Arthropod-Plant Interactions
DOI 10.1007/s11829-015-9368-x

ORIGINAL PAPER

Male bumble bees are important pollinators of a late-blooming plant

Jane E. Ogilvie · James D. Thomson

Received: 15 October 2014 / Accepted: 25 February 2015

Abstract Differences in the pollinator performance of flower visitor sexes are rarely considered. In bumble bees, males differ from workers in morphology and behaviour in ways that may affect their contribution to pollination. We compared the abundance, foraging behaviour, and pollen transfer ability of worker and male bumble bees on late-blooming *Gentiana parryi* (Gentianaceae) in subalpine meadows of the Colorado Rocky Mountains. Male bees mostly outnumbered female workers throughout blooming of the gentian. Males and workers foraged similarly, though individual males were more faithful to small foraging areas than workers. During single flower visits, males and workers caused similar levels of pollen deposition and seed production, yet female bees left fewer pollen grains in anthers to be transferred to other stigmas in the plant population. Overall, male bumble bees are common and capable pollinators of *G. parryi* and in some years and sites could be more important than workers. Male bumble bees may be important but unrecognized pollinators of other late-season plant species, and animal sexes may differ in their pollinator performance in other systems.

Keywords *Bombus* · Caste · Foraging behaviour · Pollination · Pollinator performance · Pollinator sexes

Introduction

Animals can vary in their contribution to a plant's pollination due to differences in abundance, morphology, and behaviour (e.g. Herrera 1987; Wilson and Thomson 1991; Sahli and Conner 2007), which can influence crop production (Brittain et al. 2013; Garibaldi et al. 2013) and the evolution of floral form (Whittall and Hodges 2007). Comparisons of pollinator performance tend to be between coarse taxonomic groups, such as birds and bees (e.g. Castellanos et al. 2003), flies and bees (e.g. Motten et al. 1981), or among bee genera (e.g. Thomson and Goodell 2001). However, differences in pollinator performance may occur at finer levels, such as between sexes within a species. Sexes can be dimorphic in morphology, such as body size and tongue length in bumble bees (del Castillo and Fairbairn 2011; Wolf and Moritz 2014) and hawkmoths (Agosta and Janzen 2005), or in flower-visiting behaviour and abundance. In bees, for example, females gather resources for offspring and thus may forage more often than males, who seek resources only for themselves (Michener 2000). When both sexes visit flowers, such differences may affect their value as pollinators. Few studies have examined differences in pollinator performance between sexes, though sexes are known to differ in floral trait preferences (bombyliid flies: de Jager and Ellis 2012), foraging behaviour (bumble bees: Jennersten et al. 1991; hawkmoths:

Handling Editor: Lars Chittka.

Electronic supplementary material The online version of this article (doi:10.1007/s11829-015-9368-x) contains supplementary material, which is available to authorized users.

J. E. Ogilvie · J. D. Thomson
Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada

J. E. Ogilvie · J. D. Thomson
Rocky Mountain Biological Laboratory,
Post Office Box 519, Crested Butte, CO 81224-0519, USA

Present Address:
J. E. Ogilvie (✉)
Department of Biological Science, Florida State University,
Tallahassee, FL 32306-4295, USA
e-mail: jogilvie@bio.fsu.edu

Alarcón et al. 2010), and both foraging behaviour and pollination success (bees: Ostevik et al. 2010; Cane et al. 2011).

In temperate, alpine, and arctic areas, eusocial bumble bees (*Bombus* spp.) are abundant visitors of many wild plants and some agricultural crops (Proctor et al. 1996; Goulson 2010). During the growing season, different castes forage on flowers: overwintered queens during spring, workers during mid-summer, and workers and reproductive castes (males and new queens) during late summer and autumn (Prŷs-Jones and Corbet 2011). Males often outnumber workers and new queens on flowers late in the season (Ranta and Lundberg 1981; Colla and Dumesh 2010; Ostevik et al. 2010; Prŷs-Jones and Corbet 2011; Pyke et al. 2011). Yet, despite the prevalence of bumble bees and the presence of males on flowers, very little research has examined the pollination role of *Bombus* males for late-season plants (exceptions include Jennersten et al. 1991; Ostevik et al. 2010; Wolf and Moritz 2014). Indeed, other male bee taxa are the key pollinators of some plants, such as male euglossine bees on some orchids (Dressler 1968), solitary male bees (Gaskett 2011) and male cuckoo bumble bees (Gögler et al. 2009) on some sexually deceptive orchids, and male eucerine bees on shelter-mimicking irises and orchids (Vereecken et al. 2013).

