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Understanding foraging and nesting behaviour of ground nesting bees in Dunedin, New Zealand

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Abstract: Solitary bees (Hymenoptera: Insecta) are key pollinators for natural ecosystems and agricultural crops. Unlike social bees, such as bumblebees and honeybees, solitary bees forage and build their nests independently and are more vulnerable to ongoing threats, including habitat loss and pesticides, than social bees. New Zealand has 27 native solitary bee species, and understanding foraging and nesting behaviours of native bees is critical for conservation efforts. However, few New Zealand studies have investigated the behavioural ecology of native bees. We looked at three native bee species in Dunedin: *Lasioglossum sordidum* (Halictidae), *Nesocolletes fulvescens* (syn. *Leioproctus fulvescens*), and *Nesocolletes pekanui* (syn. *Leioproctus pekanui*) (both Colletidae). These three native bee species were found at four urban nesting sites. Diurnal female nesting and foraging behaviours were observed and recorded regularly over a single summer. Both *L. sordidum* and *N. fulvescens* foraged more frequently and for longer periods in the morning than during midday and afternoon periods. Activity peaked when temperatures were between 20°C and 25°C at all four nesting sites. Wind speed significantly decreased general activity whereas ambient temperature significantly increased activity at one site. Additionally, both environmental factors influenced the number of nest entries and foraging trips of *L. sordidum*. Foraging trips of *N. pekanui* could last more than one hour, compared to *L. sordidum* and *N. fulvescens*, which foraged for c. 24 minutes on average before returning to the nest. In contrast, all three species spent similar lengths of time in the nest throughout the day. These findings contribute to an understanding of New Zealand native bees, but more research is needed to aid future conservation efforts.

Keywords: ambient temperature; foraging time; foraging trip; *Lasioglossum sordidum*; *Nesocolletes fulvescens*; *Nesocolletes pekanui*; nesting time; wind speed.

Introduction

Pollination is one of the key ecological processes that benefit human livelihoods. About 250 000 angiosperms depend on animal-mediated pollination. Insects are key pollinators for c. 75% of crops and c. 80% of wild flowering plant species, and bees are the most important insect pollinators (Potts et al. 2010; Newstrom-Lloyd 2013). While honeybees (*Apis*: Apidae) are the main pollinators for many agricultural crops (Yadav et al. 2017), there are only nine honeybee species, representing 0.04% of c. 20 000 bee species in the world (Raffiudin & Crozier 2007; Bustamante et al. 2021). Approximately 85% of bee species worldwide are described as solitary. Unlike honeybees and bumblebees (*Bombus*: Apidae), female solitary bees usually build their nesting tunnels and provision their larvae independently (Batra 1984). Some solitary bee species are more effective pollinators than honeybees for specific crops. For example, both male and female *Peponapis pruinosa* (Apidae) pollinate summer squash more effectively than honeybees, as they are adapted to work on these flowers at a faster rate (Tepedino 1981). Additionally, *Osmia lignaria*

(Megachilidae) are more efficient pollinators than honeybees for various crops, such as almond and sweet cherries (Bosch et al. 2006). *Osmia lignaria* are even managed for agricultural purposes using cavity nesting boxes (MacIvor 2017; Smagge et al. 2020). Despite the agricultural benefits that solitary bees provide for humans, their populations continue to decline worldwide due to various causes, including habitat loss and pesticides. Land changes due to agricultural intensification, urbanisation, and deforestation reduce the availability of floral resources for solitary bees as well as potential nesting habitats (Kline & Joshi 2020). Solitary bees are also more vulnerable to pesticides than honeybees because they spread the chemicals to every larvae within their nests (O'Reilly & Stanley 2023). Therefore, being able to understand foraging and nesting behaviours of solitary bees is crucial for successful conservation efforts in the future.

Most solitary bee species can produce one generation per year. After hatching, the larvae begin to feed on the mass-provisions before entering a diapause phase before winter (Bosch et al. 2010). On the other hand, some species are primitively eusocial, where individuals share the same

nesting tunnel, such as some species in the genus *Lasioglossum* (Halictidae) (Starr 2021; Nelson et al. 2022), and can produce more than one generation per year (Kukuk & Sage 1994; Cronin & Hirata 2003). In ground nesting bees, females excavate nesting tunnels underground to store their mass-provisions and raise their offspring. While solitary bees forage throughout the day, they provision their nests between trips and build additional chambers (Neff 2008). Nesting time (the time females spend in their burrows between foraging trips) could reflect the amount of provisions as well as nest construction time. However, no studies have measured the nesting time of female solitary bees.

