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ORIGINAL ARTICLE

Using citizen science data to compare flight phenology of two oligolectic bees (Hymenoptera: Andrenidae) with the flowering of their host plants

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Abstract. Understanding the relationship between solitary bee flight and flowering phenology is globally relevant for environmental management and habitat restoration. Using Swedish citizen science data over an 11-year period, the flight behaviours of two oligolectic solitary bees (*Andrena hattorfiana* and *Andrena marginata*) were compared to the flowering phenology of their hosts (*Knautia arvensis* and *Succisa pratensis*) in southern Sweden. There were 2,327 and 4,566 records of flight and flowering, respectively. While associative studies cannot resolve the degree of oligolecty, a strong temporal association of *Andrena hattorfiana* with *Knautia arvensis* and *Andrena marginata* with *Succisa pratensis* was indicated. Three conclusions emerged when comparing annual data: first, the flight period of both bee species studied overlapped with the flowering period of their corresponding host plants. Second, earlier flowering of *Knautia arvensis* corresponded with the earlier flight of *Andrena hattorfiana*. Third, the flight period duration was unaffected by the flowering period duration. For *Andrena hattorfiana/Knautia arvensis*, climate change may shift the start of flight and flowering periods to earlier dates in the year. A similar response would be expected for *Andrena marginata/Knautia arvensis*, but not for *Andrena marginata/Succisa pratensis* where there instead might be an increasing mismatch between the flight and flowering periods.

INTRODUCTION

The vast majority of flowering plants worldwide require animals for successful reproduction (Ollerton, 2011; Ayers et al., 2021). One significant group of pollinators is the bees (Apoidea), which have an intricate co-evolutionary history with their associated angiosperms (Lunau, 2004; Plant & Paulus, 2016). A key feature of this plant/pollinator relationship is the degree of specialisation, i.e., the degree to which a bee species uses many plant species (polylecty), only a single plant genus (oligolecty), or even a single plant species (monolecty) (Pekkarinen, 1997; Schlindwein, 2004; Cane, 2021). In these species, females collect pollen from selected plant species to support larval growth. Pollen from non-preferred sources can be detrimental to larval development (Praz et al., 2008; Dharampal et al., 2020). Phylogenetic studies have identified oligolecty as an ancestral trait from which polylecty have evolved numerous times (Danforth et al., 2013). Many species in the genus *Andrena* studied here are oligolectic (Larkin et al., 2008).

Considering climate change predictions (IPCC, 2014), phenological patterns may change (Benadi et al., 2014; Olliff-Yang & Mesler, 2018; Duchenne et al., 2020; Wyver et al., 2023). Warmer temperatures can cause plants and animals to flower or become active earlier in the year (Hegland et al., 2009; Bartomeus et al., 2011; Brooks et al., 2014, 2017; Kharouba et al., 2018; Blasi et al., 2023). In contrast, flowering in many plant species is determined by the photoperiod (Cho et al., 2017; Wang et al., 2021), suggesting an increasing mismatch between pollinator activity and flowering under global warming. Hence, an improved understanding of the relationship between bee flight and flowering phenology is important to better understand how the ecosystem service of pollination may be affected by climate change in the future (Gallagher et al., 2020). Oligolectic and monolectic solitary bees that rely on the flowering of a limited number of plant species and are more susceptible to phenological mismatches.

In this study, we aimed to associate the flight periods of two narrowly oligolectic solitary *Andrena* bees in Sweden with the flowering of their associated species (Dipsacaceae) using open-access citizen science data. We posed three questions:

1. Do flight and flowering periods overlap?
2. Is there a positive correlation between onset of solitary bee flight and flowering onset in different years? This would suggest that plant/pollinator adjustments correlate with climate change.

3. Is there a positive correlation between the length of the flight period and the flowering period over different years?