Once male *Bombus* eclose, they permanently leave their natal colony and spend their time searching for mates and visiting flowers for nectar to fuel their activity (Alford 1975; Goulson 2010). Foraging workers, on the other hand, act as central place foragers, collecting pollen and nectar provisions for their natal colony. Workers are morphologically and behaviourally specialized for collecting, grooming, and transporting pollen (Sladen 1912; Heinrich 1976). These differences lead to the following predictions for pollination. First, foraging males may travel further than workers and thus move pollen further, because they are not bound to a colony (Jennersten et al. 1991). Predictions for sexual differences in foraging behaviour are less clear, but selection for foraging efficiency may be limited by trade-offs with mate-finding in males (cf. Pyke 1978), which might suggest that males forage less efficiently. Males can forage more slowly on flowers than workers (Ostevik et al. 2010), though not always (Jennersten et al. 1991). Longer flower handling times may increase pollen transfer by males, but also self-pollination. Third, as males generally have longer pile (Stiles 1979) and do not groom pollen into corbiculae, their bodies may retain more loose pollen, leading to greater pollen deposition (Thomson and Plowright 1980). Ostevik et al. (2010) reported greater pollen deposition by bumble bee males in a laboratory study, while Wolf and Moritz (2014) found that free-foraging males had less pollen on their bodies (excluding legs) than workers, and the sexes differed in the prominent pollen type carried.

Although there is scattered information on the interaction between male bumble bees and flowers, no study has comprehensively compared the foraging behaviour and pollinator performance of male and worker bumble bees on a late-season blooming plant for which pollination by males is likely to be important. Thus, we made comparative observations of male and worker bumble bees on a late-blooming gentian, *Gentiana parryi* (Gentianaceae; Fig. 1). Specifically, we compared male and worker bumble bees on *G. parryi* with respect to their (1) abundance on flowers over the plant's flowering season, (2) faithfulness to foraging areas and distances moved within a meadow, (3) behaviour during foraging bouts on the flowers, and (4) pollen transfer ability during single visits to flowers (including pollen deposition, seed set, and pollen removal).

Materials and methods

Study site and system

We worked in a subalpine meadow at Schofield Park at an elevation of 3170 m, 9 km north-west of the Rocky Mountain Biological Laboratory (RMBL) in Colorado, USA (39°01′38.77″N, 107°03′10.50″W). *Gentiana parryi* Engelm. is a common herbaceous perennial in subalpine meadows around the RMBL. It has broad, tubular, vertically oriented corollas that are mostly royal blue with an area of white with dark speckles in the lower half. The protandrous flowers open for around 5.5 days, and close in cool temperatures and overnight; they are self-compatible, but require animal pollinators for high levels of seed set (Ogilvie 2014). We selected seven circular plots with a radius of 10 m (314 m^2 per plot, 2198 m^2 total area) throughout the study meadow and individually identified and mapped all flowering plants in the plots using triangulation. We carried out observations and experiments in these plots in August and September 2010, except for approximately two-thirds of the pollen removal samples, which were collected in September 2011. At the site, there were only scattered flowers of a few species also visited by *Bombus*; *G. parryi* was by far the most abundant. We saw so few new queens that we did not study their foraging behaviour and pollen transfer ability.

Bumble bee caste composition on flowers

Every 4 days in warm weather, we counted the number of open *G. parryi* flowers within each of the seven plots. We also noted the species and caste of bees visiting *G. parryi* flowers during 30-min observation periods spent walking slowly through each plot. We surveyed bees in plots during periods of foraging activity between 0930 and 1730 h and varied the order and time when each plot was observed.

Fig. 1 Photographs of a **a** female worker and **b** male *Bombus balteatus* on the flowers of *Gentiana parryi*. The male has been individually marked. The photographs show differences in the morphology between the sexes in this species, in particular the longer pile of the male

Individual bee movements within the meadow

To compare the movement distances and area-faithfulness of males and workers, we marked individual bumble bees throughout the study site and compiled resightings. During the bee surveys described above, we attempted to capture any unmarked bee into a restraining device (Kearns and Thomson 2001, p. 73) and mark it between the wing bases with a unique combination of colour spots of Sharpie solvent-based paint markers (Newell Rubbermaid, Oak Brook, Illinois, USA). We marked 0–9 individuals in each 30-min observation period. During our observations over the flowering season of *G. parryi*, we recorded the identities of marked individuals and their plot locations. We defined individual movement as the distances between a bee's marking plot and where it was resighted. We mapped the centres of the seven plots with a GPS unit and calculated pairwise plot distances as the distances between nearest plot edges. The minimum and maximum distances that bees could move between pairs of plots was 3 and 402 m, respectively.

Flower foraging behaviour

We selected individual bumble bees foraging on *G. parryi* for detailed observation of their flower foraging behaviour. We made voice recordings, noting when a bee landed on a plant, when it entered and exited each flower, and when it left a plant, until the bee exited the plot. We noted the identity of each plant visited. After transcription, we extracted the following response variables for each foraging bout: the proportion of flowers visited per plant, the number of flowers and plants visited per minute, the floral display size of visited plants, and the distance flown between sequentially visited plants. We calculated the distances travelled between successive plants as the straight-line distance between them from the mapped plant coordinates. To ensure that variables were representative of individual bees and not influenced by unusual data points at low sample sizes, we limited our analyses to those foraging bouts with three or more plant visits.

