

POLLINATION POTENTIAL OF MALE BUMBLE BEES (*BOMBUS IMPATIENS*): MOVEMENT PATTERNS AND POLLEN-TRANSFER EFFICIENCY

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Abstract—Many plant species rely on female bumble bee workers for pollen transfer. However, male bumble bees, which differ both behaviourally and morphologically from female workers, also visit many species of flowering plants and may transfer pollen differently. Males can outnumber workers on some plants, particularly those that flower late in the season. In laboratory experiments, we compared the movement patterns of male bees and female workers on an artificial flower array. We also compared the pollen transfer efficiency of males and workers foraging on *Brassica rapa* flowers. Males travelled between patches of flowers more often than workers, which may be an effective method for reducing geitonogamy in plants. Males also had lower foraging rates, longer flower handling time, and transferred more pollen from one *B. rapa* flower to the next than workers did. These caste-based differences in pollinating behaviour suggest that, under certain circumstances and on a per-visit basis, male bumble bees may be better pollen vectors than female foragers. Furthermore, our results emphasize the need to avoid species-wide generalizations of pollinator effectiveness.

Keywords: *Bombus impatiens*, foraging efficiency, geitonogamy, sexually dimorphic behaviour

INTRODUCTION

Foraging female bees are noted for their industrious focus on collecting nectar and pollen for their brood. In the sterile worker castes of eusocial species, this focus is unimpeded by distractions such as mating (Pyke 1978). Male bees, in contrast, are thought to focus on mate-finding, collecting no pollen and occasionally foraging for nectar only to fuel their own activities. Consequently, a worker will visit more flowers than a male, and in that sense will do more pollination. Most studies of bumble bee pollination concern workers (e.g., Willmer et al. 1994; Thomson & Goodell 2001; Ne'eman et al. 2006). This focus is justified, in part, because peak worker production coincides with peak flowering of many plant species. However, male bumble bees appear in the late summer and early autumn (Kearns & Thomson 2001) and may be numerically important visitors for later blooming flowers. Furthermore, male bumble bees are behaviourally and morphologically distinct from workers in ways that are likely to affect pollen transfer patterns and effectiveness.

Foraging workers are tied to their colony and return periodically throughout the day to deliver collected rewards. In contrast, male bees provide no service for their home colony; rather, they disperse shortly after eclosion (Free 1982; Kearns

& Thomson 2001). This means that males may have larger foraging ranges and disperse pollen further than workers because they are not necessarily central-place foragers (Ackerman et al. 1982; Jennersten et al. 1991). Indeed, estimates of flight ranges based on colony numbers in *Bombus terrestris* suggest that males range much further than workers in this species (Kraus et al. 2009). Other studies show that male solitary bees (*Anthophora plumipes*, *Habropoda tarsata*, and *Eucera nigrilabris*) and male euglossine bees fly longer distances between flowers (Williams & Dodson 1972; Ne'eman et al. 2006). Furthermore, it has been suggested that these bees are important agents of long distance pollen flow, although this remains to be demonstrated empirically (Williams & Dodson 1972; Ne'eman et al. 2006).

The morphology of male bees may also promote the retention of pollen on body surfaces from which transfer to stigmas is likely. Apid workers have specialized structures and behaviours for combing pollen from their body hairs into compacted corbicular pellets. This grooming process continues during foraging bouts, particularly as workers fly from flower to flower. In consequence, most pollen is quickly removed from circulation. Males, in contrast, lack corbiculae and do not collect pollen. Males also have denser and longer pile, which could cause them to retain more pollen through electrostatics (Kearns & Thomson 2001). It has been suggested that mammalian fur acts as a particularly good pollen reservoir (Muchhala & Thomson 2010), and the long pile of male bumble bees may have similar advantages.

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Taken together, these morphological and behavioural differences suggest that males are likely to disperse pollen in greater amounts and longer distances (Ne'eman et al. 2006, Kraus et al. 2009). They may make fewer flower visits than workers, but their visits may be of higher quality. This means that males may be better pollinators of some plant species or under particular ecological conditions.