MATERIAL AND METHODS

This study focused on the flowering phenology of two important, relatively late-flowering grassland plants and the flight phenology of two oligolectic solitary bees. The study area was Götaland, a region of southern Sweden covering 88,000 km^2.

Study species

The target plant species were widespread in the study area. *Knautia arvensis* has been identified as a key plant species for pollinators and was subsequently proposed as a target for ecosystem restoration and improving grassland conditions for pollinators (Franzén & Nilsson, 2008). *Knautia arvensis* and *Succisa pratensis* are both visited by a wide range of pollinators (Adams, 1955; Franzén & Larsson, 2009; Varga et al., 2022).

Andrena hattorfiana is considered monolectic in Sweden, i.e., strictly confined to a single species (*Knautia arvensis*) for pollen (Larsson, 2005). However, in southernmost Sweden, *Andrena hattorfiana* reportedly exploits the rare *Scabiosa columbaria* (Holmström et al., 2018b); therefore, "narrow oligolectic" may be a more accurate description. However, most *Andrena hattorfiana* in Sweden use only a single plant species. *Andrena hattorfiana* inhabits open, dry and sandy ground near *Knautia arvensis* (Holmström et al., 2018b).

Andrena marginata collects pollen from several different Dipsacaceae (Westrich, 1990), yet only *Knautia arvensis* and *Succisa pratensis* were common and widespread in the study area. In addition to garden plants of these genera, two rare native species, with limited geographic distributions, also exist (*Scabiosa canescens* and *Scabiosa columbaria*). *Andrena marginata* nest sites are found near the flowers of *Knautia arvensis* and *Succisa pratensis* (Holmström et al., 2018a).

In both bee species, larvae develop during late summer, overwinter as adults, and remain in the nests until their relatively late flight period begins.

Flight and flowering data

Data on flowering and solitary bees was obtained from Artportalen (the Swedish Species Observation System; www.artportalen.se). We preferred to use the data source where observers had originally uploaded information, rather than secondary sources like GBIF (Global Biodiversity Information Facility) or iNaturalist. We believe this decision means less duplication and generally a more uniform data set. In Artportalen, both professionals and amateurs can contribute to species observations. With over 100,000,000 reports, it has become a powerful potential data source for Swedish species research. There is a validation system for rare species or those that are difficult to identify (using photographs, collected specimens, detailed reports, or known expert status). In the present study, 2.9% and 13.4% of *Andrena hattorfiana* and *Andrena marginata* observations, respectively, had been validated.

The underlying assumption tested was that temporal patterns of observations in Artportalen, within and between years, were useful for understanding phenology and potential changes.

Observation data of the solitary bees *Andrena hattorfiana* and *Andrena marginata* was downloaded in March 2021. We selected the years 2010–2020 due to data availability and only reported imago or adult individuals, thereby excluding dead individuals, larvae, and nests. Reports can include several specimens, however, we only considered the report date without consideration of the number of animals reported. Finally, sex was reported in approximately 75% of the total reports. However, as male *Andrena hattorfiana* and *Andrena marginata* made up only 12% and 15% of the observations, respectively, their numbers would not allow a meaningful comparison between sexes. Therefore, we ignored sex in this study so as to retain as many observations as possible.

Flowering data for *Knautia arvensis* and *Succisa pratensis* was downloaded in March 2021. Reports often included a statement on flowering stage, therefore, reports of non-flowering individuals or those that lacked flowering information were excluded.

Temperature data

The monthly average daily temperature data from all Swedish weather stations in Götaland was downloaded from the Swedish Meteorological & Hydrological Institute (www.smhi.se). A joint monthly dataset for Götaland was compiled for each year between 2010 and 2020. As the two bee species have slightly different flight periods, species-specific temperature data was compiled: May to August for *Andrena hattorfiana* and *Knautia arvensis* and June to September for *Andrena marginata* and *Succisa pratensis*. The annual summer temperatures were expressed as a deviation from the long-term average within the reference period 1961–1990.