Pollen transfer ability

We compared the pollen transfer ability of male and worker bumble bees on *G. parryi* by examining single-visit pollen deposition on stigmas, seed set, and pollen removal. To measure seeds produced from single bee visits to flowers, plants with unopened buds were excluded from flower visitors with sandbag-style exclusion bags (Thomson et al. 2011). When flowers had receptive stigmas, we removed the bags and waited for bees to visit the virgin flowers. When a bee visited, we noted its species and sex, marked the flowers visited, and then rebagged the plants for fruit harvest 4 weeks later. We counted the number of mature seeds and undeveloped ovules under a dissecting microscope. Ovule number in *G. parryi* ranged from 455 to 1324, so we calculated proportional seed set as the number of mature seeds divided by the total number of ovules per flower and compared this for male and worker visits. Some flowers sampled towards the end of the flowering season produced no mature seeds, and as we were uncertain whether these resulted from insufficient viable pollen deposition or a maternal plant effect (e.g. resource exhaustion at the end of the growing season, or frost hindering fruit maturation), we excluded these fruits from our analyses.

To measure pollen deposition and pollen removal during single bee visits to flowers, we presented virgin cut flowers held in tubes attached at the end of an "interview stick" (Thomson 1981) to foraging bees. For pollen deposition measurements, female-phase flowers were cut from bagged plants and then presented to bees. For each visit, we noted the bee's species, sex, and duration. We kept the cut stems fresh in water for 24 h to let pollen tubes develop. We excised the bilobed stigmas and stored them in 70 % ethanol. Later, we stained the stigma lobes with lactophenol–aniline blue (Kearns and Inouye 1993), mounted them on microscope slides, and photographed them under a high-magnification dissecting microscope. We used a qualitative scale from 0 (no pollen grains) to 5 (maximum coverage of pollen grains) to score each of the two lobes of a stigma from the images. One person scored all samples, blind to bee sex, and then re-scored the samples to ensure that his qualitative scoring was not drifting during the process.

For pollen removal measurements, we cut male-phase flowers from bagged plants and kept them fresh in water. From each flower, we randomly harvested one of five undehisced anthers—a "control" to estimate total pollen available in a flower—and placed it into a microcentrifuge tube to dehisce, after which we added 0.5 ml of 70 % ethanol. When the remaining four anthers were completely dehisced, we presented the flowers to bees as previously described. We then stored the visited anthers in a tube as above. In preparation for counting, we added 19.00 ml of 0.9 % NaCl solution to each sample and dislodged pollen grains from the anthers by vortexing and sonicating the samples. We then counted the pollen grains in these samples with a Coulter Multisizer 3 particle counter (Beckman Coulter Inc., Brea, California, USA). Repeated subsamples (1.00 ml) of each pollen sample were passed through a 200-µm aperture, and the number of particles in a 10-µm range around the particle-size peak was used as the pollen grain count (typical range 20–30 µm). We multiplied the mean of three or four subsample counts by the total sample volume to estimate the pollen grain count of each sample. We multiplied each control sample estimate by the total anther number in a flower when presented to a bee (typically four). We used the proportion of pollen grains remaining in flowers as our response variable (estimated pollen grain number remaining over the total pollen number available). We discarded 30 samples for which estimates of pollen number remaining were greater than the total pollen available.

Data analysis

We used R version 3.0.2 for all analyses (R Core Team 2013). Because all response variables had non-normal distributions and we often had multiple measurements from known individual bees or plants, we used generalized linear mixed models (GLMMs) with sex as a fixed effect, and the repeatedly sampled unit (i.e. individual bee or plant) and *Bombus* species as random effects. We included *Bombus* species as a random effect, to account for the variation related to different species in our samples and because our main interest was in the differences between sexes and not species. However, preliminary analyses revealed no differences among species in any response variable. For proportional and binomial data (flower foraging behaviour: proportion of flowers visited on plants; pollen transfer ability: proportion seed set and proportion grains remaining in anthers), we specified binomial errors and a logit link function, using the R package *lme4* (Bates et al. 2013), while for all other response variables, we specified negative binomial errors and a log link function in R package *glmmADMB* (Skaug et al. 2011). Proportional seed set in flowers declined progressively when a bee visited multiple flowers on a plant, so we included the sequence of the flower visit nested within the individual bee visit as a random effect. Our results are qualitatively the same when analysing only the first and second flowers visited. For the pollen removal data, flowers differed in their estimated total pollen available between the two sampling years, so we included year as a random effect. We obtained all P values from Wald Z tests. We used two-by-two contingency tables to compare the number of marked workers and males that we did and did not resight, and to compare the number of workers and males that were resighted only in their marking plot or in another plot.