While the foraging behaviour of solitary bees has not been as well studied as the foraging of social bees, we do know that solitary bee species actively forage during spring and summer seasons when floral resources are highly abundant. Individual female solitary bees mass-provision their offspring for the coming winter and autumn (Ne'eman et al. 2006). They place the provisioned food in brood cells or chambers, and seal them off when completed (Danforth et al. 2019). Generally, solitary bees have smaller foraging ranges than honeybees. Honeybee workers are able to forage more than 9 km, though most workers forage between 6–7.5 km (Beekman & Ratnieks 2000). An Australian study observed that honeybees forage for 23–64 minutes on average per trip (Colin et al. 2022). In contrast, solitary bees forage for 6–28 minutes on average per trip at shorter distances, from 70–600 m (Gathmann & Tschardt 2002; Bennett et al. 2018), though a Swiss study found that some species, such as *Hylaeus punctulatus* (Colletidae), *Chelostoma rapunculi* (Megachilidae), and *Hoplitis adunca* (Megachilidae) can forage more than 1000 m (Zurbuchen et al. 2010). Floral availability in habitats can affect the total time solitary bees spend on foraging. For instance, a German study showed that high floral availability close to their nests reduces the foraging trip duration of *Osmia bicornis* (Megachilidae) (Gathmann & Tschardt 2002). Hence, solitary bees prefer to forage in habitats with high floral availability within their short foraging distance, as they can forage more efficiently and visit floral resources more frequently (Ne'eman et al. 2006). However, solitary bees must also adapt their foraging behaviour in habitats with low floral availability to forage longer distances.

Here we aim to investigate the foraging and nesting behaviour of native, ground nesting, solitary bees in Dunedin, New Zealand. Compared to the number of international studies that have investigated the foraging ecology of solitary bees (Cameron et al. 1996; Putra & Nakamura 2009; Zurbuchen et al. 2010; Schäffler & Dötterl 2011; Hennessy et al. 2020), few New Zealand studies have primarily focused on foraging and nesting ecology of native solitary bees (Donovan et al. 2010; Donovan & Maynard 2010; Donovan 2016; Bennett et al. 2018). We studied three species of native bee at various locations around Dunedin: *Lasioglossum sordidum* (Halictidae), *Nesocolletes fulvescens* (Colletidae; syn. *Leioproctus fulvescens*) and *Nesocolletes pekanui* (Colletidae; syn. *Leioproctus pekanui*) (Almeida 2008; D. Ward, Manaaki Whenua, pers. comm.). For nesting behaviour, we investigate how much time females spend in their nesting tunnels between foraging trips. For foraging behaviour, we investigate how many foraging trips each individual bee takes throughout the day and the length of each foraging trip. Measuring foraging and nesting times allow us to monitor the movements of female bees and understand how their movements change throughout the day. Additionally, several international studies show that

environmental factors, such as ambient temperature and wind speed, can affect the activity of solitary bees (Potts & Willmer 1997; Stone et al. 1999; Vicens & Bosch 2000). Hence, we aim to investigate how ambient temperature and wind speed (Arnell et al. 2019) affect the foraging and nesting behaviour of native solitary bees.

Methods

Study species:

Lasioglossum sordidum is a small native bee, 4.9–6.1 mm in body length, and mostly black in colour (Donovan 2007; Appendix S1 in Supplementary Material). *Nesocolletes fulvescens* are known for their yellow-orange coloured body hairs and are only distributed in the South Island (Donovan 2007; Appendix S1). *Nesocolletes pekanui* are also mainly found in the South Island. Unlike *N. fulvescens*, they are black in colour, similar to other *Leioproctus* species (Donovan 2007; Appendix S1). No New Zealand study has investigated the foraging range of these *Nesocolletes* species.

Sampling locations

This study took place at four sites in Dunedin, New Zealand: Leven Street, Helensburgh Road, and two sites within the Dunedin Botanic Gardens (Appendix S1). Sites were located by word of mouth following requests for native bee sightings via social media and from the membership of the Otago branch of the New Zealand Entomological Society. We began to monitor the sites for the emergence of bees in late October 2022.

Leven Street

This nesting site was located along Leven Street, Roslyn, on the edge of the Dunedin town belt, which is an area of largely native forest (Appendix S1) adjacent to Robin Hood Park. The nesting site was a small clay bank which sloped down towards the road. The clay bank extends for c. 16 m and vegetation consists of tussock grasses (Appendix S1). This public area is managed by the Dunedin City Council. Both *L. sordidum* and *N. fulvescens* were found building their nesting tunnels along the clay bank during summer. *Lasioglossum sordidum* appeared first around late October, followed by *N. fulvescens* around early to mid-December.

