

Phenological and social characterization of three *Lasioglossum* (*Dialictus*) species inferred from long-term trapping collections

Lyllian A.-J. Corbin¹, David N. Awde², Miriam H. Richards¹

1 Department of Biological Sciences, Brock University, St. Catharines, Ontario, Canada **2** Department of Entomology, University of Kentucky, Lexington, Kentucky, USA

Corresponding author: Lyllian Corbin (lyllian.corbin@gmail.com)

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Abstract

Detailed social and phenological data collected from nesting aggregations exist for relatively few sweat bee species because nesting aggregations are rarely found in large numbers, even when local populations are highly abundant. This limits researchers' abilities to assess the social status of many species, which in turn, limits our ability to trace the sequence of evolutionary steps between alternative social states. To address this problem, we demonstrate the utility of rehydrated, pinned specimens from pan trap and netting collections for generating inferences about the phenology and social status of a well-studied sweat bee species, *Lasioglossum* (*Dialictus*) *laevissimum*. A detailed comparison of phenology and reproductive traits, between pinned specimens and those in a previous nesting study, produced similar results for bivoltine foraging activity and eusocial colony organization typical in this species. We then used pinned specimens from monitoring studies to describe, for the first time, the foraging phenology and social behaviour of two additional *Dialictus* species, *L. hitchensi* and *L. ellisiae*. Both *L. hitchensi* and *L. ellisiae* each exhibited two peaks in abundance during their breeding seasons, indicating two periods of foraging activity, which correspond to provisioning of spring and summer broods. Differences in body size, wear, and ovarian development of spring and summer females indicated that *L. hitchensi* is most likely eusocial, while *L. ellisiae* is either solitary or communal. This study demonstrates that analyses of specimens obtained from flower and pan trap collections can be used for assessing the phenology and social organization of temperate sweat bees in the absence of nesting data. The phenological and social lability of many sweat bee species make them ideal for studying geographic and temporal variability in sociality, and analyses of pan trap collections can make these studies possible when direct observations are impossible.

Keywords

Eusociality, pan traps, social reversal, solitary, sweat bees

Introduction

In temperate zone sweat bees (Hymenoptera: Halictidae), flight phenology is closely linked to sociality. Univoltine species are virtually always solitary or communal, whereas the necessity of producing a worker brood requires that eusocial species are bivoltine, or multivoltine, if multiple worker broods are produced. While the term “voltinism” technically refers to the number of generations per year, in studies of halictid bees, it has taken on an additional usage in phenology, and is frequently used to refer to the number of broods produced each year (Richards et al. 2010). In this study, we use voltinism to refer to the latter. Facultative social sweat bees exemplify the strong connection between phenology and sociality. Some species, like *Lasioglossum calceatum* and *Halictus rubicundus*, exhibit a bivoltine, eusocial life history at low altitudes and a univoltine, solitary life cycle at high altitudes (Sakagami and Munakata 1972; Eickwort et al. 1996). Others exhibit social and phenological polymorphism within populations, with solitary nest foundresses provisioning a single brood of reproductives, while eusocial foundresses produce a worker brood that subsequently provisions the second brood (Packer et al. 1989; Packer 1990). The strength of the link between a bivoltine phenology and eusociality is well known phylogenetically, leading to the hypothesis that in halictine bees evolutionary transitions to eusociality involved two major steps: an initial transition from univoltinism to bivoltinism, and a subsequent step from solitary breeding to eusociality (Brady et al. 2006).

The subgenus *Lasioglossum* (*Dialictus*) is well known as a vast and socially diverse group of halictid bees, with over 250 species existing in North America (Ascher and Pickering 2020). *Dialictus* includes species categorized as solitary, communal, semisocial, eusocial, and socially parasitic (Batra 1966; Breed 1976; Eickwort 1986; Wcislo 1997; Gibbs 2010, 2011). Phylogenetic analyses suggest that *Lasioglossum* as a whole is ancestrally eusocial, implying considerable evolutionary lability in social traits and multiple reversions from social to solitary behaviour (Gibbs et al. 2012). However, the behaviour of many *Dialictus* remains unstudied. The social status of some species has been broadly categorized based on presumed similarities among closely related taxa, but the lability of halictid sociality means that closely related species might exhibit very different types of social behaviour. Moreover, broad social categories are limited in their usefulness for precisely tracing the sequence of evolutionary changes that must have occurred in transitions between alternative social states, such as caste-based or casteless sociality (Dew et al. 2016; Richards 2019). More detailed studies of solitary and social halictine bees are required to provide this kind of behavioural data.

Ideally, to study colony social organization in sweat bees, large numbers of colonies are observed from start to finish of at least one complete breeding season (Rehan et al. 2013;

Onuferko et al. 2015; Awde and Richards 2018). The activity of foragers at nest entrances established flight phenology and the timing of brood provisioning phases. Nests are excavated at various times to obtain ‘snapshots’ of colony development and brood production, as well as to collect adult females. Adult females are examined to investigate body size, wing wear, mandibular wear, and ovarian development status, traits that relate to caste and reproductive status. However, a major challenge is that sweat bee nests are rarely found together in large enough numbers that biologists are likely to devote the time to studying them, even in areas where local populations are highly abundant. Museum collections provide an alternative source of specimens that can be used to investigate both phenology and reproductive activities of halictid and other bees. Passive collection methods, such as regular pan-trapping or sweep-netting, provide large numbers of halictids specimens (Portman et al. 2020) that can be counted and used for estimating the relative abundance of foraging females from spring to autumn. Preserved specimens, including pinned specimens, can be rehydrated in water, allowing females to be dissected and their ovarian development measured (Packer et al. 2007; Richards et al. 2010, 2015).