Results

Bumble bee caste composition on flowers

During the main flowering period of *G. parryi* (mid-August to early September; Fig. 2a), there were 12–667 flowers in each plot, and 258–1704 flowers open during each census. We observed 386 bumble bees visiting *G. parryi* flowers during 28 h of observation. Male bumble bees were most common (58.0 %), followed by female workers (40.2 %) and a few new queens (1.8 %). Males predominated on all days except one (Fig. 2b). Of five bumble bee species recorded, *Bombus balteatus* Dahlbom, *B. appositus* Cresson, and *B. flavifrons* Cresson accounted for 93.8 % of the visits (Supplementary Table 1). Of these three species, we saw bees of all castes (female workers and new queens, and males); male bees outnumbered females in the two most common bee species, *B. balteatus* and *B. appositus*. Of the two uncommon *Bombus* spp. visiting *G. parryi* (*B. sylvicola* Kirby and *B. californicus* Smith; 6.2 % of visits), we observed only workers.

Individual bee movements within the meadow

We resighted 61 (40 %) individual bees again, on 1–13 occasions over a period of 1–18 days. Of bees that we resighted, males significantly outnumbered workers (41/77 males and 20/77 workers seen again; two-by-two contingency table, $\chi^2 = 11.97$, $P = 0.0005$). When individuals were seen again, males were more often seen only in their marking plot compared to workers (26/41 males and 7/20

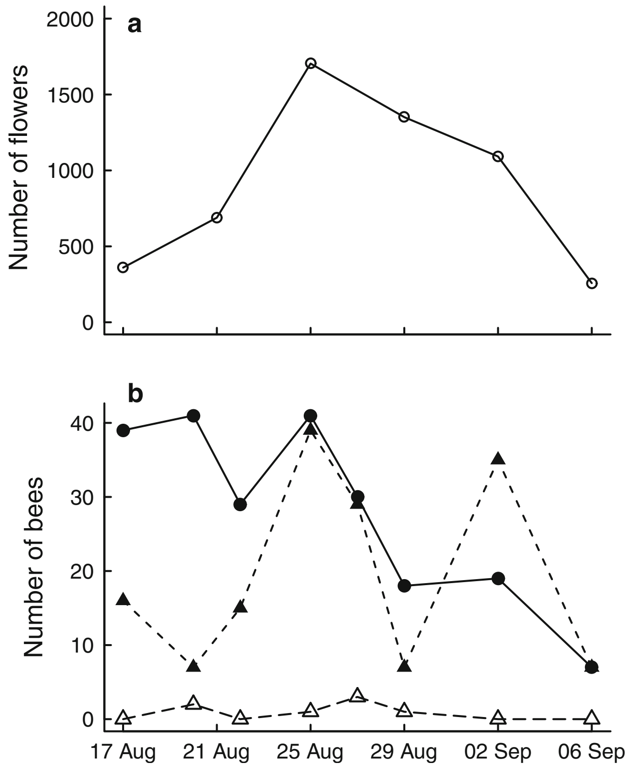

Fig. 2 Number of **a** *Gentiana parryi* flowers, and **b** male, worker, and queen bumble bees observed visiting *G. parryi* flowers, in seven 314 m^2 plots in Schofield Park, Colorado, over the plant's flowering season in 2010. In **b**, the *filled circles* and *solid line* are males, *filled triangles* and *short dashed line* are workers, and the *open triangles* and *long dashed line* are queens

workers; two-by-two contingency table, $\chi^2 = 4.37$, $P = 0.037$), indicating that males have higher site fidelity. In addition, workers were seen at further distances from their original location than males: 45.3 ± 16.2 versus 8.0 ± 4.3 m (mean ± SE, $n = 46$ and 132, respectively; GLMM, $Z = 3.20$, $P = 0.0014$; Fig. 3).

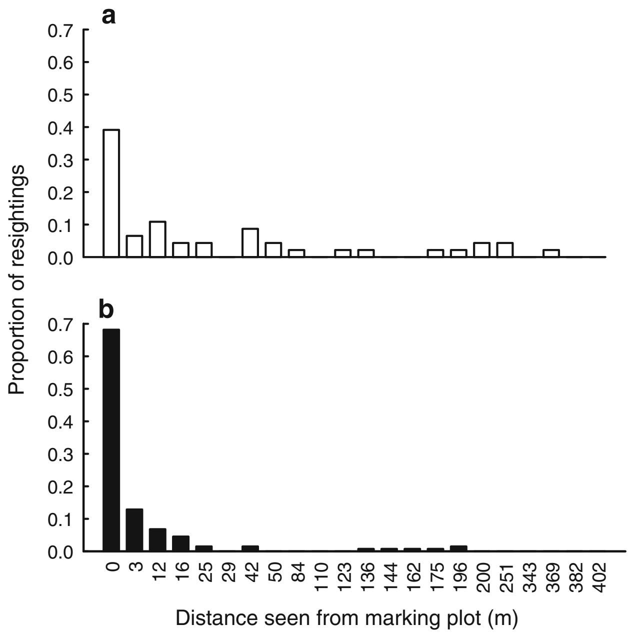

Fig. 3 Proportional frequency distributions showing the number of marked individual **a** worker and **b** male bumble bees seen at particular distances from their original marking location while foraging on *Gentiana parryi* flowers in a subalpine meadow. All bee sightings within each caste were pooled; $n = 132$ and 46 sightings for males and workers, respectively. Workers were seen at significantly further distances than males (GLMM, $P = 0.0014$)

