Local Weather Conditions Affect Forager Size and Visitation Rate on Bramble Flowers (*Rubus fruticosus*) in Bumble Bees *(Bombus spp)*

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Abstract Bumble bees (*Bombus*; Hymenoptera) are crucial pollinators for many agricultural crops, but their numbers have declined - with climate change as a possible driver. Different aspects of local weather conditions can have substantial effects on bumble bees' ability to forage. Here we made 501 observations of bumblebee workers on bramble flowers (*Rubus fruticosus*) to explore how the characteristic sizes of foragers active and their individual rate of movement between flowers were correlated with aspects of weather. Firstly, we found that increased ambient temperature is correlated to reduced activity in larger workers. Moreover, while higher humidity was linked to an increase in smaller workers, an increase in cloud cover led their numbers to decrease. Visitation rate and temperature showed a significant negative relationship whereas no other weather aspect affected visitation rate significantly. Our results suggest that predicted rises in ambient temperatures will adversely affect bumble bee foraging, and particularly so for larger-bodied workers. We anticipate that this study can be used as a foundation for longer-term and more detailed studies on bumble bee foraging and colony performance. Such work is vital to identify management measures to mitigate pollinator declines and preserve food security.

Keywords bumble bees · pollinators · climate change · foraging

Introduction

Pollination is one of the key services that maintain ecosystems (Klein et al. 2007) and is crucial for the sexual reproduction of about 70% of tropical and 84% of European crops (Williams 1994; Roubik 1995). Thus, human food security is largely dependent on the diversity and efficiency of pollinating animals (of which most are flying insects). While the global land-cover used to grow pollination-dependent crops has increased (Aizen et al. 2009), the number of flying insects has substantially decreased in the last thirty years (Potts et al. 2010; Dirzo et al. 2014; Hallmann et al. 2017). Pollinators are threatened by a range of human-induced changes such as the increased use of pesticides, a reduction of hedgerows and fragmentation of habitat (Potts et al. 2010; Feltham et al. 2015; Goulson et al. 2015). Moreover, climate change is also thought to be a major cause of pollinator loss (Warren et al. 2001; Memmott et al. 2007); and so investigating the effects of weather on pollinators is vital.

Climate change is causing shifts in local weather conditions all over the world (Howe 2018). Average

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ambient temperature is predicted to rise by 1.5-2 °C by the end of the century (Collins et al. 2013), while wind speeds are expected to increase by 1 up to 5 m s^{-1} within the next one hundred years (Robinson et al. 2017). Short-term weather effects are also becoming more extreme; with increasing frequencies of drought in summers while winters have had a rise in recorded rainfall (Jenkins et al. 2008). As mentioned, these changes can have detrimental effects on pollinating insects as, for example, high wind speeds can adversely affect their ability to fly and forage efficiently (Combes and Dudley 2009; Chang et al. 2016). On the other hand, higher temperatures can limit the ability of some large or well-insulated pollinators to forage, due to their limited ability to lose heat effectively (May 1979; Heinrich and Esch 1994; De Marco et al. Jr 2005). This may also have caused the observed range changes of pollinators towards higher latitudes (Chen et al. 2011).

One pollinator group that is vital for pollinating a large number of crops are bumble bees (Velthuis and Van Doorn 2006). Bumble bees are eusocial insects that make up the genus *Bombus*, which comprises ~ 255 species in the family of Hymenoptera (Goulson 2010) and are primarily found in the northern hemisphere (Williams et al. 2009). They are characteristically larger and hairier than other species of Hymenoptera and the resulting insulation due to the lower surface area to volume ratio decreases heat loss (Heinrich 2004). Furthermore, they are facultatively endothermic and can raise their internal body temperature to over 30 °C by contracting their flight muscles simultaneously to generate heat (Heinrich 1993) and by substrate cycling catalyzed by the enzyme fructose bisphosphatase (Newsholme et al. 1972; Clark et al. 1973). These adaptations allow them to forage in lower ambient temperatures than other pollinating insects (Ahn et al. 1988) and enables a successful provision of nectar and pollen to the colony even during colder spring months.

However, even with their ability to warm up their flight muscles, most bumble bee workers are restricted to foraging at ambient temperatures of about 12 °C (Goulson 2010). On the other hand, recent rises in average temperature especially during the summer (Jenkins et al. 2008) have increased their risk of overheating due to their larger, well-insulated bodies. A thoracic temperature of about 42 °C is lethal (Heinrich and Heinrich 1983) and despite

having some methods of releasing heat (countercurrent heat exchange through the petiole: Heinrich (2004); black fur on thorax: Williams (2007), the foraging activity of many workers may be limited in high temperatures as well. Moreover, as well as air temperature, they are affected by a range of other aspects of local weather. Crall et al. (2017) showed that wind and turbulence can significantly affect bumble bee body stability and wing kinematics which, in turn, affect their ability to land on flowers precisely. High wind speeds, especially when coming from the side, also cause the need for constant adjustment to prevent yaw and roll, and workers are more likely to have high-impact landings on flowers under these conditions (Chang et al. 2016). The effects of humidity are less well resolved, as studies indicate contradicting results (Sanderson et al. 2015; Yankit et al. 2020). Evidence does suggest, however, that air humidity affects which resource is collected by bumble bees and lower humidity seems to be preferable for pollen collection (Peat and Goulson 2005). Further, bumble bees are restricted by their low visual acuity, which decreases their ability to see in low light conditions (Kapustjanskij et al. 2007). Although some workers were observed to leave the nest during twilight (less than 10 lx), it was shown that their ability to successfully search for flowers is adversely affected by low light intensities (Hall et al. 2021).