In this study, we used pinned specimens previously collected and identified for a long-term monitoring study in the Niagara region of southern Ontario, Canada (Richards et al. 2011; Onuferko et al. 2015) to evaluate the social status of three sympatric *Dialictus* populations. Of 33 *Lasioglossum* (*Dialictus*) species present locally, only seven are known to be eusocial (including *L. laevisimum*), 17 are predicted to be eusocial (including *L. hitchensi* and *L. ellisiae*), one is possibly communal, four are cleptoparasites or social parasites, and four have undescribed social statuses (Onuferko et al. 2015). None of the species are described as solitary. Thus our primary objective was to describe the phenology and social behaviour of two species, *L. (Dialictus) hitchensi* and *L. (D.) ellisiae*, both predicted to be eusocial on phylogenetic grounds (Gibbs et al. 2012; Onuferko et al. 2015). Our second objective was to further validate the use of pinned specimens collected using passive collecting methods, such as pan traps and sweep nets, when nests are not available. We do this by explicitly comparing social trait inferences from pan trap collections of *L. (D.) laevisimum*, to those from a study based on detailed behavioural observations and nest excavation from a sympatric population (Awde and Richards 2018).

Methods

Study sites and specimen collections

All specimens were collected from grassy meadows as part of a monitoring study from 2003 to 2006 and from 2008 to 2013 at four sites in southern Ontario: Brock University (43.1178°N, 79.2473°W) and the adjacent Glenridge Quarry Naturalization Site in St. Catharines (43.1197°N, 79.2390°W), the Elm Street Naturalization Site in Port Colborne (42.9235°N, 79.2579°W), and the Station Road Naturalization Site in Wainfleet (42.8847°N, 79.376°W; Onuferko et al. 2015). Descriptions of collecting

sites and the local bee assemblage, which includes 33 *Dialictus* species, are available in Richards et al. (2011) and Onuferko et al. (2015).

We used specimens collected via pan traps, netting from flowers, and sweep-netting to examine the social status of *L. laevissimum*, *L. hitchensi* and *L. ellisiae*. *Lasioglossum laevissimum* was used for a comparison of social trait inferences from monitoring studies with the ‘gold standard’ of nest-based observations from a previous study in the same region (Awde and Richards 2018). *Lasioglossum hitchensi* and *L. ellisiae* were selected because large numbers of specimens had been identified and collected, and because these two species are likely to be phylogenetically informative in future studies.

Collection methods were compared and described in detail in Richards et al. (2011). Pan trapping and sweep netting were carried out each year either weekly or biweekly from spring (April or May) to fall (September or October), for a total of 10 years of collections, covering the entire flight season for the local bee community. Specimens were preserved in 70% ethanol before being pinned and identified using taxonomic keys by Gibbs (2010, 2011) for *Lasioglossum* (*Dialictus*) in combination with online keys on Discover Life (Onuferko et al. 2015; Ascher and Pickering 2020). Specimens caught in 2003 were identified by Dr. Jason Gibbs (Richards et al. 2011) and those caught from 2004–2013 were identified by Dr. Thomas Onuferko (Onuferko et al. 2015), with additional confirmations by Ms. Nora Romero. All specimens are currently in the collection of the Brock Bee Lab, at Brock University, Canada.

Flight phenology

In the Niagara region of southern Ontario, halictid bees generally begin spring brood provisioning activity in late April or early May and summer flight activity peaking in July (Richards et al. 2010, 2015; Proulx 2020). Locally, univoltine sweat bee populations can be identified in weekly (or biweekly) pan trap collections as those showing a single peak in female abundance (pan traps are presumed to mainly attract foragers) from spring to summer, whereas bivoltine sweat bee populations exhibit two peaks, one in spring and one in summer.

Flight phenology (whether bees were univoltine or bivoltine) was inferred solely from weekly abundances of female and male bees caught in pan traps, pooling samples over the ten years from 2003 to 2013 (bees were not collected in 2007). Total numbers of pan trapped specimens were 51 females and 1 male for *L. laevissimum*, 1473 females and 7 males for *L. hitchensi*, and 54 females and 13 males for *L. ellisiae*. For each species, we decided which week to designate as the end of the spring provisioning and the beginning of summer provisioning periods, based on several key factors: the re-appearance of unworn females suggesting emergence of Brood 1, the appearance of males (most eusocial species produce at least a few males in Brood 1), and whether population sizes seemed to be increasing (reviewed in Awde and Richards 2018; Breed 1976; Packer 1992; Richards et al. 2010). We also plotted mean weekly abundance of females and males (the number of bees caught per calendar week divided by the total number of collections per calendar week, pooling over years), and then used a local

polynomial regression (Loess) smoother to evaluate the number of peaks in female bee abundance and foraging activity from spring to summer (geom_smooth command, package: ggplot2). Since data were pooled over ten years of collections over which the timing of spring activity might differ considerably, the designated cutoff dates between spring and summer provisioning are approximate.

Female traits related to social behaviour

Female traits were examined in females collected by all three methods (Table 1). We examined female traits frequently used to evaluate colony social organization in halictid bees, including body size, mandibular and wing wear, and degree of ovarian development (Packer 2007; Richards et al. 2010, 2015). Pinned female specimens were measured and dissected using a Zeiss stereomicroscope, equipped with an ocular micrometer at 8–66× magnification. Head width (HW) was measured as the widest distance across the head, including the compound eyes. Costal vein length (CVL) was measured on the right forewing, from the base of the costal vein to the stigma (Suppl. material 1). If the right wing was damaged, the left wing was used instead. Since HW and CVL were positively correlated in all species (Pearson's product-moment correlation; *L. laevissimum*: $t=4.75$, $df=91$, $p=7.322e-06$; *L. hitchensi*: $t=21.65$, $df=120$, $p<2.2e-16$, *L. ellisiae*: $t=15.93$, $df=78$, $p<2.2e-16$), HW was used for size comparisons. Size differences between spring and summer females were calculated using the formula:

$$[(\text{mean spring HW} - \text{mean summer HW}) / \text{mean spring HW}] \times 100$$

We assessed the amount of burrow digging and flight activity performed by each female by examining the level of wear that accumulated on their mandibles and forewings respectively (Suppl. material 2). Mandibular wear (MW) and wing wear (WW) were scored on a scale from 0 to 5 (i.e., unworn to completely worn), using whole numbers only. A total wear (TW) score for each female was obtained by summing MW + WW. We classified 'worn' bees as those having MW or WW scores ≥ 2 (Richards et al. 2010); we rarely observed bees with distinctly different levels of wear on their mandibles and wings among all species.