Statistical analysis

For a general description of flight and flowering, data from all 11 years was merged in order to present a temporal pattern by fitting a lowes function (stiffness = 0.1) to the frequency data (using Statistica 64, TIBCO, Cloud Software Group, Inc).

To illustrate the interannual variation and annual overlap of flight and flowering, we arbitrarily defined the flight and flowering period to encompass 70% of the observations occurring in a year (i.e., by excluding the first and last 15% of records in a year). Different cutoff thresholds were tried, but because the number of observations in a year could be few, lower cutoff values resulted in the more extreme date outliers being too influential.

Furthermore, to test whether summer temperatures drive flowering and flight phenology, we calculated the correlation with annual temperature. Response data included the start date (excluding the first 15% of data), median date, and length of flight/flowering (15%–85% of observations).

RESULTS

The recorded sightings of bee species and plants varied annually (Table 1), and the lowest recorded annual sighting was 37 for *Andrena marginata*.

When 11 years of data were combined, the flight period of *Andrena hattorfiana* overlapped well with the flowering period of *Knautia arvensis*, and the same was true for *Andrena marginata* and *Succisa pratensis* (Fig. 1). There was an approximately one-month difference in flight periods. For both pairs, the flowering period started two weeks before the flight period, and the peaks in flowering and flight periods were relatively close, while the flowering period continued until the beginning of September, well beyond the flight period of both *Andrena* species.

When the data were broken down into annual patterns, the flight periods were much shorter (average number of days from 15% to 85% of the records; SD) for *Andrena hattorfiana* (26.1; 3.4) and *Andrena marginata* (27.8; 7.2) than for the flowering of *Knautia arvensis* (56.5; 11.5) and *Succisa pratensis* (48.0; 7.6). The flowering of the two species overlapped to a much larger extent than did the flight periods (Fig. 2). Although the flowering periods of the two

Table 1. Observation counts for the four species between 2010–2020.

	Knautia arvensis	*Succisa pratensis*	*Andrena marginata**	*Andrena hattorfiana***
2010	79	47	44	88
2011	62	68	37	234
2012	57	72	67	174
2013	47	1072	46	438
2014	92	95	43	98
2015	176	170	37	163
2016	214	204	37	165
2017	243	236	82	170
2018	225	161	40	58
2019	288	258	37	122
2020	360	340	74	73

*Females and males accounted for 59% and 15% of observations, respectively. **Females and males accounted for 63% and 12% of the observations, respectively.

plant species overlapped to some extent in all years, the flight period of the two bee species did not overlap in eight out of eleven years (Fig. 2). In four of the years, there was no overlap between the flight period of early flying *Andrena hattorfiana* and the late flowering *Succisa pratensis,* whereas late flying *Andrena marginata* overlapped with the early flowering *Knautia arvensis* in all years except one (Fig. 2).

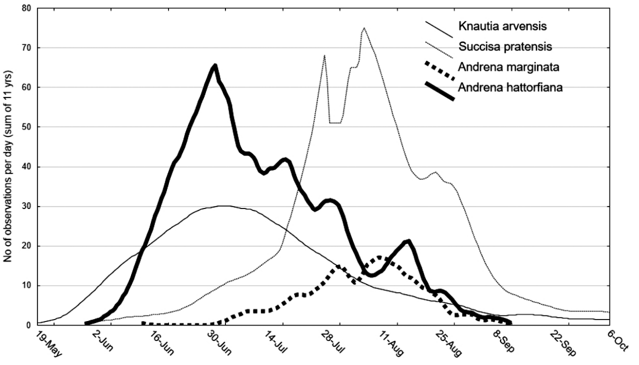

Fig. 1. Temporal patterns of the flight period of two *Andrena* species and flowering period of two Caprifoliaceae (Dipsacaceae) summed over 11 years, as reflected in citizen science data.