Helensburgh Road

This site was in the front garden of a residential house. *Nesocolletes pekanui* were found building their nesting burrows in the sand between the bricks in the owner's garden (Appendix S1). This species emerged at the start of January 2023.

Dunedin Botanic Gardens

Established in 1863, the Dunedin Botanic Garden is New Zealand's oldest botanical garden. With the assistance from the Botanic Garden staff, we located two nesting sites for native bees. Location A was in the New Zealand native plant collection, in the upper gardens. The staff reported that they had made land modifications at Location A earlier in 2022. Location A was the smallest of the four nesting sites (c. 2 m²). *Lasioglossum sordidum* were found digging nesting tunnels between small pebbles (Appendix S1). Their nesting tunnels were on top of a rockery with light exposure due to no forest cover. Location B was located in the lower gardens right beside the Water of Leith. It was a cliff face of loose dirt with native

Veronica spp. shrubs at the base (Appendix S1). *Nesocolletes fulvescens* were found nesting here. The loose soil and steep gradient made it difficult to navigate the entire site.

Field Monitoring

We visited each of the four nesting sites once per week from 05/11/2022 to 29/01/2023 (Appendix S1). We arrived early in the morning, usually between 8:45 a.m. and 9:00 a.m. Upon arrival, we identified the native bees to the lowest possible taxonomic level and randomly selected a nesting site to monitor activity. Once a female bee entered a nesting tunnel with pollen, we marked the tunnel with a coloured push pin and started recording using a GoPro camera (Fig. 1). We recorded activity at the marked nesting tunnels three times through the day: morning (between 10:00–11:00 a.m.), midday (between 11:00 a.m.–12:00 p.m.) and afternoon (usually between 12:00–01:00 p.m.). Each recording period was about one hour long, though the recording period was sometimes shorter due to technical issues with the cameras (battery, overheating, etc.). For both Leven Street and Helensburgh Road, we placed three GoPro cameras recording three separate locations within each site per day, whereas each location in the Botanic Gardens had one GoPro camera, due to the small size and accessibility of the nesting sites.

We instantaneously measured the temperature and wind speed with a handheld Kestrel monitor (KESTREL 3000) at the start of the day and then every 20 minutes until the end of the day. This was done away from shade and was oriented toward the wind direction. We also randomly placed a quadrat (50 cm × 50 cm) within the nesting site and counted the number of bees flying within the quadrat for 5 seconds. This was done 13 to 16 times throughout the day.

Additionally, we caught emerging female bees before and during the afternoon recording period to confirm whether there was more than one female residing in a nesting tunnel, as other New Zealand studies have observed that two or more female *Lasioglossum* spp. can share a single nesting tunnel (Donovan 1980; Donovan 2007; Nelson et al. 2022). The first emerging female was caught, and we observed any further activity at the nesting tunnels. If another female bee exited from the same nesting tunnel, then this confirmed that more than one female shared the same tunnel. The first female caught was then released after the final recording period. This sampling occurred from early December 2022 to late January 2023 (*L. sordidum*, $n = 5$ nesting tunnels; *N. fulvescens*, $n = 6$ nesting tunnels; *N. pekanui*, $n = 5$ nesting tunnels) and from late October to mid-December 2023 (*L. sordidum*, $n = 24$ nesting tunnels).

Data extraction from videos

While reviewing the videos, we recorded both exit and entry times from the marked nesting tunnels. Exit time was noted when a female bee left its tunnel entrance. Entry was noted when a female bee returned with pollen on its scopae. Subtracting exit time from entry time provided the foraging time of one foraging trip per individual. The time from entry to exit provided the nesting period, when the female bee was presumed to be provisioning the nest with pollen and nectar for their larvae or excavating soil to build branching chambers.

Statistical analysis

Statistical analyses were carried out using R (v 4.0.3) (R Core Team 2020). We used linear mixed-effects models (one model per species) to investigate how the fixed effects of



Figure 1. Field nesting location. Go Pro camera recording marked nesting tunnels at Leven Street.

time of day (morning, midday, afternoon) and site influenced the foraging and nesting time (which both showed a normal distribution during exploratory data analysis) of *L. sordidum* and *N. fulvescens* (site was excluded for *N. pekanui* as it was only found at a single site). Day of the year (Julian date) was included as a covariate. Nest ID was included as a random factor, to account for repeated measures of individual nesting tunnels. The number of foraging trips and nest entries (both count data) were modelled using generalised linear mixed-effects models with a Poisson distribution, using the same fixed and random effects as above. When significant effects in foraging time and number of foraging trips were detected for *L. sordidum* and *N. fulvescens*, we used posthoc testing, using the multcomp package (v. 1.4-25), to detect significant differences between time periods throughout the day. Unfortunately, we were not able to conduct statistical analysis of foraging trips and foraging time for *N. pekanui*, as the bees foraged for longer than the 1 hour recording period.