Ovarian development score was assessed to distinguish sterile and reproductive females (Suppl. material 3). Pinned specimens were rehydrated in a jar of distilled water for 24 hours, then dissected. Thin or only slightly thickened ovaries were

Table 1. Numbers of pinned specimens used for examining female social traits.

Species	Collection years	Collection method			Total
		Pan traps	Netting from flowers	Sweep-netting	
<i>L. laevissimum</i>	2003–2013*	34	43	18	95
<i>L. hitchensi</i>	2009	124	0	0	124
<i>L. ellisiae</i>	2003	40	9	33	82

* Bees were not collected in 2007.

given a score of 0. For all females with developing oocytes, each oocyte was scored by its size relative to a fully developed oocyte (0.25, 0.50, 0.75, or 1), and then scores for all oocytes within an individual were summed to create a total ovarian development (OD) score. This scoring method has frequently been used to assess potential reproductivity of halictid bees (e.g. Richards et al. 2010, 2015). Following Breed (1976), any female whose largest oocyte was at least 1/2 size (scored as 0.5), was classified as “fecund”.

While rehydrated ovaries from pinned specimens appeared similar in size to those of specimens stored in liquid preservative (Packer 2007; Richards et al. 2010), it is possible that the ovaries of pinned specimens do not return to their pre-desiccation size, which could result in pinned specimens appearing to have lower OD. We avoid this potential bias by using fractional scores to calculate total OD, which is, in effect, a relative ranking of females’ ovarian development, and by avoiding comparisons of absolute oocyte size across studies.

Inferring colony social organization

Univoltine populations of non-parasitic halictids are most likely to be either solitary or communal. In both solitary and communal species, the distributions of body size and ovarian development are expected to be unimodal, so nest observations are required to distinguish between these possibilities.

Bivoltine populations of non-parasitic halictids are most likely to be either solitary or eusocial. Locally, the only known communal sweat bee (*Agapostemon virescens*) is univoltine (MH Richards, unpub. data), whereas at least one solitary species (*Lasioglossum zonulum*) is bivoltine (Proulx 2020). We use the term foundress to refer to overwintered females that establish nests and forage in spring after emerging from hibernation (Eickwort et al. 1996). Based on previous studies of solitary and eusocial sweat bees (Danforth et al. 2003), in solitary bivoltine species, foundresses and their daughters (summer females) are predicted to be similar in size, to accumulate similar levels of wear, and to have similar levels of ovarian development (Packer 1994; Eickwort et al. 1996). In contrast, eusocial foundresses (spring queens) are predicted to be significantly larger than most of their daughter workers (summer females), to accumulate more wing and mandibular wear, and to have significantly higher ovarian development (Packer 1986; Richards et al. 2010; Awde and Richards 2018). Moreover, the distributions of ovarian development should differ between the summer foragers of solitary and eusocial species. In solitary species, summer foragers should be provisioning their own brood cells and so all females are expected to have high levels of ovarian development, consistent with laying eggs. In eusocial species, many or most summer workers provision queen-laid eggs and exhibit little or no ovarian development. Across eusocial *Dialictus* populations, the proportion of foraging workers with developed ovaries can vary from 9 to 63% (summarized in Awde and Richards 2018).

Data analyses and software

Data is available on the Brock University repository (<https://dr.library.brocku.ca/>). All statistical comparisons were performed in R, version 3.4.3 (through RStudio, version 1.1.383). Figures were created using *ggplot2*. Initial comparisons of HW, TW, and OD between spring and summer females were based on analysis of variance. Where the error term was not normally distributed, we used Kruskal-Wallis tests.

Results

Lasioglossum laevisimum

Phenology: The phenology based on pan trapped specimens of *L. laevisimum* is shown in Figure 1, with additional details presented in Table 2. Spring females (foundresses) were mostly caught from April to early May (weeks 0 to 3). Two large, worn females collected in week 6 were classed as foundresses. Thus, the spring brood-provisioning phase for Brood 1 extended to about the end of May. Summer females (females produced in Brood 1) were first pan-trapped in week 8, suggesting that the Brood 2 provisioning phase began in mid-June. No males were caught until week 19, suggesting that males were not produced in Brood 1. The single male caught in week 19 likely was produced in Brood 2, so its capture suggested the onset of Brood 2 emergence. A slight increase in the numbers of foragers caught during weeks 23–25 suggests the possibility that late foragers (possibly produced in Brood 2) might be provisioning a third brood (Brood 3). Females were caught in pan traps until October (week 25).

Colony social organization: Traits of spring and summer females are shown in Table 2. Spring females were 3.6% larger than workers based on mean head width (ANOVA, $F=4.62$, $df=1,93$, $p=0.034$). Spring and summer females had similar wear scores (ANOVA, $F=0.62$, $df=1,92$, n.s.). Spring females, on average, had significantly higher OD scores than summer females (Kruskal-Wallis, $H=5.45$, $df=1$, $p=0.020$) and were more likely to be fecund (Figure 2).

The bivoltine or multivoltine phenology inferred from pan trapped specimens, as well as the larger size and greater ovarian development of spring females, are consistent with eusociality, in agreement with the results from nest observations and excavations for a sympatric population (Table 2).