The extent to which bumble bee workers are affected by local weather conditions is also partly influenced by their individual size (Heinrich and Heinrich 1983; Heinrich 2004; Kapustjanskij et al. 2007; Goulson 2010; Willmer and Finlayson 2014). Bumble bees divide the work in the colony at least to some extent based on alloethism, meaning that tasks are divided based on worker size; rather than age as seen in, for example, honeybees (Wilson 1971). Individual body mass can vary up to ten-fold within a single nest (Alford 1975) where smaller workers conduct nest-based tasks whereas larger workers are primarily foragers (Goulson 2010). However, even within foragers there is large variation in sizes and some studies have recorded a more than two-fold difference in mass between the smallest and largest forager active at one time in the same colony (Goulson et al. 2002; Spaethe and Weidenmüller 2002). Some studies suggest that larger workers are better foragers, as they can carry more nectar and have a higher foraging efficiency in comparison to smaller ones (Spaethe and

Weidenmüller 2002; Willmer and Finlayson 2014), and are better equipped to tolerate colder conditions due to their lower surface area to volume ratio (Heinrich 2004). Contrary to this, Peat and Goulson (2005) found no significant effect of increasingly poorer weather conditions on worker size. Nonetheless, Hall et al. (2021) and Kapustjanskij et al. (2007) found that larger bees were more successful foragers than smaller bees in lower light conditions due to their larger eye size (Taylor et al. 2019). Additionally, Crall et al. (2015) observed that larger workers fly faster in windy conditions but have greater need to perform corrective maneuvers if obstacles are in their flight path. Thus, further research is required to solve the discrepancies in previous studies and directly investigate the effects of weather conditions on the same population of bumble bees.

The aim of this study is to investigate the effects of weather conditions on the size distribution of actively foraging workers and their visitation rate in the field. Most studies investigating the effects of weather conditions on worker size did so by monitoring and measuring bees as they left and arrived at the nest (Goulson et al. 2002; Spaethe and Weidenmüller 2002; Peat and Goulson 2005; Hall et al. 2021). Although this allows an accurate measuring of time spent outside the nest and bee weight by using integrated scales in nest entrances and ID-tags, one cannot say for sure whether workers leaving the nest do so to forage, or for example for defecation or orientation flights (Cisarovsky 2013; Philippides et al.

2013). Hence, we aim to research bumble bee foraging behavior on flowers in the field to focus solely on foraging workers. We did this by recording weather conditions regularly throughout the day while observing bumble bee foragers on bramble flowers (*Rubus fruticosus* agg.) and documenting their species, size, and flower visits per minute. Based on previous work, we predict that larger workers would be more common at colder temperatures, lower light conditions and higher wind speeds. Moreover, we expect that the rate at which different flowers are visited would be negatively correlated with temperature as well as higher wind speeds.

Methods and Materials

Worker Size

During a one-week period from the 23 to the 30 May 2021, 102 bumble bees of a range of different species were caught opportunistically on flowers and their thorax width at its widest point measured to the nearest 0.1 mm (Goulson et al. 2002; Peat and Goulson 2005) using electronic Vernier calipers (RoHS, England). By determining peaks in a size-frequency histogram (Fig. 1) and using visual classification (Willmer and Finlayson 2014), the bees were categorized (using an ad hoc classification) as either small (≤5.5 mm thorax width), medium (>5.5 to 7.0 mm), large (>7.0 to 9.0 mm) and extra-large (>9.0 mm).

Fig. 1 Histogram showing the size distribution of a total of 102 bumble bees that were caught and the thorax width was measured at its widest point using Vernier calipers. Size categories were chosen based on peaks in the histogram as well as visual cues. Thus, workers were categorized into small (≤5.5 mm), medium (5.6 to 7.0 mm), large (7.1 to 9.0 mm) and extra-large (>9.0 mm) bees were considered gynes and, hence, not considered during the main data collection period
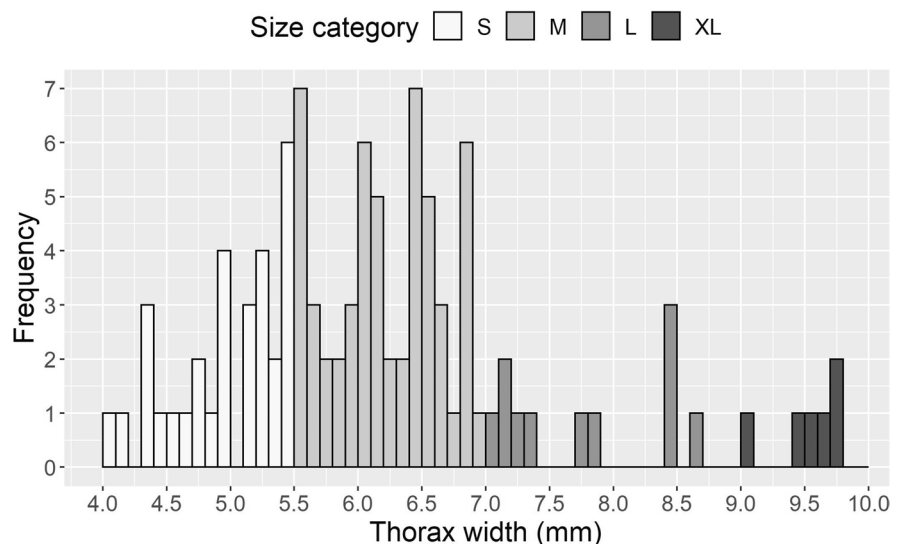
All but extra-large individuals were considered workers with extra-large bees being counted as gynes. Measured bees were larger on average than found in previous UK studies (Goulson et al. 2002; Del Castillo and Fairbairn 2012), but it has been suggested that bumble bees are larger in Scotland as it is colder than England (Peat et al. 2005), which was also supported by the findings of Willmer and Finlayson (2014). Another 100 bees were then caught, and size was classified based on visual inspection before measuring the individual, to determine accuracy of visual categorization of the observer. Over 90% of these bees had a thorax width within the range expected according to the visual classification On this basis, we assume that bees during the main observations were categorized reasonably accurately on the basis of visual inspection. This avoided the need to catch them during the main observation period which would have influenced their subsequent foraging behavior. Another 50 bees were caught after three weeks of data collection to ensure that accuracy remained high, and again more than 90% of individual had a thorax width within the range expected according to the visual classification.