We used linear models to investigate the relationship between the environmental factors (ambient temperature and wind speed), the total number of bees per quadrat, and the number of entries and foraging trips per bee species throughout the day. We transformed the count data using a log transformation. When investigating the number of entries and foraging trips, we calculated the average wind speed and ambient temperature for each recording period and used these as predictors; we included nesting site as a fixed effect.

Results

Foraging and nesting time

A total of 175 nesting tunnels were observed throughout the

2022/23 summer (74 tunnels from Leven Street, 39 tunnels from Helensburgh Road, and 64 tunnels from the Dunedin Botanic Gardens). We monitored *L. sordidum* at Leven Street less often than at the Botanic Gardens A due to time constraints, since there were more *L. sordidum* individuals at Leven Street than at Botanic Gardens A.

Number of female bees per nesting tunnel

A total of 41 female bees were caught while they were emerging from their nesting tunnels during afternoon recording periods. Both *N. fulvescens* ($n = 6$) and *N. pekanui* ($n = 5$) nesting tunnels were considered to contain only one female bee, as no activity was observed after a female bee was caught. On the other hand, ten *L. sordidum* nesting tunnels were observed to contain more than one female, as activity was observed after the first emerging female was caught (2022 summer: $n = 1/5$ nesting tunnels, 2023 summer: $n = 9/24$ nesting tunnels); hence foraging and nesting times are an underestimate for *L. sordidum*.

Lasioglossum sordidum

A total of 81 nesting tunnels were monitored for *L. sordidum* females. Time of day significantly affected the total time *L. sordidum* females spent foraging at both sites (Fig. 2a, $t = 3.580$, $p < 0.0001$; Appendix S1). Females spent less time foraging during the afternoon periods than during the morning ($p = 0.001$) and midday periods (Fig. 2a, $p = 0.002$). *Lasioglossum sordidum* females made more foraging trips in the mornings ($p < 0.001$) and midday ($p < 0.001$) than afternoon, and there were significant differences between sites, with females making more foraging trips at Leven Street (Fig. 2b, $t = 2.540$, $p = 0.011$; Appendix S1) and foraging more often earlier in the summer season (Appendix S1, $t = 1.125$,

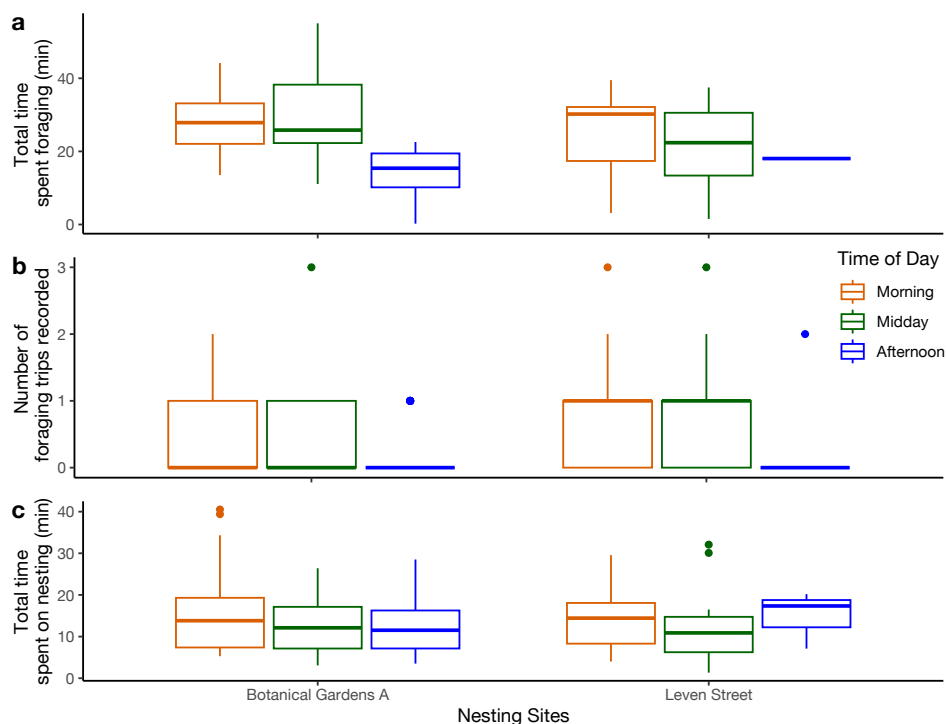


Figure 2. Effect of time of day on total foraging time (a), number of foraging trips (b), and total nesting time (c) for *Lasioglossum sordidum* females from both nesting sites. Botanic Gardens A ($n = 52$ nesting tunnels across 8 days), Leven Street ($n = 29$ nesting tunnels across 5 days).