Lasioglossum hitchensi

Phenology: The spring provisioning period began in early April and lasted until late June (weeks 0 to 8). The summer provisioning period lasted from late June to September. The capture of a male in week 6 (2011) indicates that nests initiated very

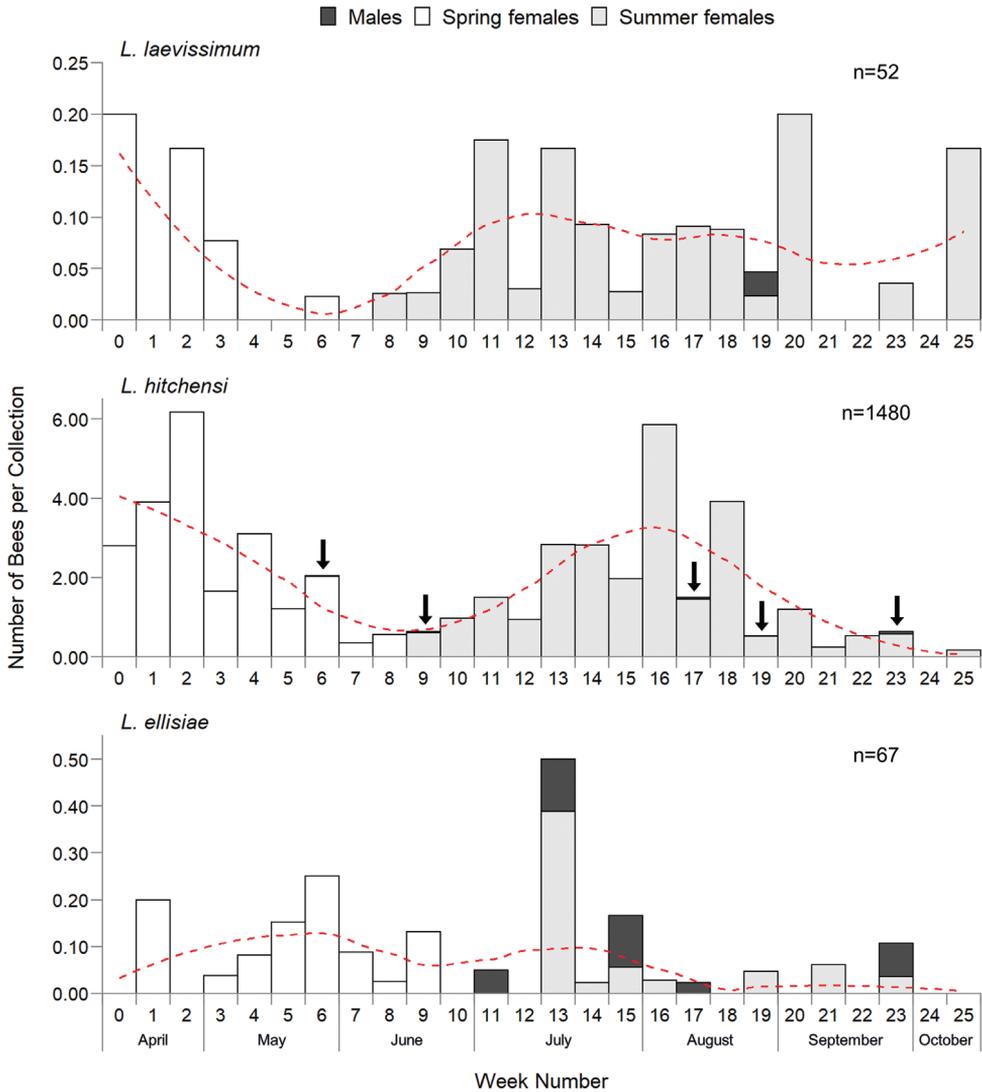


Figure 1. Bivoltine flight phenologies of *L. laevissimum*, *L. hitchensi* and *L. ellisiae*, inferred from pan trap collections, 2003–2013. The number of bees collected per week represents the average number of bees collected in pan traps, across sites and years, from 2003 to 2013. A total of 52 *L. laevissimum* bees, 1480 *L. hitchensi* bees, and 67 *L. ellisiae* bees were collected. Dark grey bars represent males, white bars represent spring females and light grey bars represent summer females. The red polynomial regression (drawn using the *geom_smooth* function, Loess method, in R) was used to help visually identify the number of abundance peaks for each species. Black arrows indicate the weeks when *L. hitchensi* males were collected in pan traps.

early in spring may produce Brood 1 offspring several weeks earlier than the population average. The males caught in week 17 would likely have been produced in Brood 2 emergence. Thus, *L. hitchensi* exhibits a bivoltine phenology.

Table 2. Phenological events and social traits of *L. laevissimum* females inferred from passive collections and nest excavations. Spring females from Awde and Richards (2018) were queens collected from nests in summer that would have been foraging in spring, while summer females were workers collected from nests in summer. Statistical comparisons are for pinned females assessed in this study versus females collected from nests in Awde and Richards (2018).

	Pan traps, sweeps, and flower collections (this study)	Nest excavations and observations (Awde and Richards 2018)	Statistical comparisons
Phenology			
First foraging trip by spring female	late April (week 0)	late April (week 1)	–
Quiescent period between spring and summer foraging	mid-May – early June (week 4 – 7)	mid-May – late June (week 6 – week 10)	–
First foraging trip by summer female	mid-June (week 7 or 8)	late June (week 10)	–
First adult male	late August (week 19)	mid-July (week 13)	–
First adult gyne	mid-July (week 12)	mid-July (week 12)	–
Last foraging trip by summer female	early October (week 25)	early October (week 25)	–
Spring female traits			
Head width (mm) (mean ± SD, n)	1.65 ± 0.06, n=10	1.67 ± 0.08, n=24	KW=0.07, df=1, p=0.79
Median total wear score (range, n)	4 (1 – 8, n=10)	4.5 (2 – 9, n=24)	KW=0.27, df=1, p=0.60
Median OD score (range, n)	1.125 (0 – 2.5, n=10)	2.5 (0.75 – 3.5, n=24)	KW=6.88, df=1, p=0.009
Proportion fecund (largest oocyte at least 1/2 size)	5/10 (50%)	21/24 (87.5%)	$\chi^2=0.36$, df=1, p=0.5474
Proportion mated	NA	24/24 (100%)	–
Summer female traits			
Head width (mm) (mean ± SD, n)	1.59 ± 0.09, n=85	1.61 ± 0.89, n=135	KW=4.34, df=1, p=0.037
Median total wear score (median, range, n)	4 (0 – 8, n=84)	3 (0 – 10, n=132)	KW=11.66, df=1, p<0.001
Median OD score (range, n)	0 (0 – 2.25, n=85)	0 (0 – 3.25, n=133)	KW=0.78, df=1, p=0.38
Proportion fecund (largest oocyte at least 1/2 size)	11/85 (12.9%)	23/133 (17.3%)	$\chi^2=0.3$, df=1, p=0.5813
Proportion mated	NA	52/133 (39.1%)	
Queen-worker size difference	3.6%	4.6% (n=21 comparisons within colonies)	

Colony social organization: Reproductive traits of spring and summer females are presented in Table 3. Spring females on average were 3.2% larger than summer females based on head width. Wear did not differ significantly between spring and summer females. Median ovarian development scores were substantially higher in spring compared to summer females, as most spring females had at least one ¾ or fully developed oocyte, while most summer females had undeveloped oocytes.