Weather and Visitation Rate

Data collection occurred between the 10 June and 04 July 2021 around St Andrews, Scotland. Observations were made between 10am to 5pm, the peak foraging time for pollinators (Garbuzov et al. 2017), in all conditions except heavy rain that prevented any foraging activity. However, if no bumble bees were seen for 30 min the conditions were considered unsuitable and data collection ended for that day. Bumble bees were observed on bramble (*Rubus fruticosus*), a common plant locally that flowers between June and July and is frequently visited by bumble bee species (Goulson et al. 2005; Wignall et al. 2020). We surveyed at two sites (Site 1: Botanical Garden St Andrews, 56°20'09.8"N 2°48'17.0"W; Site 2: East Sands Coastal Path, St Andrews, 56°19'53.3"N 2°46'11.8"W) which were assigned a number based on the flowering start date of the present bramble. Bramble at the Botanical Garden bloomed first and was, thus, site 1. Data was collected there until another site was in peak bloom. As sites were added, they were surveyed on alternating days (Day 1: Site 1, Day 2: Site 2, etc.).

Temperature, humidity, and wind speed were measured with hand-held instruments every 30 min; and light intensity every 15 min due to higher variability because of cloud cover changes. Wind speed and light intensity measurements occurred at 1 m above ground but the thermohydrometer was placed on the ground to ensure shade coverage and prevent overestimates due to the effects of direct sunlight on the thermometer. The thermohydrometer (Vaisala HM40, SW version 1.7, Finland) was left for about 10–15 min before recording the first data to give it time to adjust to conditions. Wind speed (Anemometer, RS AM-4201, United Kingdom) was measured by recording it for 60 s and the highest recorded value was documented as the current wind speed. Light intensity (ATP ETI-1301, United Kingdom) was measured while facing the sun but holding the device horizontal. Cloud cover was categorized in okta (number of eighth of the sky covered in clouds) and was assessed immediately after each foraging observation.

When a bumble bee was seen foraging on a flower, we started a stopwatch (Garmin, vivoactive 4s) and recorded the number of flowers visited during the foraging event. The maximum time of observation for each individual bee was 5 min. For each worker, we recorded date, time of start of observation, bumble bee species, size category, total number of flowers visited, duration of observation, presence or absence of pollen in pollen baskets, and the relevant weather data. Bee species were identified using Pinchen (2006), and *Bombus terrestris* and the morphologically very similar *Bombus lucorum* were both recorded as *B. terrestris/lucorum* due to the high risk of misidentification in the field (Wolf et al. 2010). We recorded the total number of flower visitations without consideration of whether a recorded sequence of visits involved different plants on the same patch or return visits to the same flower. Visitationrate was then calculated per minute by dividing the number of flowers visited by the duration in seconds and multiplying the result by 60.

On some occasions the workers visited flowers that were hidden from view by leaves or within the bushes so that accurate flower visitation could not have been recorded. In these cases, the stopwatch was paused, and we waited about 30 s for the bee to reappear into our field of view. If it did, the stopwatch was resumed, and the observation continued. If not, this individual observation was considered finished. If bees foraged for longer than 5 min, we tried to ensure not to record the same bee twice. Given typical values for the size