$p = 0.003$). In contrast, *L. sordidum* females spent similar amounts of time in their nesting tunnels throughout the day between foraging trips at both sites (Fig. 2c, $t = -0.490$, $p = 0.138$; Appendix S1). For both the total time spent foraging and nesting, there were no significant differences between sites (Fig. 2c, $t = 0.262$, $p = 0.793$), and day of the year ($t = 0.237$, $p = 0.264$) was non-significant (Appendix S1).

Nesocolletes fulvescens

A total of 55 *N. fulvescens* nesting tunnels were monitored. Time of day significantly influenced the total time spent foraging (Fig. 3a, $t = -3.436$, $p < 0.0001$; Appendix S1) and number of foraging trips (Fig. 3b, $t = -4.818$, $p < 0.0001$; Appendix S1), with females foraging for longer periods of time and more frequently during the morning recording periods than during midday (foraging time: $p = 0.001$, Fig. 3a; foraging trips: $p < 0.001$, Fig. 3b) or afternoon recording periods (foraging time: $p < 0.001$, Fig. 3a; foraging trips: $p < 0.001$, Fig. 3b). In contrast, *N. fulvescens* spent similar amounts of time in their nesting tunnels between foraging trips throughout the day (Fig. 3c, $t = 0.930$, $p = 0.644$; Appendix S1). There were no significant differences between sites, and day of the year did not influence total time spent foraging or nesting (Appendix S1).

Nesocolletes pekanui

A total of 39 nesting tunnels belonging to *N. pekanui* were observed at Helensburgh Road. Unfortunately, there was insufficient data on both the total time spent foraging and the number of foraging trips for an analysis across time of day, as the foraging trips were so long that the re-entry times were often not recorded. *Nesocolletes pekanui* were monitored visually and found to forage, on average, for 146.3 ± 6.4 SE minutes ($n = 16$ nesting tunnels) throughout the day, with a range of 10.5 to 229.6 minutes. There were no significant differences

in nesting time throughout the day (Fig. 4, $t = -0.390$, $p = 0.898$; Appendix S1).

Environmental Factors

Higher wind speeds decreased the number of *L. sordidum* female nest entries (Appendix S1, $t = -5.100$, $p < 0.0001$) and foraging trips (Appendix S1, $t = -3.008$, $p = 0.003$), while higher ambient temperature increased the number of nest entries (Appendix S1, $t = -2.055$, $p = 0.041$). No significant differences between nesting sites were detected ($t = -0.719$, $p = 0.473$). Additionally, there were no significant differences between morning and afternoon recording periods on either environmental factor (wind speed: $t = 0.224$, $p = 0.823$; temperature: $t = 1.386$, $p = 0.182$).

Wind speed and ambient temperature had no significant effect on *N. fulvescens* nest entries (Appendix S1, temperature: $t = -0.076$, $p = 0.940$; wind speed: $t = -1.125$, $p = 0.262$) or foraging trips (Appendix S1, temperature: $t = 0.255$, $p = 0.799$; wind speed: $t = -0.357$, $p = 0.721$). There was also no difference in ambient temperature ($t = 0.674$, $p = 0.507$) or wind speed ($t = -0.494$, $p = 0.626$) between morning and afternoon recording periods and no significant difference between sites in number of foraging trips ($t = 0.970$, $p = 0.334$) and entries ($t = 1.405$, $p = 0.162$).

A total of 269 quadrats were sampled from all four nesting sites throughout the field season. Both ambient temperature (Appendix S1, $t = -1.898$, $p < 0.001$) and wind speed (Appendix S1, $t = 4.452$, $p < 0.001$) significantly affected bee activity, although these effects were apparent only at Botanic Gardens A (Appendix S1, Temperature: $p = 0.010$; Appendix S1, Wind speed: $p = 0.010$), where bee activity increased with site temperature (Appendix S1, $R^2 = 0.246$, $p < 0.001$) and decreased with increasing wind speed (Appendix S1, $R^2 = 0.103$, $p = 0.014$).