The average size difference between spring and summer females belied a curious pattern, evidenced by a distinct drop in summer female head width in week 16 (Suppl. material 4). We therefore divided the summer females into early (collected from weeks 10 to 15) and late groups (collected from week 16 onward) for further comparisons (Figure 3). Early summer females were as large as spring females, and significantly larger than late summer females (ANOVA, $F=24.107$, $df= 2,119$, $p=1.62e-09$). However, all three groups had exhibited a similar degree of wear (TW: ANOVA, $F=1.70$, $df=2,119$, $p=0.188$). Spring females had significantly higher OD scores than both early and late summer females (Kruskal-Wallis, $H=21.27$, $df=2$, $p=2.41e-05$).

The combination of a bivoltine phenology, greater size, and higher ovarian development of spring than summer females suggests that *L. hitchensi* is eusocial.

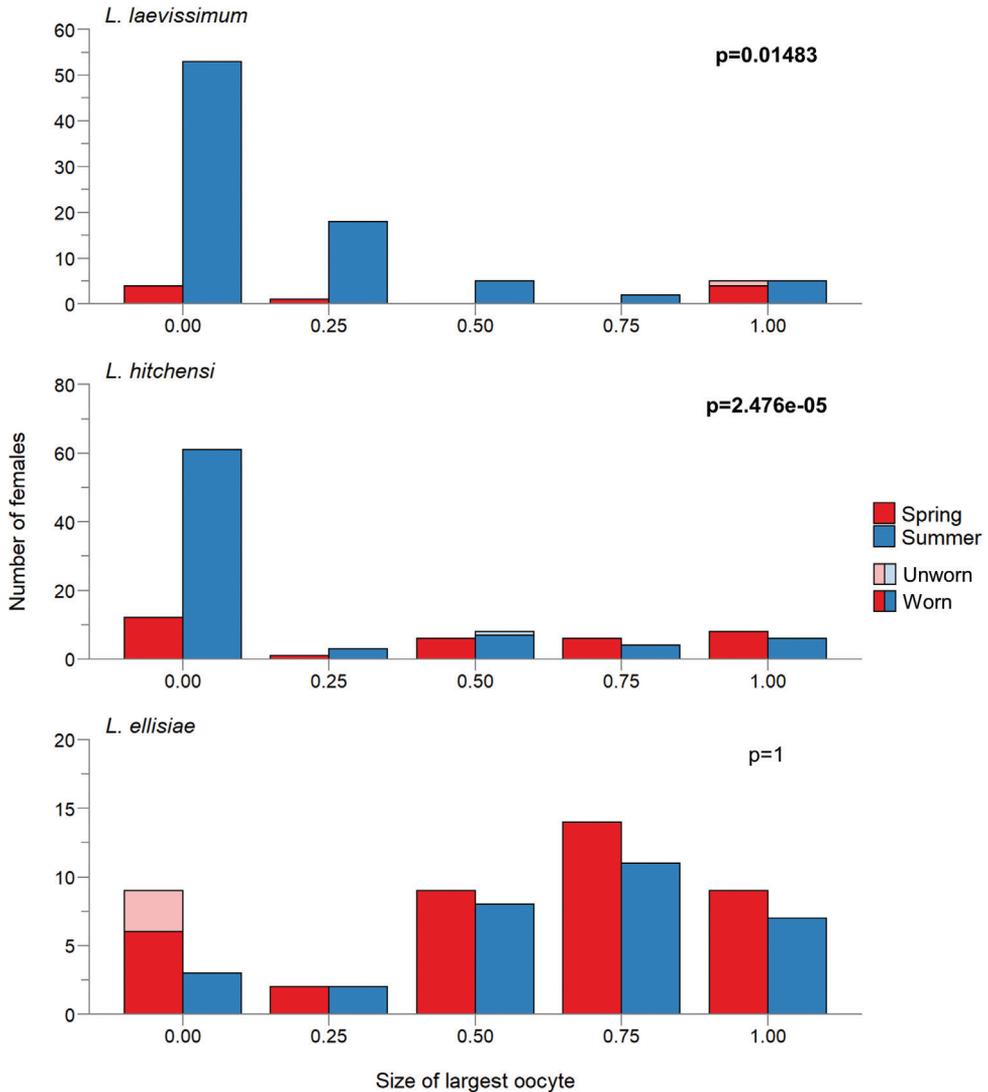


Figure 2. Wear and ovarian development of adult females caught in spring and summer. Fisher exact tests were used to compare the proportions of spring and summer females in each ovarian category. Unworn summer females with no ovarian development were excluded, as these females likely were newly eclosed. In *L. laevissimum* and *L. hitchensi*, spring females were significantly more likely to be fecund (largest oocyte at least 1/2-developed), while in *L. ellisiae*, spring and summer females showed similar levels of ovarian development (see Table 3 for statistics).

Lasioglossum ellisiae

Phenology: The brood-provisioning phase for Brood 1 began in mid-April and continued until mid-June (weeks 1 to 9; Figure 1). The second brood-provisioning phase began in mid-July (week 13) and continued until late September (week 23).

Table 3. Body size and reproductive traits of *L. hitchensi* and *L. ellisiae* females with statistical comparisons between spring and summer. Head width is given as the mean and standard deviation. Total wear and ovarian development scores are given as the median and range. Statistical comparisons are for spring versus summer females.