Fig. 2 (**A**) Number of observations of each bumble bee species and respective size distribution within the species. The most commonly recorded species was *Bombus hypnorum* (n = 193), followed by *B. terrestris/lucorum* (n = 122), *B. pascuorum* (n = 75), *B. pratorum* (n = 54), *B. soroeensis* (n = 36), *B. hortotum* (n = 14), and lastly *B. lapidarius* (n = 7). (**B**) Percentage distribution of size categories within each species. The species with the highest proportion of large workers were *B. terrestris/lucorum* (67.2%), *B. soroeensis* (66.7%), and *B. hortotum* (50.0%) whereas *B. soroeensis* (5.5%) and *B. terrestris/lucorum* (5.8%) had the lowest percentage of small workers
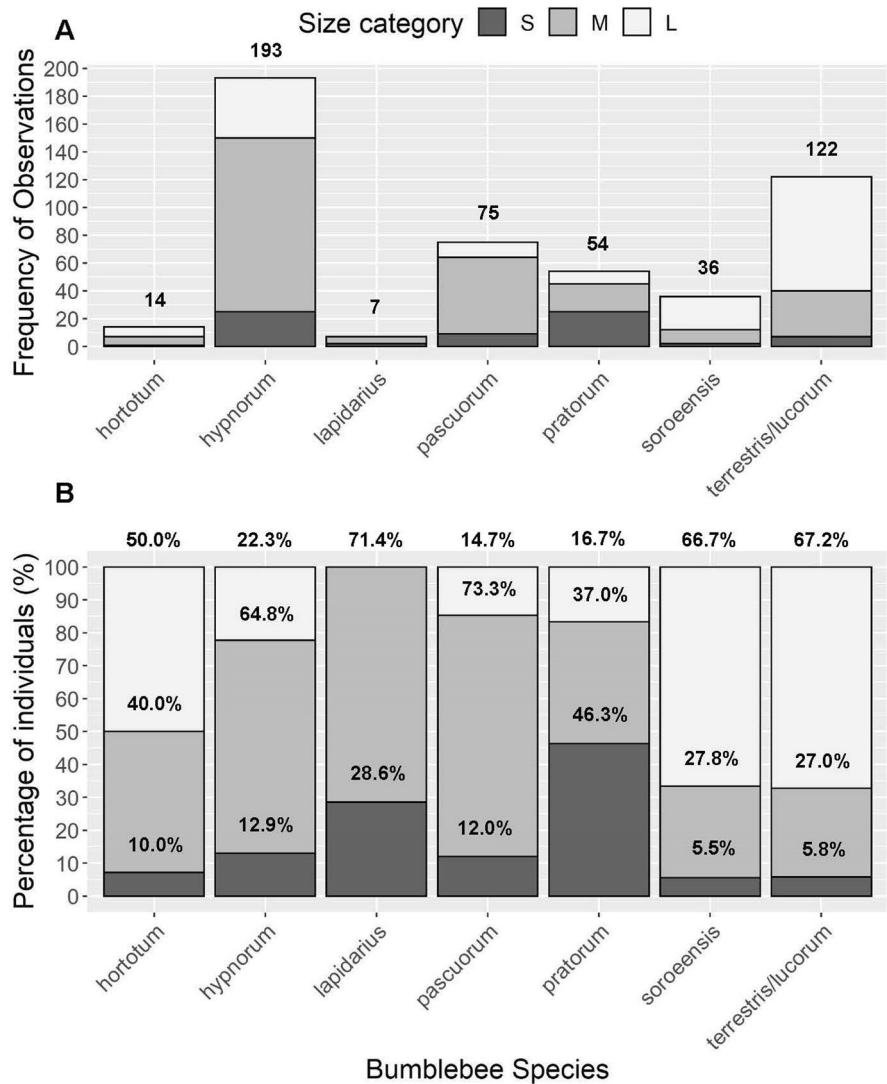
of bumble bee colonies, the turnover of workers within colonies, typical visitation rate, and density of colonies, we except that the bulk of our observations will involve different individuals.

Statistical Analysis

All data was analysed and using R v. 4.1.0 (R Core Team 2021) and significance was taken as p < 0.05.

Plots were created using the *ggplot2* package (Wickham 2016).

To investigate whether the size of foraging worker bees was affected by local weather conditions a multinomial logistic regression with size of workers as the response variable and all recorded weather conditions and location as predictor variables was used (Model 1). This model was run using the *nnet* package in R (Venables and Ripley 2002).

multinom(Worker size ~ Location + Temperature + Humidity + Wind Speed + Cloud Cover + Light, data = data)　　　(Model 1)

The model was run a total of three times, each time with a different worker size as the intercept. Worker size levels were changed using the *relevel* function in R and allowed for pairwise comparison between the different response variable factors. All predictor variables were kept in the model, even if they had no significant effect on worker size as they were all considered important explanatory variables. The same was done for all other models run (see below).

To investigate the effects of local weather conditions on species composition Kruskal Wallis tests followed by pairwise Mann-Whitney U tests for pairwise comparisons were used. These were chosen as data distribution for all weather conditions was non-parametric (Shapiro-Wilk, p<0.05 for all conditions). As species distribution differed with weather conditions (see Results), the above explained multinomial logistic regression was repeated but included the three most common species (*B. hypnorum, B. terrestris/lucorum, B. pascuorum)* as explanatory variables to investigate whether the changes seen in size were due to weather conditions rather than the species make-up of the actively foraging bee population.

We examined whether there were significant differences in visitation rate between worker sizes and species by using a Kruskal Wallis test, as data for visitation rate was non-parametric (Shapiro-Wilk, W=0.927, p<0.001). Moreover, to model the effects of local weather condition and location on the visitation rate a GLM with an inverse Gaussian family and identity link function was fitted. Hence, just like in Model 1 all weather conditions and location were included as factors, but also presence of pollen in pollen baskets and the number of open flowers were explanatory variables in the model to predict visitation rate (Model 2). Data for visitation rate was not normally distributed (Shapiro-Wilk, W=0.927, p<0.001) but right-skewed and log-transforming the data did not make it parametric (Shapiro-Wilk, W=0.994, p=0.038). Thus, the inverse Gaussian family was chosen as it deals with strictly positive, right-skewed data (Dunn and Smyth 2018) and the assumptions of the model for variance of residuals and a linear relationship between the response and the linear predictor were met.