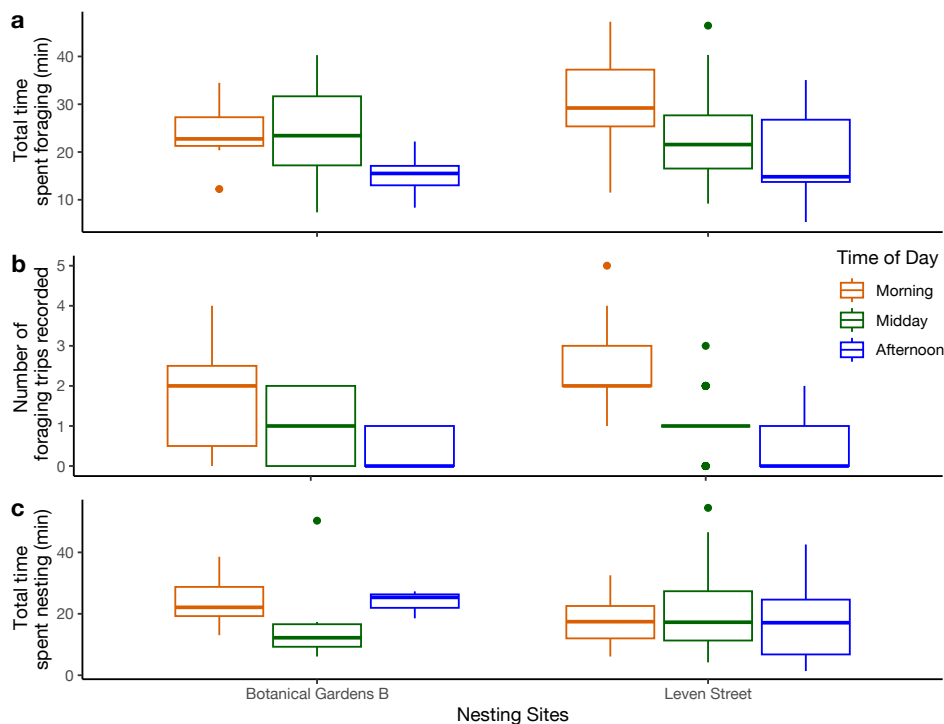


Figure 3. Effect of time of day on total foraging time (a), the number of foraging trips (b) and total nesting time (c) for *Nesocolletes fulvescens* females from both nesting sites. Botanic Gardens B ($n = 11$ nesting tunnels across 3 days), Leven Street ($n = 44$ nesting tunnels across 5 days).

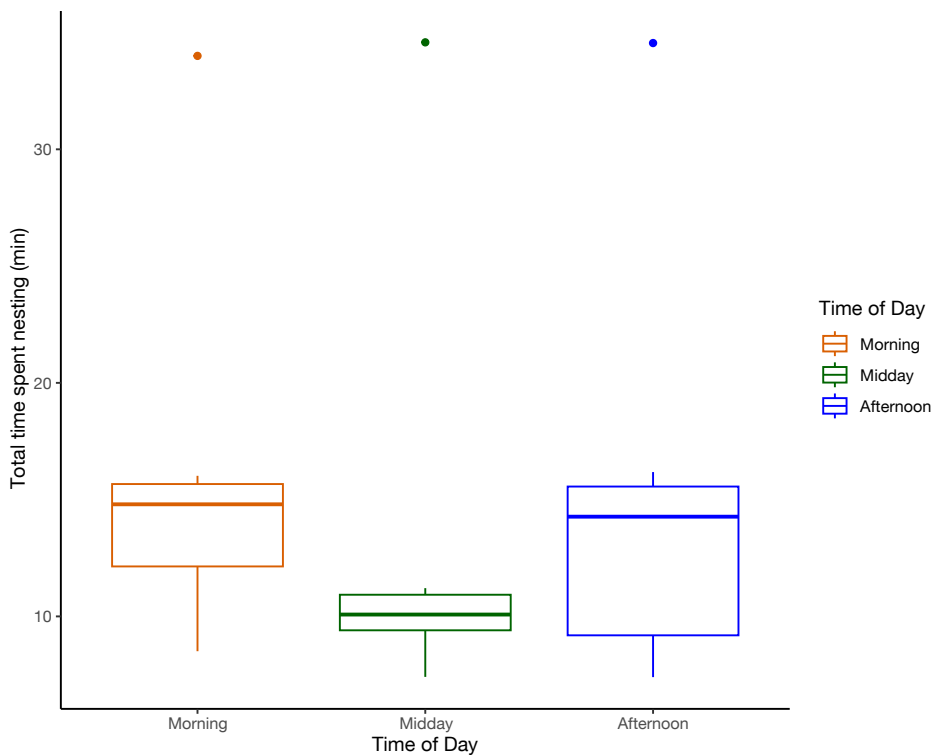


Figure 4. Effect of time of day on total nesting time for *Nesocolletes pekanui* females from Helensburgh Road ($n=39$ nesting tunnels across 5 days).