Species and trait	Spring females	Summer females	Statistical comparisons
<i>L. hitchensi</i>			
No. specimens	34	90	
Head width (mm)	1.58 ± 0.09	1.53 ± 0.09	ANOVA, F=7.40, df=1,120, p=0.007
Total wear score	4.0 (2–8)	4.0 (0–10)	ANOVA, F=0.385, df=1,120, p=0.536
OD score	0.75 (0–3.25)	0.0 (0–2)	Kruskal-Wallis, H=19.99, df=1, p=7.80e-06
Proportion fecund	21 / 34 (62%)	18 / 88 (20%)	Fisher test, p=2.48e-05
<i>L. ellisiae</i>			
No. specimens	46	36	
Head width (mm)	1.43 ± 0.05	1.38 ± 0.04	ANOVA, F=21.05, df=1,79, p=1.66e-05
Total wear score	4.0 (0–7)	5.0 (0–10)	ANOVA, F=3.88, df=1,78, p=0.052
OD score	0.75 (0–2.25)	1.0 (0–1.75)	Kruskal-Wallis, H=0.01, df=1, p=0.923
Proportion fecund	32 / 43 (74%)	26 / 35 (74%)	Fisher test, p=1

Males first appeared in week 11 so Brood 1 was definitely emerging by this time. Thus, *L. ellisiae* females exhibit a bivoltine phenology.

Colony social organization: Reproductive traits of spring and summer females are presented in Table 3. Spring females were 3.5% larger than summer females based on head width. However, spring and summer females had similarly high wear and OD scores and 76% of females from each group were fecund (Figure 2, Table 3). The similar wear and ovarian development of spring and summer females suggest that both spring and summer females were engaged in nest construction, brood provisioning, and egg-laying (Table 3). Thus, *L. ellisiae* likely is solitary or communal.

Discussion

The value of monitoring studies for inferring colony sociality: evidence from *L. laevisimum*

Observations of bees at nests are the ‘gold standard’ for investigating colony social organization. However, the social status of many sweat bee species has remained unstudied because nests have not been found in large enough numbers to persuade biologists to spend time studying them. The widespread growth of monitoring studies based on collections of foragers, provides an alternative source of social information. In this study, one of our objectives was to demonstrate that specimens collected in monitoring studies provide detailed information about sweat bee social behaviour that compares well with studies based on nest observations.

Table 2 provides a detailed comparison of the phenology and sociality of *L. laevisimum* in southern Ontario inferred from nest and non-nest-based observations (for convenience, we refer to specimens from the current study as ‘trapped’). Based on

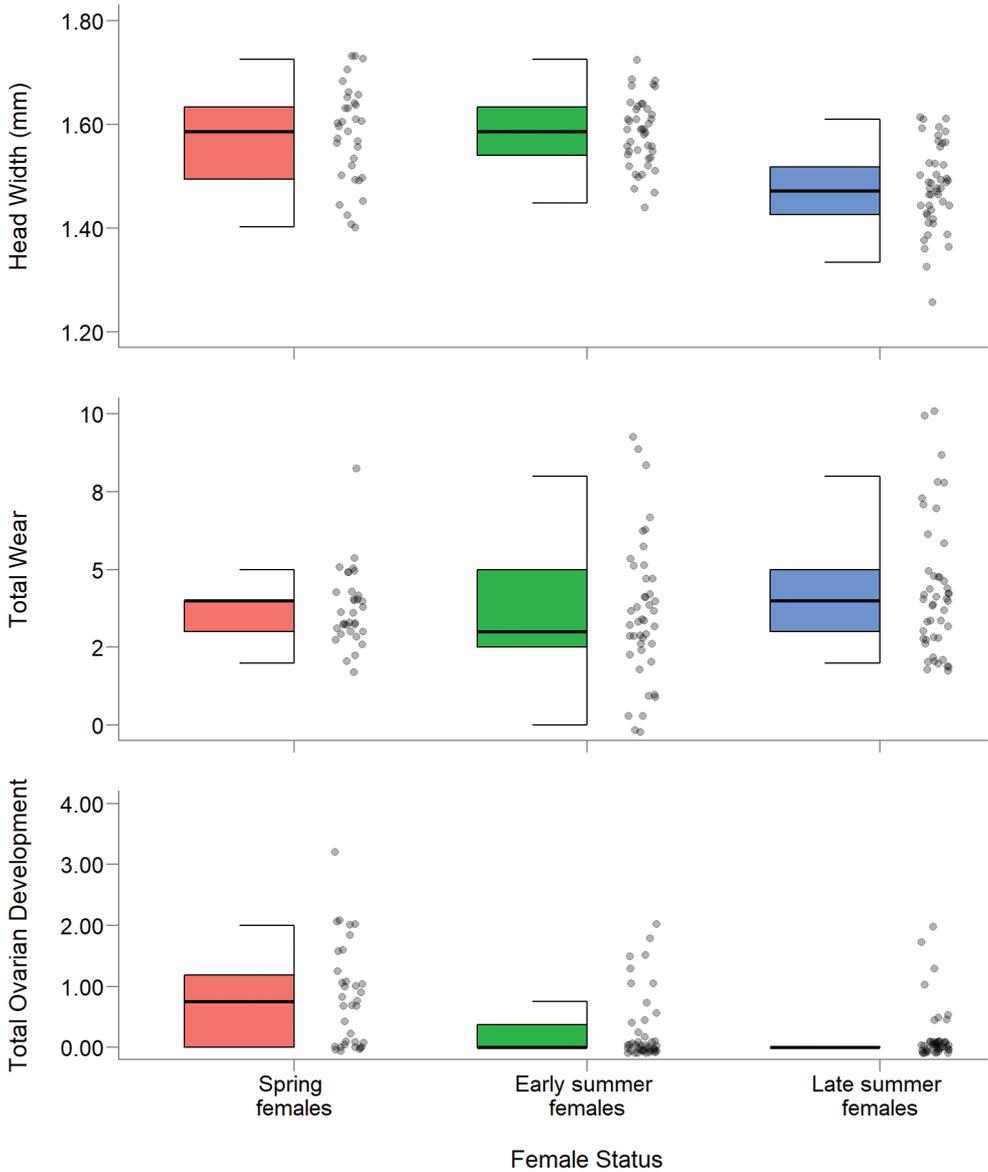


Figure 3. Social trait comparisons among spring, early summer and late summer females of *L. hitchensi*. Spring females were caught in weeks 0 to 8, early summer females in weeks 10 to 15, and late summer females from week 16 onward. Early summer females were larger than late summer females but showed similar signs of wear and ovarian development. See Table 2 for statistical analyses.