Flower foraging behaviour

Both males and workers foraged on *G. parryi* flowers for nectar. They moved in and out of the flowers in a similar way. Workers occasionally actively collected pollen from the anthers (15 % of all worker visits in our abundance observations; all workers of the short-tongued *B. sylvicola* foraged solely for pollen), though some workers did accumulate small pollen loads when it appeared that they were only nectar foraging. During foraging bouts on *G. parryi*, the sexes did not differ in the number of flowers visited per minute (GLMM, $Z = 0.74$, $P = 0.46$), the number of plants visited per minute (GLMM, $Z = -0.43$, $P = 0.67$), the proportion of flowers visited per plant (GLMM, $Z = 0.43$, $P = 0.67$), nor the floral display size of visited plants (GLMM, $Z = 1.45$, $P = 0.15$; Table 1). However, males tended to move further distances between sequentially visited plants (GLMM, $Z = -1.92$, $P = 0.055$; Table 1). While males moved shorter distances between areas than workers, within areas, males tended to move further distances between plants.

Pollen transfer ability

Male and worker bumble bees deposited similar amounts of pollen on stigmas (mean pollen load 0–5 score: males = 2.4 ± 0.17, workers = 2.39 ± 0.24, $n = 45$ and 33; GLMM, $Z = 0.60$, $P = 0.548$; Fig. 4a). In addition, the sexes did not differ in the proportion of seed set during single visits to flowers (males = 0.40 ± 0.06, workers = 0.41 ± 0.04, $n = 28$ and 60; GLMM, $Z = 0.08$, $P = 0.933$; Fig. 4b). However, males left 14 % more pollen in a flower after a visit than workers did (males = 0.87 ± 0.02, workers = 0.76 ± 0.03, $n = 39$ and 36; GLMM, $Z = 5.32$, $P = 1 \times 10^{-7}$; Fig. 4c).

Discussion

Male bumble bees contribute to the pollination of *G. parryi*, as do workers, and in some sites and years, males may contribute more than worker bees do. First, during our

Table 1 Summary of the flower foraging behaviour of male and worker bumble bees

Response variable	Male			Worker		
	Mean	SE	*N* bouts	Mean	SE	*N* bouts
No. of flowers visited per minute	5.40	0.34	29	5.86	0.39	31
No. of plants visited per minute	2.76	0.20		2.73	0.24	
Prop. of flowers visited per plant	0.58	0.02		0.61	0.03	
Floral display size of plants	4.56	0.29		5.05	0.29	
Distance moved between plants (cm)	246	30		179	12	

Data are means of individual foraging bouts, which varied in the number of plant and flower visits. Bumble bee species were pooled

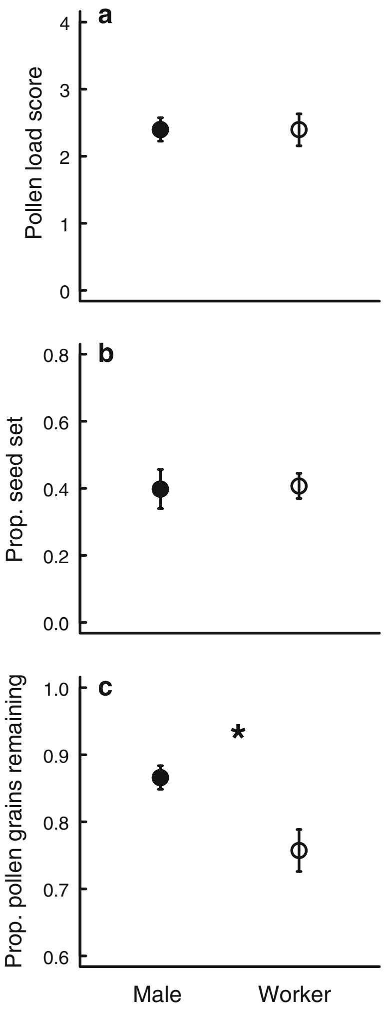

Fig. 4 Pollination performance of male and worker bumble bees visiting *Gentiana parryi*. Means (±SE) of the **a** amount of pollen deposited on stigmas, **b** proportion of mature seeds produced, and **c** estimated proportion of pollen grains remaining, after single visits to flowers. The *asterisk* indicates a significant difference ($P = 1 \times 10^{-7}$, GLMM). Samples sizes for males and workers are **a** 45 and 33, **b** 28 and 60, and **c** 39 and 36