Discussion

Foraging and nesting behaviour in three species

Despite their ecological importance, there is less knowledge about the foraging and nesting behaviour of solitary bees than there is about social bees. To address these knowledge gaps, we observed the behaviour of three native bee species in urban Dunedin: *Lasioglossum sordidum*, *Nesocolletes fulvescens*, and *Nesocolletes pekanui*. Both *L. sordidum* and *N. fulvescens* females mostly foraged in the mornings. On the other hand, all three native bee species nested for similar amounts of time throughout the day. Ambient temperature and wind speed significantly affected some of the behaviours of *L. sordidum* females, but not *N. fulvescens* females.

The foraging activity of *L. sordidum* and *N. fulvescens* females decreased throughout the day, with maximum foraging effort between 10 a.m. and 11 a.m. Other studies have observed similar foraging patterns. Another New Zealand study observed that the number of kiwifruit pollen grains collected and the activity of honeybees and *Lasioglossum* spp. peaked between 10 and 11 a.m., and then decreased in the afternoon (Howlett et al. 2017). Likewise, a study from Scotland found that foraging trip duration and time spent foraging on raspberry flowers peaked between 10 a.m. and 12 p.m., and subsequently decreased in the afternoons (Willmer et al. 1994). Increased foraging efforts in the mornings could be associated with reduced availability of nectar and pollen in the afternoon. Several studies have observed diurnal patterns of nectar availability (Timewell & Mac Nally 2004; Muniz et al. 2013; Xu et al. 2021). Experimental studies have also shown that when floral visitors are excluded, nectar volume either increases or remains high throughout the day, but when exposed to floral visitors, nectar volume decreases (Herrera 1990; Barp et al. 2011). When nectar volume decreases, the nectar sugar concentration increases, possibly due to lower

water availability or increased evaporation (Fowler et al. 2016; Cavalcante et al. 2018). Hence, both *L. sordidum* and *N. fulvescens* females may be responding to high nectar and pollen availability in the mornings.

An alternative explanation for higher levels of foraging in the morning is that ambient temperature could influence foraging patterns throughout the day, though ambient temperature was similar between morning and afternoon recording periods. The bees observed in this study were most active between 20 and 25°C, with activity decreasing when temperatures exceeded 25°C. This indicates a temperature threshold where high temperatures can be detrimental to native bees (Corbet & Huang 2016; Hamblin et al. 2017). Solitary bees are ectothermic insects, meaning that external temperature can affect their metabolism and development (Forrest & Chisholm 2017; Torson et al. 2017). For example, an American study found that high temperatures, between 40°C to 46°C, can reduce activity, development and survival of *Megachile rotundata* (Hayes & López-Martínez 2021). Possibly, ambient temperatures could negatively affect the activity and health of native solitary bees in New Zealand when exceeding 25°C (Giejdasz & Fliszkiewicz 2016; Forrest & Chisholm 2017). Interestingly, in this study ambient temperature and wind speed only significantly affected the foraging behaviour of *L. sordidum*. *Lasioglossum sordidum* has a smaller body size than *N. fulvescens* (Rader et al. 2009). Higher wind speeds could cause *L. sordidum* to spend more energy to stabilise themselves (Trani et al. 2022). This could explain why the number of foraging trips and nest entries of *L. sordidum* decreased at higher wind speeds. Likewise, when looking at the effect of wind speed and ambient temperature on the overall number of active native bees at a site, we only observed significant effects at Botanic Gardens A. Compared to other nesting sites, Botanic Gardens A was more exposed throughout the day. Leven Street had tree canopy cover around the nesting site, Botanic Gardens B was a cliff facing in a northwest direction,

and the nesting site in Helensburgh Road was located by a house, which provided shade in the early morning. Botanic Gardens A was located in the middle of the rock garden with no shelter from the wind or sun. Botanic Gardens A was therefore more exposed to environmental factors than other nesting sites. This could explain why the effects of ambient temperature and wind speed on the native bee activity were mainly observed in Botanic Gardens A.

Another possible explanation for longer foraging times in the mornings could be that the returning females initially took a longer time to locate their nest entrances due to the use of coloured pins. Solitary bees have been shown to use landmarks to locate their nest entrances (Wcislo 1992); hence, the use of the coloured pins may have caused the bees to spend more time re-learning their flight paths while foraging. Future studies should first test whether coloured pins impact nest relocation.