three years of nest observations and excavations, Awde and Richards (2018) found that spring foundress provisioning lasted from late April to late June, worker provisioning activity began in late June, and males and gynes were first collected from nests in July. The timing of brood-provisioning by queens and workers inferred from the pan trap data agrees well with this colony phenology inferred from nest data (Awde and

Richards 2018). In fact, the pan trap phenology for *L. laevissimum* even confirmed subtle, but repeated observations from multiple populations, that there is a third phase of female flight activity, as previously suggested by finding newly provisioned brood cells produced in nests excavated in late summer and autumn (Packer et al. 1989; Packer 1992; Awde and Richards 2018). Discrepancies between pan traps and nest data in the timing of major events likely stem from two causes: first, sweat bees exhibit considerable variation in the timing of spring and summer foraging in response to weather and climate variation (Richards et al. 2015). Second, pan traps likely do not attract all flying bees equivalently; at our research sites, male sweat bees are captured in pan traps far less frequently than females (MH Richards, unpub. data). The lack of males in pan traps probably accounts for the large discrepancy in timing of male emergence between pan traps and nest data (Table 2). Thus, female phenology based on pan traps matched exceedingly well with nest observations, but male phenology did not. Fortunately, most conclusions about colony social organization are based on the activities of females.

Social trait inferences based on examination of female specimens from trapping and nesting studies were largely in accordance, in that both clearly point to eusocial colony organization. While several traits were similar between trapped and nest specimens (e.g., spring female size, wear, and proportion of fecund females), there were also some differences. Trapped queens had significantly lower OD scores than nest queens; this difference reflects the fact that trapping began in April when some foundresses had not yet begun ovarian development, whereas nest queens were mostly collected after the onset of Brood 2 egg-laying (Awde and Richards 2018). Trapped workers were on average slightly smaller and more worn than nest workers, which suggests that smaller workers were more likely to leave the nest as foragers, while larger workers may be more likely to remain inside the nests, waiting for reproductive opportunities (Awde and Richards 2018). Another important difference was in the queen-worker size difference, which was smaller in trapped than nest specimens. Ideally, queen-worker size difference should be calculated based on comparisons between queens and the workers in their own nests; population-level averages, whether from pan traps, netting, or nest observations, consistently underestimate nest-based estimates, because of wide overlap in the sizes of queens and workers (Dunn et al. 1998; Richards et al. 2010, 2015). This would be an important consideration in cross-species comparisons that use queen-worker size differences as a metric (Breed 1976; Packer and Knerer 1985).

Some variables important in comparative analyses of the strength of eusocial colony organization cannot be inferred without nest data, including colony size, queen longevity, the frequency of queen replacement, and the proportion of males in Brood 1 (Breed 1976; Packer and Knerer 1985; Awde and Richards 2018). The proportion of mated workers could probably be reliably estimated from trapped specimens stored in liquid; finding the spermatheca and distinguishing whether it contains sperm is difficult when specimens have been pinned and dried for years before being rehydrated and dissected (Packer et al. 2007). Although rehydrated *L. laevissimum* females were assessed for matedness, we were not confident in the results (D.N. Awde, pers. obs.). One variable that we did not report here is the timing of gyne emergence. In our

experience, it can be difficult to distinguish between gynes and late-emerging workers, even when using specimens derived from nest excavations. In fact, *L. laevissimum* presents a particular puzzle with respect to gyne behaviour. In our nest-based study, we found females that appeared to be newly emerged gynes, but which had developing ovaries. We also found newly provisioned brood cells far too late in the season for brood to complete development, an odd phenomenon also noted for a Calgary population of this species (Packer 1992; Packer and Owen 1994). In general, late-emerging workers of eusocial sweat bees, especially those that emerge into queenless nests, may frequently overwinter as gynes (Danforth et al. 2003).

The social status of *Lasioglossum hitchensi* and *L. ellisiae*

Reproductive division of labour is the crucial variable distinguishing halictine eusociality (Batra 1966; Richards 2019). In *L. hitchensi*, eusociality was indicated by the significantly higher ovarian development of spring females. Small summer foragers with low ovarian development fit the classic eusocial phenotype of workers provisioning eggs to be laid by queens. The low proportion of fecund summer foragers (20%) is comparable to that observed in *L. laevissimum* (Table 2) and suggests fairly strong queen control of worker behaviour, as measured by this criterion (reviewed in Awde and Richards 2018). A novel finding was that foragers collected in early summer (weeks 10 to 15) were as large as spring foundresses. In contrast, small body size predominated among summer foragers a few weeks later. The large size of these early summer females suggests that they could be more resistant to queens' efforts to coerce them into becoming workers (Richards and Packer 1996), but on average, the early summer workers did not have higher ovarian development scores than late summer workers, so the significance of their large body size awaits nest-based observation.

We concluded that *L. ellisiae* is either solitary or communal because summer foragers were just as likely to have highly developed ovaries as spring foragers, and because summer foragers of *L. ellisiae* had significantly more ovarian development than those of the two eusocial species, *L. hitchensi* and *L. laevissimum*. Without nest data, females of solitary and communal species are indistinguishable, because the variance among females in their degree of ovarian development should be similar to the variance in solitary species. However, we suggest that solitary behaviour is more likely for two reasons. First, the only other communal halictid at our sites, *Agapostemon virescens*, is univoltine, and univoltinism is thought to be typical of communal halictids (Abrams and Eickwort 1980). Second, evolutionary reversion from eusocial to solitary behaviour has occurred frequently in halictid bees, whereas transitions between communal and eusocial behaviour are thought to be far rarer (Richards et al. 2003).