Temperature and correlation

Only one of the two bee species (*Andrena hattorfiana*) and one of the two plants (*Knautia arvensis*) conformed to the expected pattern of response to summer temperatures, with higher temperatures causing an earlier start and earlier peak (median date; Table 2). However, the duration of the active period was affected differently at higher temperatures, leading to a shorter flight period and extended flowering period (Table 2). In contrast, the start and peak of

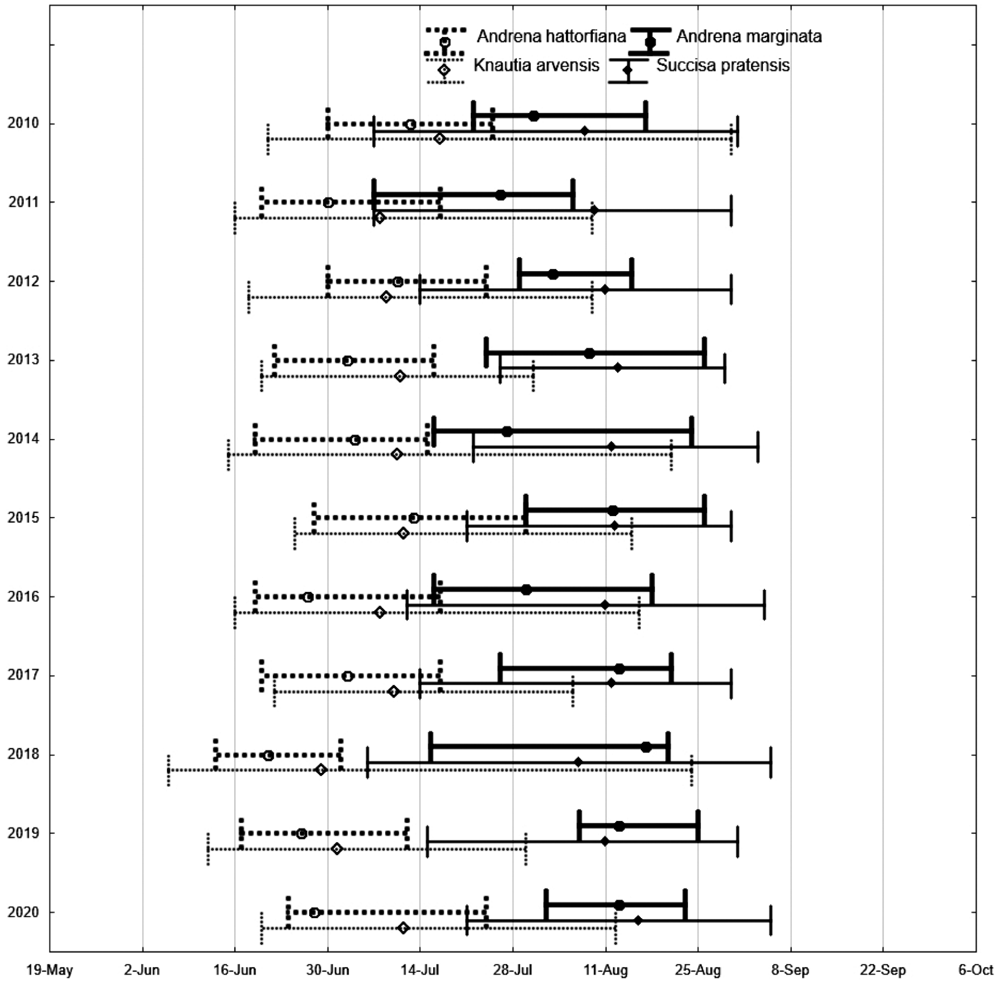

Fig. 2. Yearly observations of flight season for two *Andrena* species and of flowering for two Caprifoliaceae (Dipsacaceae). Flight and flowering times are defined as 15%–85% of data. Points represent median dates.