In this study, *N. pekanui* foraged for at least one hour, compared to the other two species (*L. sordidum* for 24.47 minutes and *N. fulvescens* for 24.74 minutes on average). Many *N. pekanui* females did not return during the morning recording session. They first exited during the morning recording periods and returned during either the midday or early afternoon recording periods. No other *N. pekanui* females were observed entering and exiting the marked nesting tunnels between recording periods. This was confirmed by continuous observation of the nesting tunnels while recording environmental factors and native bee activity at the small nesting site. Hence, we were not able to analyse the number of foraging trips or foraging trip duration. Other international studies have shown that foraging trips of some solitary bee species last longer than one hour. For example, a Colombian study recorded the foraging trip duration of *Anthophora waltheri* (Apidae) females lasting from 4 to 88 minutes (Gonzalez et al. 2006).

Nests ensure the survival of native solitary bees. They provide protection from predators and offer optimal conditions for proper development of their larvae (Almeida 2008). However, no studies on solitary bee nesting biology have recorded the nesting time of females. This study found that all three native bee species had similar nesting times throughout the day. During video monitoring, we observed both *L. sordidum* and *N. fulvescens* females digging soil out of the nesting tunnels. This suggests that females were building new brood chambers to store mass provisions (Alcock 1980; Donovan 1980; O'Neill et al. 2014). This digging behaviour occurred randomly among female bees throughout the day.

One limitation of our study was that we observed *L. sordidum* behaviours for only the early part of the nesting season. Hence, we are unable to infer how nesting and foraging behaviour changed over the season at this site. However, we observed that *L. sordidum* males started to appear around mid-December and then the sex ratio became biased towards males (Z. Lim pers. obs.). Females sometimes would not leave their nesting tunnels because males blocked the exit as they sought to mate with the females. Therefore, the presence of males would likely affect the foraging and nesting times of *L. sordidum* females. *Lasioglossum sordidum* females were also seen less often from mid-December onwards, possibly because they were avoiding males. Generally, female solitary bees tend to avoid mating with males while foraging, to reduce costs to female fitness and reproductive success (Stone 1995). For example, *Anthrenoides micans* (Andrenidae) females are intercepted and repeatedly harassed by males about once every 3 minutes, and repeated copulation of females during foraging

periods can decrease the provisioning rate (Dutra et al. 2020).

Eusociality of *Lasioglossum sordidum*

For both *N. fulvescens* and *N. pekanui*, we concluded that only one female occupied each nesting tunnel. Generally, female bees from Colletidae build nests independently (Albans et al. 1980; Wuellner & Jang 1996; Rozen et al. 2019). However, our observations suggest that more than one *L. sordidum* female was sharing the same nesting tunnel in 10 out of 29 nesting tunnels where we experimentally caught a bee to monitor nest sharing. As a result, the foraging and nesting time of *L. sordidum* females may be an underestimate in this study, and thus the findings for *L. sordidum* may be unreliable compared to findings for *N. fulvescens* and *N. pekanui*. It was not possible to differentiate *L. sordidum* females emerging from the same nesting tunnel in the videos. Alternatively, these additional females could have just been opportunistic individuals scoping out a hole that was now unguarded. Additional experimental work is required to determine the social system of *Lasioglossum* bees in New Zealand.

Our observations confirmed previous records in New Zealand that *Lasioglossum* spp. display social organisation, possibly at a primitive eusocial level (Donovan 1980; Nelson et al. 2022). Eusociality has evolved three times in sweat bees (Hymenoptera: Halictinae) (Boesi et al. 2009), a group that includes *Lasioglossum*. Most *Lasioglossum* species in temperate zones, such as *Lasioglossum zephyrus* in the USA, *Lasioglossum calceatum* in the UK and *Lasioglossum malachurum* in Germany, have a founding queen (Kukuk & May 1991; Davison & Field 2018; Steitz & Ayasse 2020). These queens, mated females, construct nests and produce workers as their first brood, followed by the reproductive brood (both females and males) (Davison & Field 2016). New Zealand is located in a temperate zone like the UK and the USA. This suggests that *L. sordidum* in New Zealand might share a similar social structure with other *Lasioglossum* species from temperate zones (Starr 2021).

Conclusions

Overall, this study showed that *N. fulvescens* and *L. sordidum* forage more actively during the morning than during midday or afternoon. On the other hand, *N. pekanui* can forage for longer periods of time than either of the other two species. All three native bee species spent similar periods nesting between foraging trips. Ambient temperature and wind speed affected the general activity of some native bees. For future research, an alternative method is required to accurately observe the behaviours of *L. sordidum* while taking their primitive eusociality into account. These findings will contribute to a better understanding of foraging and nesting behaviour of native bees and assist future conservation efforts.

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Supplementary Material

Additional supporting information may be found in the online version of this article.

Appendix S1. Supplemental figures.

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