study, males were more common flower visitors than workers over most of the plant's late-summer flowering season. Second, males and workers behaved similarly during foraging bouts on the flowers. They did not differ in the speed with which they visited flowers and plants, in the proportion of flowers visited on plants, or in the floral display sizes of visited plants. However, we found differences in how males and workers moved among plants and areas: males tended to move further between successive plants during foraging bouts, and individual males were more often resighted in the same area and moved shorter distances between focal plots in the meadow. Third, males and workers did not differ in pollen loads deposited on stigmas or in proportions of seed set during single visits to flowers. However, males removed less pollen from flowers during single visits than workers, indicating that they disperse pollen more efficiently than workers. That is, males left more pollen in the plant population while leading to similar seed set levels during a visit. Given that they tended to be more abundant flower visitors and left more pollen for dispersal to other flowers, male *Bombus* are important pollinators of *G. parryi*, and in some situations, may be more important than workers. Therefore, male bumble bees are not indolent and ineffectual drones; they are effective pollinators of *G. parryi* and likely important for the ecology and evolution of its flowers.

Abundance and foraging behaviour

Male bumble bees are often more common than female workers (and new queens) on late-season flowers (Ranta and Lundberg 1981; Colla and Dumesh 2010; Ostevik et al. 2010; Prŷs-Jones and Corbet 2011; Pyke et al. 2011). Their abundance on flowers is reasonable: bumble bee colonies often produce males, and in numbers similar to workers (Pelletier and McNeil 2003) and greater than new queens (Bourke 1997). Furthermore, males—unlike workers—must leave the colony. However, male bumble bees have species-specific strategies to find mates (Goulson 2010), which may influence the time that different species allocate to visiting flowers. Males of the two most common species that we observed, *B. balteatus* and *B. appositus*, spent much of their time foraging on flowers when it was warm, and we did not observe any obvious mate-searching or scent marking during these bouts. In other systems, males forage on flowers during only parts of the day, typically in the afternoon (Alford 1975; Svensson 1979; Jennersten et al. 1991). Regardless, all males must visit at least some flowers to fuel their own activity (Bertsch 1984), so they do have the potential to contribute to pollination.

Despite obvious differences in their motivations, males and workers were remarkably similar in their behaviour during foraging bouts. They visited flowers and plants at the same rate, which is contrary to the longer flower handling times of male *Bombus impatiens* on artificial and *Brassica rapa* flowers (Ostevik et al. 2010), and the fewer pollen grains on male *B. terrestris* and *B. lapidarius* bodies (Wolf and Moritz 2014). In another study, workers and males of *B. terricola* on milkweed and *B. pratorum* on fireweed mostly did not differ in their flower-visiting behaviour, while *B. terricola* males visited more flowers per inflorescence and fewer inflorescences per minute on goldenrod (Jennersten et al. 1991). Thus, male foraging behaviour will vary with species and context, though males of at least some species forage at the same pace as workers. Although we predicted that workers may be faster foragers due to stronger selection pressure for foraging efficiency, it may likewise be beneficial for males to forage efficiently, because they could spend more time mate-searching. We did, however, find that males tended to fly farther between successive plants than workers (mean of 246 vs. 179 cm, respectively). If pollen carryover is longer for males, as would be expected because males do not groom pollen off their bodies into corbiculae, this difference in distance may be meaningful for gene flow in *G. parryi*.

We resighted more marked individual males than workers, and of those individuals that we resighted, workers were seen at further distances than males (8 vs. 45 m for males and workers). This result counters the prediction that males would move further than workers and thus contribute more to long-distance pollen dispersal (Jennersten et al. 1991). Population genetic studies suggest that males disperse further than workers at a population level (Kraus et al. 2009; Wolf et al. 2012). Though, importantly, these studies do not have the resolution to infer individual movement distances over small spatial and temporal scales, as we do. However, our results do not preclude the possibility that male bumble bees initially disperse long distances when leaving their natal nest and then “settle” into an area. That our males were area-faithful is not unusual; males of some species patrol regular routes as a mating strategy (Goulson 2010). There are obvious advantages for the male bees in our study to have a regular foraging area: it should take less energy and time to return to a familiar area than to learn a new one (Osborne and Williams 2001), and if males are visiting flowers to encounter mates, it may be advantageous to occupy a resource-rich area attractive to potential mates. Males foraging more locally than workers may mean that males lead to more restrictive pollen movement for *G. parryi*.