Body size patterns in eusocial and secondarily solitary sweat bees

Comparisons between eusocial and secondarily solitary sweat bees should help us to understand trait changes hypothesized to have been important in evolutionary tran-

sitions between solitary and social behaviour (Plateaux-Quénu and Plateaux 1985; Plateaux-Quénu et al. 1989). Body size differences between queens and workers are almost ubiquitous in eusocial Hymenoptera. In eusocial sweat bees, the larger size of queens enables them to aggressively manipulate the behaviour of their smaller daughters, forcing them to behave as workers (Richards and Packer 1996; Smith et al. 2019). Thus, in eusocial species there is clearly a selective advantage for queens in producing workers smaller than themselves.

Although solitary halictines are not expected to produce spring and summer females of different sizes, since they are all the same caste (Lin and Michener 1972), there may be reasons why spring and summer females of solitary species differ in size. For instance, larger body size of spring females might be an advantage in surviving hibernation, while smaller body size might be an advantage for summer females that forage in higher temperatures (Richards and Packer 1994, 1995). We found that in *L. ellisiae*, spring females were larger, as is also true in another secondarily solitary species, *L. (D.) villosulum* (Plateaux-Quénu et al. 1989). Secondarily solitary species might advantageously retain a spring-summer size difference inherited from a eusocial ancestor. In contrast, spring and summer females of two largely solitary species in another subgenus, *L. (Lasioglossum) scitulum* and *L. (L.) mutilum*, do not differ in size (Miyayama et al. 1998, 2000). In these two species, the reversion to solitary behaviour may be associated with a switch to similarly sized spring and summer females, which would depend on whether ancestrally eusocial halictines always displayed this size difference. In the most strongly eusocial halictine, *Lasioglossum marginatum*, queens and workers are the same size (Plateaux-Quénu 1959, 1962).

Linkages between phenology and social behaviour

Bivoltinism is necessary for eusociality in sweat bees, because in virtually all known species, daughters born in the first brood, remain in their natal nest to help rear a second brood during the same brood-rearing season, after which colonies die out. The only known exception to this rule is *Lasioglossum marginatum*, which lives in perennial colonies that produce a single brood of workers each year for several years, before producing reproductives only in the last year of a colony's life (Plateaux-Quénu 1959, 1962); the phylogenetic position of *L. marginatum* clearly indicates that its univoltine, perennial life history is derived. While it seems that halictine eusociality requires bivoltinism, the converse is not true. There have been reversions to solitary behaviour occurring in *Dialictus* (Danforth 2002; Danforth et al. 2003; Gibbs et al. 2012), and species like *L. ellisiae* and *L. villosulum* show social reversion is not always associated with reversions to univoltinism. Indeed, phylogenetic relationships within *Dialictus* indicate that there may have been multiple evolutionary changes back and forth in both phenology and sociality. *Lasioglossum ellisiae* is closely related to *L. vierecki*, which is also bivoltine and solitary, but other closely related species are eusocial (*L. parvum*, *L. umbripenne* and *L. gundlachii*; Wille and Orozco 1970; Eickwort and Eickwort 1971; Eickwort 1988; Gibbs et al. 2012), so either solitary or eusocial behaviour might

be secondary in this group. *Lasioglossum villosulum* is related to the solitary univoltine bees *L. lucidulum* and *L. lustrans*, implying that it might be secondarily bivoltine (Daly 1961; Knerer 1981; Plateaux-Quénu 2008; Gibbs et al. 2012).

Conclusions

The first study to compare specimens from pan trap and nest data in assessing colony social organization, focused on the eusocial behaviour of *Halictus confusus* (Richards et al. 2010). Systematic pan trap collections have now been used to describe solitary and eusocial behaviour of five species for which nests were not available: *Halictus tripartitus* (Packer et al. 2007), *H. ligatus* (Richards et al. 2015), *L. ellisiae* and *L. hitchensi* (current study), and *L. zonulum* (Proulx 2020). Given the phenological and social lability of many sweat bee species, it has long been a goal of social insect biologists to examine geographic and temporal variability in sociality, within and among species (Danforth et al. 2013; Kocher et al. 2014). Using specimens collected in monitoring studies, including dissections of rehydrated, pinned specimens, can make achieving this goal realistic.

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Supplementary material I

Figure S1. Right forewing of an *L. hitchensi* female.

Authors: Lyllian A-J Corbin

Data type: Image

Explanation note: Forewing of a *Lasioglossum (Dialictus) hitchensi* adult female with labels indicating the stigma, costal vein, and costal vein base. Image was captured using a Ziess stereomicroscope, with an AmScope camera attachment, at 40× magnification.

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Link: <https://doi.org/10.3897/jhr.88.73220.suppl1>

Supplementary material 2

Figure S2. Scoring systems for mandibular wear (MW) and wing wear (WW).

Authors: Lyllian A-J Corbin

Data type: Image

Explanation note: Diagram showing wear scores assigned to *Lasioglossum (Dialictus)* females based on the amount of accumulated wear on their mandibles and wing margins.

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Link: <https://doi.org/10.3897/jhr.88.73220.suppl2>

Supplementary material 3

Figure S3. Scoring systems for ovarian development scores.

Authors: Lyllian A-J Corbin

Data type: Image

Explanation note: Diagrams illustrating oocyte sizes (0, 0.25, 0.5, 0.75, and 1) scored in female specimens to assess ovarian development

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Link: <https://doi.org/10.3897/jhr.88.73220.suppl3>

Supplementary material 4

Figure S4. Head width comparisons among weeks suggest a mix of social traits in *L. hitchensi* summer females

Authors: Lyllian A-J Corbin

Data type: Image

Explanation note: Head width comparisons in *Lasioglossum (Dialictus) hitchensi* spring and summer females based on week collected. Figure shows boxplots, coloured by spring and summer female groups, on weeks that females were collected in pan traps in 2009. The black arrow indicates a decrease in summer female head width started on week 16, in which early summer females (collected in weeks 10 to 15) were larger than late summer females (collected in weeks 16 to 23).

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