to establish nests solitarily in Phase 1, likely in June. Nest founding is asynchronous, and new nests may be initiated as late as early July. Females seem to prefer nest sites in and beside footpaths and other areas with harder packed soil and sparse vegetation. Most foundresses finish provisioning Brood 1 by early July, then close their nest entrances, remaining inside the nests until the emergence of Brood 1 adults in early August. Brood 1 comprises both females and males, whose emergence as adults marks the beginning of Phase 2, when adult females reactivate their nests and begin provisioning Brood 2. No new nests are founded in Phase 2, so Brood 1 daughters evidently remain in their maternal nests. Most Phase 2 foragers are Brood 1 daughters, but a few are long-lived foundresses that resume foraging to provision a second brood.

About half of all nests reactivated during Phase 2. Nests that did not reactivate appear to represent a truly solitary and univoltine life history, although early mortality of all nest occupants could also explain why they do not reopen in Phase 2. In contrast, nests that did reactivate in Phase 2 clearly represent a bivoltine life history. A mix of univoltine and bivoltine life histories frequently occurs in both solitary and eusocial sweat bees (Miyayama *et al.*, 1998, 2000; Proulx & Richards, 2024). Even in obligately eusocial species, some females are functionally solitary. Most frequently, eusocial colonies become functionally solitary if the foundress dies during Phase 1 and is replaced by a single daughter who provisions Brood 2, while other daughters leave the natal nest or enter hibernation. Very rarely, in species like *Halictus ligatus* Say, foundresses whose workers die before emergence can resume brood provisioning during Phase 2; in this way, they behave like solitary females that live long enough to provision two successive broods (Richards & Packer, 1994). Similarly, when *H. ligatus* workers lose their nests, they may dig their own new nests, in effect adopting a solitary bivoltine nesting strategy (Rehan *et al.*, 2013).

The activity of adult females during Phase 2 is key to understanding the nature of colony social organisation in bivoltine sweat bees (Schwarz *et al.*, 2007; Corbin *et al.*, 2021). We observed several nests in which multiple females were active outside the nest, with at least one of them collecting pollen. We did not observe any nests in which more than one female collected pollen on the same day. Given our small sample sizes, it would be premature to hazard a guess at the proportion of Brood 1 daughters that provision brood during Phase 2. However, most dissected Phase 2 foragers had developing ovaries, suggesting they were collecting provisions for their own eggs. In fact, the proportion of fecund Brood 1 daughters in *L. sablense* (84%) is the highest of any *Lasioglossum* (*Dialictus*) yet studied (Breed, 1976; Awde & Richards, 2018) suggesting that multifemale associations during Phase 2 were often communal. Nevertheless, in our sample of 15 dissected Phase 2 females, we did find three small, worn females with no ovarian development, which likely were workers provisioning eggs laid by a nestmate, suggesting that at least a few colonies become eusocial. In some ways, the behaviour of *L. sablense* resembles that of the primarily solitary species, *L. figueresi* Wcislo (Wcislo *et al.*, 1993). In this species, sociality develops when Brood 1 daughters remain together in their natal nest. The Brood 1 daughters usually provision their own brood and the colony becomes communal, but very rarely, one female lays eggs that are provisioned by her sisters, creating a semisocial colony. *Lasioglossum*

figueresi foundresses almost always die before their daughters emerge, so colonies usually cannot become eusocial. In *L. sablense*, the long lives of many foundresses likely increase the potential for overlapping maternal and daughter generations, so colonies could potentially become either communal or eusocial during Phase 2.

Conclusions

The preliminary data presented here provide a tantalizing outline of the phenology and social behaviour of *L. sablense*, which will aid in long-term monitoring of this threatened, endemic species. It will also contribute to the long tradition of comparative studies of sweat bee social behaviour. The Sable Island Sweat Bee is part of the *viridatum* group of *L. (Dialictus)* (Gibbs, 2010), which includes the behaviourally uncharacterized *L. novascotiae*, the only other sweat bee found on Sable Island, and well studied species such as *L. laevissimum* (Packer, 1992; Awde & Richards 2018), which seems to be obligately eusocial and thus less socially variable than *L. sablense*. The fact that *L. sablense* is endemic to an isolated island that is only about 10,000 years old, suggests that it evolved as a separate species quite quickly and so might become a fascinating model for investigating the time course and sequence of social evolutionary changes in these bees. More detailed studies of *L. sablense*, *L. novascotiae*, and other members of the *viridatum* group would be valuable for testing this hypothesis.

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SUPPLEMENTAL MATERIAL

Table 1S. Linear models analysing the influence of body size (head width) on total wear scores of Phase 1 and 2 females (Fig. 3). The association between size and wear was significant, when all females were included (left), but not when the five probable foundresses collected in Phase 2 were excluded (right).

Table 2S. Linear models analysing the influence of body size on total ovarian scores of Phase 1 and 2 females (Figs. 5, 6, 7). Ovarian development scores were not significantly associated with head width (left) but were significantly associated with costal vein length (right).

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