Pollinator performance

Male and worker bumble bees may differ in their pollinator performance for *G. parryi*. Although their visits produce equivalent seed production, males left more pollen in flowers, meaning that they left more grains in the active pool for transfer to other flowers (they used fewer grains for similar numbers of seeds produced). We do not know the significance of males leaving 14 % (on average) more pollen in flowers to *G. parryi* pollination, but these pollen grains could contribute to additional pollination events. This pattern likely arises from differences between the sexes in morphological and behavioural adaptations for pollen collection. Although most workers were actively foraging for nectar on *G. parryi* (except for the short-tongued *B. sylvicola*, which foraged principally for pollen), nectar-seeking workers are still fastidious pollen groomers that regularly divert pollen from stigmas by packing it into corbicular pellets (sensu lato Harder and Wilson 1998). Foraging worker bumble bees rapidly lose pollen from their bodies when they groom, reducing pollen carryover (Thomson and Plowright 1980; Thomson 1986). Males lack both motivation and equipment for pollen grooming, so a grain on a male’s body has a greater chance of ending up on a stigma. The sexual difference should be even greater when more workers engage in active pollen collection.

Flower visitor sexes of the same species can differ in morphological and behavioural traits important for plant pollination and floral evolution (Temeles and Kress 2003; Alarcón et al. 2010; de Jager and Ellis 2012), yet animal sexes are not routinely stated in pollination studies. Given the likely meaningful differences we found between bumble bee sexes, we caution pollination biologists against lumping flower visitor sexes if it is feasible to distinguish them. Indeed, the sexes within a species may differ more than individuals of the same sex from different species (especially congeneric). Our study supports the premise that selection could favour later flowering if male bumble bees are better pollinators than workers (Ostevik et al. 2010). Furthermore, our data suggest that differences in the foraging behaviour and pollen transfer ability between animal sexes may contribute to a finer level of pollinator diversity, which can influence crop and wild plant pollination (Biesmeijer et al. 2006; Garibaldi et al. 2013).

For *G. parryi*, male bumble bees are common and capable pollinators. Many temperate-zone plant species have the tails of their flowering season during the time when male bumble bees are common on flowers, and there are other plant species, like *G. parryi*, which flower entirely when male bumble bees are active. The Gentianeae tribe in particular has many late-flowering species in temperate areas; these are likely to be commonly visited by male bumble bees. We suggest that male bumble bees are more important pollinators of late-season nectar-producing plant species than has been recognized.

Acknowledgments We thank the RMBL for field support, especially Jennie Reithel and billy barr; Brett Harris for field help; and Kareem Jarrah, Sarah Kim, and Patricia Lee for help with laboratory work. We are grateful to Jessica Forrest, Ben Gilbert, Takashi Makino, Randy Mitchell, Ali Parker, and an anonymous reviewer, for helpful discussion or manuscript comments. We also thank Neal Williams and his laboratory for assistance and use of the particle counter, and Megan Frederickson and her laboratory for use of the dissecting microscope. This work was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to JDT.

References

Agosta SJ, Janzen DH (2005) Body size distributions of large Costa Rican dry forest moths and the underlying relationship between plant and pollinator morphology. Oikos 108:183–193

Alarcón R, Riffell JA, Davidowitz G, Hildebrand JG, Bronstein JL (2010) Sex-dependent variation in the floral preferences of the hawkmoth *Manduca sexta*. Anim Behav 80:289–296

Alford DV (1975) Bumblebees. Davis-Poynter, London

Bates D, Maechler M, Bolker BM, Walker S (2013) Linear mixed-effects models using Eigen and S4. R Package, version 1.0–5. http://lme4.r-forge.r-project.org/

Bertsch A (1984) Foraging in male bumblebees (*Bombus lucorum* L.): Maximizing energy or minimizing water load? Oecologia 62:325–336

Biesmeijer JC, Roberts SPM, Reemer M et al (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354

Bourke AFG (1997) Sex ratios in bumble bees. Philos T Roy Soc B 352:1921–1933

Brittain C, Williams N, Kremen C, Klein AM (2013) Synergistic effects of non-*Apis* bees and honey bees for pollination services. Proc R Soc B Biol Sci 280:20122767

Cane JH, Sampson BJ, Miller SA (2011) Pollination value of male bees: the specialist bee *Peponapis pruinosa* (Apidae) at summer squash (*Cucurbita pepo*). Environ Entomol 40:614–620

Castellanos MC, Wilson P, Thomson JD (2003) Pollen transfer by hummingbirds and bumblebees, and the divergence of pollination modes in *Penstemon*. Evolution 57:2742–2752

Colla SR, Dumesh S (2010) The bumble bees of southern Ontario: notes on natural history and distribution. J Entomol Soc Ont 141:38–67

de Jager ML, Ellis AG (2012) Gender-specific pollinator preference for floral traits. Funct Ecol 26:1197–1204

del Castillo RC, Fairbairn DJ (2011) Macroevolutionary patterns of bumblebee body size: detecting the interplay between natural and sexual selection. Ecol Evol 2:46–57

Dressler RL (1968) Pollination by euglossine bees. Evolution 22:202–210

Garibaldi LA, Steffan-Dewenter I, Winfree R et al (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339:1608–1611

Gaskett AC (2011) Orchid pollination by sexual deception: pollinator perspectives. Biol Rev 86:33–75