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glm(Visitationrate ~ Temperature + Humidity + Wind Speed + Cloud Cover + Light + Location

   +Pollen + Number of open Flowers, data = data, family = inverse.gaussian(link = εidentityε))   (Model 2)

Results

Effects of Weather on Worker Size

There are a total of 501 observations from 17 days of data collection, 394 of which were made at the Botanical Garden and 107 at the Coastal Path near East Sands. Medium workers were the most common (254 individuals), followed by large (176) and lastly small (71) individuals. *Bombus hypnorum* and *Bombus terrestris/lucorum* were the most common species, with *Bombus lapidarius* being the least common as it was only recorded 7 times. *Bombus terrestris/lucorum* and *soroeensis* showed the greatest proportion of large workers, whereas *pratorum* and *lapidarius* have the largest proportion of small workers (Fig. 2).

Weather conditions varied substantially over the course of data collection. Air temperatures ranged from 12.8 to 27.5 °C with a median of 16.7 °C, with humidity fluctuating between 42.2% and 92.9% (median=73.2%). The maximum wind speed record

was 6.8 m s^{-1} and the minimum was 0 m s^{-1}, with median wind speed being 1.3 m s^{-1}. Light intensity varied approximately 10-fold and ranged from 12,600 to 129,700 lx and a median of 52,900 lx. Cloud cover ranged between 1 and 8 oktas with a median of 6.

The effects of weather conditions on the presence of differently sized workers were modelled using a multinomial logistic regression (Table 1) and showed that temperature significantly affected the size of workers present at the bramble patches. With rising temperatures there were significantly more small workers active in comparison to both medium (Multinomial logistic regression, *estimate ± SE*: -0.081±0.039, p=0.03) and large worker bees (*estimate ± SE*: -0.169±0.041p<0.001). Moreover, there were also significantly fewer large than medium workers observed (*estimate ± SE*: -0.087±0.029, p<0.01) as temperature increased. Humidity also significantly influenced observed worker size and small workers were only substantially more common than large (*estimate ± SE*: -0.029±0.012, p=0.01), but not

Table 1 Coefficient summaries of models used to explain changes in worker size with shifts in local weather conditions

Response variable	Predictor variable	Coefficient	Std. Error	p-value
Worker size				
small vs. medium	Size S (Intercept)	3.347	0.014	< 0.001***
	Temperature	-0.081	0.039	0.034*
	Humidity	-0.016	0.011	0.150
	Wind speed	0.038	0.106	0.718
	Light intensity	0.000006	0.0005	0.904
	Cloud cover	0.089	0.086	0.297
	Location (site 2)	-0.081	0.379	0.830
small vs. large	Size S (Intercept)	4.873	0.015	< 0.001***
	Temperature	-0.169	0.041	< 0.001***
	Humidity	-0.029	0.012	0.01**
	Wind speed	0.030	0.112	0.785
	Light intensity	0.00005	0.0006	0.936
	Cloud cover	0.204	0.095	0.031*
	Location (site 2)	-0.309	0.410	0.450
medium vs. large	Size M (Intercept)	1.527	0.012	< 0.001***
	Temperature	-0.087	0.029	0.003**
	Humidity	-0.014	0.008	0.083
	Wind speed	-0.008	0.075	0.917
	Light intensity	0.00002	0.0004	0.964
	Cloud cover	0.115	0.070	0.103
	Location (site 2)	-0.228	0.299	0.445

A multinomial logistic regression was used to model the relationships between worker sizes and weather conditions and location. The model was run three times, each with a different worker size as intercept for pair-wise comparisons. Significant p-values are highlighted with apostrophes, with the number of apostrophes relating to the significance of the relationship

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

medium individuals (*estimate ± SE*: -0.016 ± 0.011, p = 0.15) as humidity rose. There was no significant difference between frequencies of observation of medium and large workers (*estimate ± SE*: -0.014 ± 0.008, p = 0.08) with changes of humidity. A similar pattern can be seen for cloud cover. Medium workers were not significantly more common than small ones during higher cloud scores (*estimate ± SE*: 0.089 ± 0.086, p = 0.297), but large worker bees were (*estimate ± SE*: 0.204 ± 0.095, p = 0.031). Although larger bees were more common than medium-sized individuals at higher cloud cover, this difference was not significant (*estimate ± SE*: 0.115 ± 0.070, p = 0.1). Medium sized workers were more common relative to small and large ones with increasing wind speed, but there was no significant difference between any bee sizes as a function of wind speed (p > 0.05 for all estimates). Moreover, light intensity and location did

not significantly affect the size of workers foraging on bramble (p > 0.05 for all estimates, Table 1).