Table 2. Correlation between flight, flowering, and summer temperatures. For *Andrena hattorfiana* and *Knautia arvensis,* average temperatures for May to August were used, and for *Andrena marginata* and *Succisa pratensis,* average temperatures for June to September were used.

	Andrena hattorfiana	*Knautia arvensis*	*Succisa pratensis*	Summer temps
Start of flight/flowering				
Andrena marginata	0.326	0.451	0.313	–0.271
Andrena hattorfiana	–	0.763**	0.169	–0.786**
Knautia arvensis		–	0.441	–0.875***
Succisa pratensis			–	–0.303
Median of flight/flowering				
Andrena marginata	–0.300	0.185	–0.418	0.250
Andrena hattorfiana	–	0.772**	0.091	–0.799**
Knautia arvensis		–	0.337	–0.710*
Succisa pratensis			–	–0.311
Lenght of flight/flowering				
Andrena marginata	–0.227	0.421	0.473	0.421
Andrena hattorfiana	–	–0.438	–0.406	–0.718*
Knautia arvensis		–	0.725*	0.607(*)
Succisa pratensis			–	0.541(*)

(*)P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.

Andrena marginata and *Succisa pratensis's* activity were unrelated to summer temperatures, whereas the length of flowering tended to increase with temperature (Table 2).

DISCUSSION

The main finding in this study was that the citizen science data carried a phenological signal that could be biologically interpreted. Despite using a large geographic study region and only 11 years of data, we demonstrated consistent differences in phenology between the two bee species and two of their potential plant species. Furthermore, interannual variation in phenology in two of the studied species could be explained by the temperature data. Therefore, this type of data is well suited to phenological study.

Flower availability for the bees

The flowering period of *Knautia arvensis* began approximately a month before *Succisa pratensis*, and the flight period of *Andrena hattorfiana* started approximately a month before that of *Andrena marginata*. Given the relatively short flight period (approximately 30 days) and temporal flight and flowering patterns, *Andrena hattorfiana* would mainly have access to *Knautia arvensis*, while *Andrena marginata* would mainly have access to *Succisa pratensis*. However, in most years, both bee species could potentially use both plant species. According to faunistic literature, *Andrena hattorfiana* is narrowly oligolectic, almost exclusively using *Knautia arvensis*, while *Andrena marginata* is oligolectic and uses both plant species considered in this study (www.artfakta.se). However, according to our data, only the late-flowering *Succisa pratensis* would be available for *Andrena marginata* in some years. Associative data cannot clarify the degree to which flower specialisation varies among bee species, but may indicate whether a species is behaviourally or functionally confined to a single species. Reportedly, for example, *Andrena hattorfiana* does not visit *Succisa pratensis* despite the widespread presence of it's flowers in the study area. Furthermore, the late flight period of *Andrena marginata* prevents it from exploiting *Knautia arvensis* in some years.

Onset of flight and flowering

Global warming may affect the synchronisation between the flight seasons of narrowly oligolectic pollinators and flowering in several ways. Firstly, both pollinator and associated plant host might shift towards earlier activity periods (Bartomeus et al., 2011); secondly, pollinator flight period and flowering could become more synchronised if one of them adapts to changes (Freimuth et al., 2022); and thirdly, flight and flowering might become less synchronised (Forrest, 2016). Earlier activity periods may be expected under warming climate conditions at the time scale of decades to centuries, as previously shown for European pollinators and Swedish bumblebees (Ogilvie et al., 2017; Duchenne et al., 2020; Blasi et al., 2023). In the current study, the flowering period of *Knautia arvensis* began earlier in warmer years, similar to the flight period of *Andrena hattorfiana*. Although a temperature cue to trigger the start of the flight period is expected for species that overwinter as imagos (e.g., temperature sum; Schäffler & Dötterl, 2011), such an effect was not observed in *Andrena marginata,* nor in the flowering period of *Succisa pratensis*. Based on these findings, earlier activity for *Andrena hattorfiana/Knautia arvensis*, but not for *Andrena marginata*/*Succisa pratensis*, may occur as global warming progresses. In addition, the flowering of *Knautia arvensis* may become unavailable to *Andrena marginata* under climate change. Whether this would mean a substantial loss of food for *Andrena marginata* and a trend towards this species becoming limited to a single host plant remains to be established. Previous studies have shown that desynchronisation between bee flight and flower phenology causes fitness loss in one or both species (Hegland et al., 2009, Villagomez et al., 2021). Fitness in the current plant species is unlikely to be affected, as they are visited by a wide range of pollinators (Adams, 1955, Franzén & Larsson, 2009, Varga et al., 2022).