Gögler J, Stökl J, Sramkova A et al (2009) Ménage à trois—two endemic species of deceptive orchids and one pollinator species. Evolution 63:2222–2234

Goulson D (2010) Bumblebees: behaviour, ecology, and conservation. Oxford University Press, Oxford

Harder LD, Wilson WG (1998) Theoretical consequences of heterogeneous transport conditions for pollen dispersal by animals. Ecology 79:2789–2807

Heinrich B (1976) The foraging specializations of individual bumblebees. Ecol Monogr 46:105–128

Herrera CM (1987) Components of pollinator "quality": comparative analysis of a diverse insect assemblage. Oikos 50:79–90

Jennersten O, Morse DH, O'Neil P (1991) Movements of male and worker bumblebees on and between flowers. Oikos 62:319–324

Kearns CA, Inouye DW (1993) Techniques for pollination biologists. University Press of Colorado, Niwot

Kearns CA, Thomson JD (2001) The natural history of bumblebees. University Press of Colorado, Boulder

Kraus FB, Wolf S, Moritz RFA (2009) Male flight distance and population substructure in the bumblebee *Bombus terrestris*. J Anim Ecol 78:247–252

Michener CD (2000) The bees of the world. Johns Hopkins University Press, Baltimore

Motten AF, Campbell DR, Alexander DE, Miller HL (1981) Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. Ecology 62:1278–1287

Ogilvie JE (2014) Bee foraging in space and time: linking individual behaviour to pollination. PhD Dissertation, University of Toronto, Canada

Osborne JL, Williams IH (2001) Site constancy of bumble bees in an experimentally patchy habitat. Agric Ecosyst Environ 83:129–141

Ostevik KL, Manson JS, Thomson JD (2010) Pollination potential of male bumble bees (*Bombus impatiens*): movement patterns and pollen-transfer efficiency. J Poll Ecol 2:21–26

Pelletier L, McNeil JN (2003) The effect of food supplementation on reproductive success in bumblebee field colonies. Oikos 103:688–694

Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Timber Press, Portland

Prŷs-Jones OE, Corbet SA (2011) Bumblebees. Pelagic Publishing, Exeter

Pyke GH (1978) Optimal foraging in bumblebees and coevolution with their plants. Oecologia 36:281–293

Pyke GH, Inouye DW, Thomson JD (2011) Activity and abundance of bumble bees near Crested Butte, Colorado: diel, seasonal, and elevation effects. Ecol Entomol 36:511–521

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/

Ranta E, Lundberg H (1981) Resource utilization by bumblebee queens, workers and males in a subarctic area. Ecography 4:145–154

Sahli HF, Conner JK (2007) Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, *Raphanus raphanistrum* (Brassicaceae). Am J Bot 94:203–209

Skaug H, Fournier A, Nielsen A, Magnusson A, Bolker BM (2011) glmmADMB: generalized linear mixed models using AD model builder. R Package, version 0.7. http://glmmadmb.r-forge.r-project.org, http://admb-project.org

Sladen FW (1912) The humble-bee, its life-history and how to domesticate it. Macmillan, London

Stiles EW (1979) Evolution of colour pattern and pubescence characteristics in male bumblebees: automimicry vs. thermoregulation. Evolution 33:941–957

Svensson BG (1979) Patrolling behavior of bumble bee males (Hymenoptera, Apidae) in a subalpine-alpine area, Swedish Lapland. Zoon 7:67–94

Temeles EJ, Kress WJ (2003) Adaptation in a plant-hummingbird association. Science 300:630–633

Thomson JD (1981) Field measures of flower constancy in bumblebees. Am Midl Nat 105:377–380

Thomson JD (1986) Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. J Ecol 74:329–341

Thomson JD, Goodell K (2001) Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. J Appl Ecol 38:1032–1044

Thomson JD, Plowright RC (1980) Pollen carryover, nectar rewards, and pollinator behaviour with special reference to *Diervilla lonicera*. Oecologia 46:68–74

Thomson JD, Forrest JRK, Ogilvie JE (2011) Pollinator exclusion devices permitting easy access to flowers of small herbaceous plants. J Poll Ecol 4:24–25

Vereecken NJ, Dorchin A, Dafni A, Hötling S, Schulz S, Watts S (2013) A pollinators' eye view of a shelter mimicry system. Ann Bot 111:1155–1165

Whittall JB, Hodges SA (2007) Pollinator shifts drive increasingly long nectar spurs in columbine flowers. Nature 447:706–709

Wilson P, Thomson JD (1991) Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. Ecology 72:1503–1507

Wolf S, Moritz RFA (2014) The pollination potential of free-foraging bumblebee (*Bombus* spp.) males (Hymenoptera: Apidae). Apidologie 45:440–450

Wolf S, Toev T, Moritz RLV, Moritz RFA (2012) Spatial and temporal dynamics of the male effective population size in bumblebees (Hymenoptera: Apidae). Popul Ecol 54:115–124