Relative species prevalence was also influenced by a variety of weather conditions. More specifically, after conducting pairwise comparisons using Mann-Whitney U tests after initial Kruskal Wallis tests, we found that workers of the characteristically medium bodied, brown-black-white colored species, *Bombus hypnorum*, differed most from others. They were relatively more common than half of the other observed species (Pairwise Mann-Whitney U, *B. pratorum, B. terrestris/lucorum* and *B. soroeensis*: p < 0.001) at higher temperatures. Furthermore, they were significantly more frequent at higher wind speeds in comparison to all species except the small to medium sized red-tailed species of *B. lapidarius* (for *B. hortotum, B. pascuorum* and *B. terrestris/lucorum*: p < 0.001; *B. pratorum*: p = 0.03; *B.*
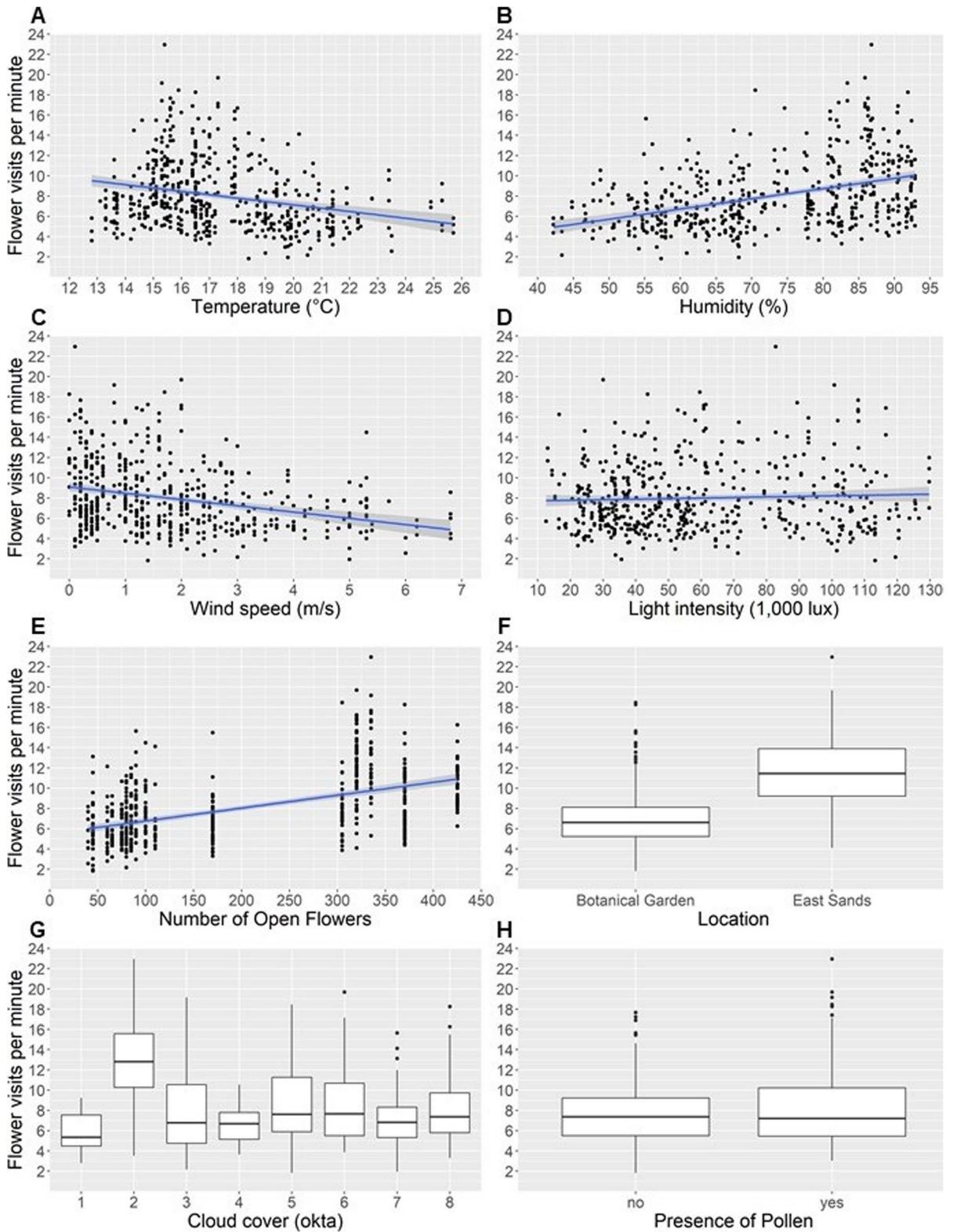
◄**Fig. 3** The relationships between different weather conditions and location on the visitation rate of bumble bee workers on bramble. Data was collected over 17 days in June to July 2021 in St Andrews, Scotland from a total of 501 worker bees. Individual plots present the effect of (**A**) Temperature, (**B**) Humidity, (**C**) Wind speed, (**D**) Light intensity, (**E**) Number of open flowers, (**F**) Cloud cover, (**G**) Location, and (**H**) Presence of pollen on flower visits per minute. Lines in (**A**) to (**E**) present the lines of best fit using a linear regression with standard errors being represented by shaded areas

soroeensis: p = 0.04). On the other hand, they became significantly less common than four out of the six other species *(B. lapidarius*: p = 0.01; *B. pascuorum, B. soroeensis* and *B. terrestris/lucorum*: p < 0.001) as humidity rose; and less likely to forage in higher cloud cover than the two characteristically large-bodied white-tailed species *B. terrestris/lucorum* (p = 0.002) and *B. soroeensis* (p = 0.01). The usually medium sized red-tailed workers of *B. pratorum* became significantly rarer than *B. terrestris/lucorum* (p < 0.001) and *B. soroeensis* (p = 0.003) with increasing temperature. Moreover, workers of this species (p = 0.002), as well as worker of two other species (for *B. hypnorum* and *B. pascuorum*: p < 0.001), were also significantly less likely to forage in more humid conditions than the three-banded workers of *B. hortotum*. Light intensity was the only weather condition that did not affect the presence of any specific species during observations (Kruskal Wallis, H = 236.42, df = 218, p = 0.187).