Another potential consequence of global warming could be that an oligolitic bee might become exposed to plant species that expand into their geographic range. For example, if *Scabiosa canescens* and/or *Scabiosa columbaria* became more widespread and abundant in Sweden, *Andrena marginata,* which can use various Dipsacaceae (Westrich, 1990), would have more food alternatives. Phenological changes may also occur within bee species due to global warming. Kehrberger et al. (2019) showed that only males of *Osmia cornuta* responded to global warming. The type of citizen science data used in this study, covering easily-sexed bees, is useful for exploring this potentially important effect of gender further. Males comprised 10% and 15%, and reports of the current species and females were 65% and 59%, respectively.

Length of flight period and flowering

Generally, flowering periods are much longer than flight periods, suggesting that mismatches with the main plant species are unlikely (cf. Iler et al., 2013, Olliff-Yang

& Mesler, 2018). An expected consequence of climate change and warmer, dryer conditions is the narrowing of the activity period (Duchenne et al., 2020). The current data showed that the flight period of *Andrena hattorfiana* decreased with increasing temperatures, e.g., due to more active flight activity during warm periods, whereas both plant species flowered longer under warmer conditions, which are also invariably dryer, in Sweden. This might increase or decrease the mismatch of flowering and flight periods and may be further investigated using longer time periods of citizen science data.

Data assessment

The degree of temporal resolution in this study, which encompassed a relatively large geographic region, surpassed expectations. Consequently, we are optimistic about the value of such data for phenological studies.

However, the data contained some shortcomings. The most critical aspect is that observations reflect where and when observations are made and only partly reflect species activity. Spatial bias occurs when certain areas or habitats are more frequently visited by observers and constitutes a major limitation of citizen science data, requiring complex data analyses to resolve (e.g., Snäll et al., 2011; Bradter et al., 2018). However, spatial bias is unlikely to undermine our conclusions regarding phenological issues. More importantly, there is a temporal bias in reporting, where some periods of field activity are more popular with observers. Insect and plant observations in early autumn are subject to a negative bias, and unusually early and late observations are more likely to be reported than observations during peak activity. This motivated us to exclude early and late observations. However, if we assume this temporal bias to be constant between years, the data could still provide a comparable interannual description of flight and flowering, although the accuracy of the estimates might be poor.

Species differ in the probability of their being reported, and in our study, there was a surprising lack of reports on the common plant species *Knautia arvensis.* Such potential differences must be considered when comparing species. The correct identification of organisms is one of the main challenges facing citizen science data (Ratnieks et al., 2016; López-Guillén et al., 2024). However, the species included in the current study are relatively easy to identify. Therefore, we believe that misidentifications were not a major concern in the present study.

In this study, the three phenological variables used (first flight/flowering, median flight/flowering, and length of flight/flowering) were sensitive to the number of observations and, therefore, we excluded the earliest and latest data. This reduces, but does not eliminate, the bias caused by the low number of observations. Furthermore, we included a relatively large geographic region in order to obtain meaningful analysis data. The drawback is that this region contains both a temperature gradient (south to north) and a rainfall gradient (west to east), which potentially rendered patterns less distinct.

The citizen science data used here seem useful for evaluating phenological patterns and changes due to weather or climate change, but only for frequently reported species.

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