As species distribution differed significantly with certain weather conditions, the multinomial logistic regression to predict worker size category was repeated but included only data from the three most common species. Species was then also added as a explanatory factor to the model, to investigate whether the differences were in fact due to changes in local weather conditions rather than bumble bee species. In comparison to *B. hypnorum, B. terrestris/lucorum's* were significantly more likely to be large rather than small in size (*estimate ± SE*: 2.99 ± 0.42, p < 0.001), but there was not a significantly higher chance of being medium than small (*estimate ± SE*: 0.123 ± 0.39, p = 0.76). No other species was a significant predictor of size (p > 0.05 for all estimates) so it seems we can conclude that results from the original multinomial logistic regression were due to changes in weather conditions affecting bumble bee on the basis of size more than on the basis of other species-related traits.

Effects of Weather, Size, and Species on Visitation Rate

There was no significant difference in the visitation rates between different species (Kruskal Wallis, H = 346.9, df = 323, p = 0.173) and sizes (Kruskal Wallis, H = 325.9, df = 323, p = 0.44). However, the GLM used to investigate the effect of local weather conditions on visitation rates (Fig. 3) showed that higher temperatures were significantly correlated to a decrease in flower visits per minute (GLM, *estimate ± SE*: -0.149 ± 0.056, p = 0.008). During increased humidity there was a rise in visitation rate,

Table 2 Model summary of the GLM with an inverse Gaussian family and identity link function, used to investigate the effects of local weather conditions, location, presence of pollen in pollen baskets and the number of open flowers on visitation rate

Response variable	Explanatory variable	Coefficient	Std. Error	p-value
Visitation rate	Intercept	10.18	1.896	<0.001***
	Temperature	-0.149	0.056	0.008**
	Humidity	0.012	0.013	0.500
	Wind speed	-0.060	0.069	0.387
	Light intensity	0.0002	0.0005	0.632
	Cloud cover	-0.057	0.079	0.471
	Open Flowers	0.006	0.002	<0.001**
	Location (site 2)	3.619	0.570	<0.001***
	Presence of pollen	-0.610	0.237	0.01**

Significant p-values are highlighted with apostrophes, with the number of apostrophes relating to the significance of the relationship

* p < 0.05, ** p < 0.01, *** p < 0.001

but this was not significant (GLM, *estimate* ± *SE*: 0.012 ± 0.013, p = 0.5). Neither wind speed, light intensity or cloud cover significantly affected visitation rate (GLM, p > 0.05 for all coefficients, Table 2). However, flower visits per minute were significantly affected by location and were higher at site 2 (East Sands) than at site 1 (Botanical Garden, GLM, *estimate* ± *SE*: 3.619 ± 0.570, p < 0.001, Fig. 3). Additionally, the presence of pollen in pollen baskets resulted in a significantly lower visitation rate in workers (GLM, *estimate* ± *SE*: -0.610 ± 0.237, p = 0.01) whereas the number of open flowers was significantly positively correlated to visitation rate (GLM, *estimate* ± *SE*: 0.0006 ± 0.0002, p < 0.001).

Discussion

Plant-pollinator interactions have co-evolved for a long time (Johnson and Anderson 2010) but these fine-tuned mutualistic relationships may now be threatened by rapid shifts in local weather conditions as a result of climate change (Memmott et al. 2007). Thus, it is crucial to investigate the effects of these changes on the ability of pollinators such as bumble bees to pollinate plants, reproduce and survive. In this study, by observing bumble bee workers on bramble flowers, we investigated whether changes in the recorded weather conditions affected worker size and visitation rate.

Worker Size

We found that the size of foraging workers decreases as temperature increases. This supports the hypothesis of Heinrich (2004) that larger workers have a lower surface area to volume ratio and are thus less able to lose heat efficiently, causing them to overheat in high temperatures. Interestingly, although our study showed a similar ambient temperature range as the one done by Peat and Goulson (2005), we did find a significant correlation between worker size and air temperature when they did not. Their use of commercial bumble bees allowed them to measure all workers to the nearest 0.1 mm, which provides more accurate size measurements than our three size categories. Regardless, our results indicate that larger workers may be crucial foragers during low temperature periods and also due to their increased capacity to carry

pollen and nectar (Goulson et al. 2002). However, although they offer benefits, individually larger workers are more costly to rear (Goulson 2010) as they require more food during larval stages and a higher incubation temperature (Couvillon and Dornhaus 2009). This is specifically difficult to maintain when queens rear the first batch of workers as she regularly must leave the nest to forage, causing the eggs to cool down while she is gone (Goulson 2010). Hence, many colonies may not be able to rear high quantities of larger foragers at the start of the colony cycle when they are needed which can in turn lead to less overall workers in the summer and a decreased chance of successful queen rearing.

Climate change is used in some studies to refer to temperature changes only (Gérard et al. 2020), although a multitude of other aspects of weather are also affected (IPCC 2021). Thus, we investigated the effects of a range of other weather conditions and found, for example, no correlation between wind speed and forager size. This may be as body size is directly correlated to the size of other body parts such as wing length (Medler 1962) and, thus, all bumble bees, regardless of size, should show a similar body stability. Contrary to this, Crall et al. (2015) found that larger bumble bees have to adjust more when flying through obstacles in windy condition. However, although larger workers had to expend more energy in those situations, this may not stop them from foraging entirely. Furthermore, Riley et al. (1999) found that bumble bees have adapted to higher wind speeds by flying lower to the ground in windier conditions. Therefore, we may not have seen a size difference as workers show similar body stability and have developed behavioral adaptations during high wind speeds which allow all size spectra to forage in such situations.

Increasing cloud cover was linked to a higher number of large in comparison to small workers which may be due to the correlation between cloud cover and temperature. It is often warmer when there are no or little clouds, both of which were associated with an increased number of small foragers on bramble. Light intensity, on the other hand, had no effect on observed forager size. Other studies found that larger bumble bee workers were more likely to leave the nest in lower light intensities, due to their increased visual acuity as a result of bigger eyes (Kapustjanskij et al. 2007). The same pattern was also found in a study

of stingless bees where larger species had longer foraging days due to their ability to fly earlier in the morning and later in the evening than smaller species (Streinzer et al. 2016). The lack of a significant association in our study was probably caused by the decreased light intensity range in comparison to these other studies. Kapustjanskij et al. (2007) recorded that the minimum light intensity for foraging is less than 10 lx, whereas our lowest documented light intensity was 12,600 lx. Thus, all size categories were presumably able to see and, hence, based on our results one should not consider light intensity an unimportant factor in predicting bumble bee worker size, as this may have been due to limitations in methodology rather than the lack of an existing relationship.

Lastly, there were significantly more active smaller workers in higher humidity in comparison to large ones. This was unexpected as humidity is often negatively correlated to temperature (Chambó et al. 2017), meaning that lower ambient temperatures are usually associated with higher air humidity. Moreover, smaller foragers are most commonly pollen foragers (Goulson et al. 2002) and as pollen is primarily collected in low humidity (Peat and Goulson 2005; Chambó et al. 2017) small workers should be less active with increasing humidity. Although the relationship was not as strong as the one seen for temperature, the trend was in the opposite direction, and we would have predicted to see more smaller workers when humidity was low. Nevertheless, due to the proximity to the coast we can expect higher than average humidity measurements at our sites, regardless of temperature (Pepler 2011). Thus, small workers may have adapted to high humidity conditions, but it may also the case that worker size is not solely affected by changes in weather conditions but also by other factors such as plant development, human interference, or differences in foraging efficiency of differently sized workers.

Visitation Rate

Temperature was a strong negative predictor of visitation rate which may be the result of an increased need to lose heat as temperatures increase. This is crucial to prevent overheating and may cause bumble bees to pause between visiting flowers, thereby decreasing the number of flowers visited per unit time. No other weather conditions significantly affected

visitation rate but there was a negative correlation between the presence of pollen in the pollen baskets and their foraging speed. This is in line with results of previous studies which showed that foragers rarely forage solely for pollen (Goulson et al. 2002), meaning that they collect both nectar and pollen which increases the amount of time spent on each individual flower. The number of open flowers increased visitation rate which is expected as it decreases the need to fly between inflorescences when they are in crawling distance. This relationship may also explain the large difference in visitation rate between the two observation sites. Most bramble flowers at East Sands (site 2) started blooming within a day or two of each other whereas at the Botanical Garden (site 1) blooming onset occurred more steadily with only about 50 flowers blooming when observations started. Hence, inflorescences were further apart, and workers always had to take off to visit another flower which negatively affected visitation rate.

Although we did not expect cloud cover and light intensity to have major effects on the number of flower visits per minute, we were surprised about the lack of a significant relationship with wind speed. Based on observations during data collection, workers seemed to struggle to fly and land as wind speeds increased and some individuals were even blown off flowers or unable to reach an inflorescence at all. Moreover, previous research found that bumble bee workers were negatively affected by increasing wind speeds and it took them longer to approach flowers (Chang et al. 2016). The lack of a relationship may be due to the large number of open flowers, which, as explained above, decreases the need to fly between inflorescences which may have been linked to high visitation rates even during strong wind. Hence, wind may still negatively affect bumble bee foragers, specifically on plants where inflorescences are not in close proximity and studies looking into flight ability in the field rather than wind tunnels could help us to better understand the exact effects of wind on pollinators.

Individual Bumble Bee Species

While not a main focus of this study, we found that species prevalence was differently affected by certain aspects of weather. Interestingly, our results indicate that the invasive tree bumble bee *Bombus hypnorum*

is more resistant to higher wind speeds and temperatures than native species. *Bombus hypnorum* was first documented in the UK in 2001 (Goulson and Williams 2001) and has since then rapidly spread across many parts of mainland England, Scotland and Wales (Crowther 2017). This rapid expansion of this species may be due their better adaptations to urbanization as they nest in above-ground cavities which are abundantly found in towns (Crowther et al. 2014) whereas ground-nesting sites are lacking (Fitch et al. 2019). Additionally, some hypotheses suggest that certain species are not as negatively affected by climate change, although the reasons for that are unclear (Crowther et al. 2014). Hence, further research into the adaptations of individual species to changes in local weather conditions may allow us to understand which physiological and behavioral traits are crucial to survival in a changing world.

Limitations and Further Studies

In this study, data was only collected at two sites within the same town over a short period of time. Thus, one should take care in generalizing the results to other species and habitats. Moreover, it would have been beneficial if the study had run throughout the same time as the colony cycle of most species. This would have given us an idea as to whether worker size changes throughout the colony life cycle which could have been incorporated as an explanatory factor in the models. However, such study would also need to consider a broader range of flowering species and aspects of flower choice, as there may be an interaction between local weather conditions, worker size and plant species.

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Declarations

Conflict of Interest   The authors have no competing interests to declare that are relevant to the content of this article.

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