Little is known about whether these differences between male and worker bees actually translate into different pollination efficiencies. Previous studies have compared visual pattern discrimination in males and workers (Church et al. 2001), while others have reported differences in temporal foraging patterns (Jennersten et al. 1991) and foraging ranges (Kraus et al. 2009) between the castes. However, these works failed to connect these differences to pollination efficiency. In this study, we compare differences in the foraging behaviour and pollen transfer efficiency of the female workers and males of *Bombus impatiens*.

MATERIALS AND METHODS

Late-season survey of caste frequencies

As part of a larger study of species distributions, on 20-23 August 2007 Barbara and James Thomson collected all bumble bee individuals found on all species of flowering plants along three hiking trails near the Rocky Mountain Biological Laboratory at Gothic, Colorado. Elevations ranged from 2900 to 3750 m. At those dates and elevations, the growing season was coming to a close, and only the latest-flowering plant species remained in bloom.

Flight-distance experiment

We obtained individual adult males and two *Bombus impatiens* colonies from Biobest Canada (Leamington, ON, Canada). We attached each colony box to a flight cage (2.2 x 2.2 x 2.4 m) using a gated screen tube that controlled female worker access to the cage. Approximately 50 eclosed males were housed and trained in the same flight cage but without access to a nest. Within the flight cage, we set up a foraging array comprising five patches of twelve artificial flowers each (Fig. 1). Individual artificial flowers were made using 1.5 mL microcentrifuge tubes for nectar reservoirs, with 3.5cm diameter rings of yellow construction paper attached to the mouth of the tube to provide advertisement and a landing surface, following Gegear et al. (2007). For two to three days before the experimental bouts, we allowed bees to forage on artificial nectar distributed throughout the array *ad libitum*.

For each experimental bout, we released a single bee into the foraging array. Individual female workers used in the experiment were bees that were observed foraging during the training period and had been marked on the thorax with liquid paper. Individual males used in the experiment were selected from those actively foraging in a second flight cage at the time of the experiment. We used a different bee for each foraging bout.

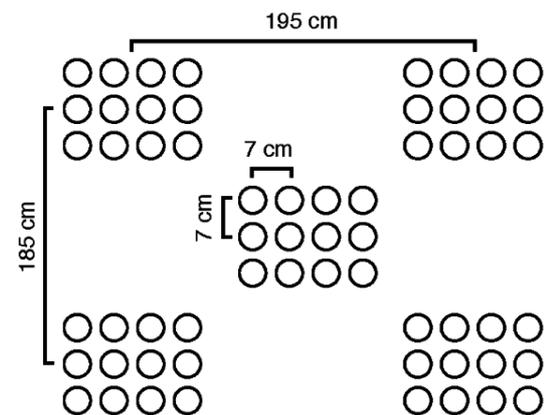


Fig. 1. Schematic of the artificial flower array used in foraging experiments. Each circle represents an artificial flower and each group of 12 flowers makes up a patch.

At the beginning of a foraging bout, each flower in the foraging array was stocked with 1 μ L of honey diluted with water to a 55% sucrose-equivalent concentration as determined by refractometry. If the honey water in any flower had been exposed for more than two hours, we replaced it. We did not refill flowers during experimental bouts.

We defined foraging bout length as the time between when a bee landed on the first flower it visited and when it left the last flower it visited before it stopped foraging for approximately five minutes (for males) or it returned to the colony (for workers). We recorded the sequence of all flowers visited and the length of time spent within the tube of each flower using a voice recorder. We noted three visitation behaviours: bees landing on flowers, landing and exploring flowers, or landing and entering the flower to collect honey water. This last behaviour is closest to a true, decisive visitation event (hereafter referred to as 'entered'). However, in some real flowers, exploratory landings without entry into flower corollas can cause pollination. For this reason, we also kept a dataset that included all three behaviours (hereafter referred to as 'visited'). Using the sequence of flowers visited and the positions of each flower in the array, we calculated the distances travelled between each flower visited or entered. We calculated four summary statistics for each bee used in the experiment: visitation rate (number of flowers visited/foraging bout length), median distance travelled between patches, number of flowers visited per patch, and the proportion of inter-flower movement that occurred within patches (number of movements between flowers in the same patch/total number of movements between flowers). We collected data from the foraging bouts of 12 male and 12 worker bees.

We took the natural logarithms of the median distances travelled between patches, the number of flowers visited per patch, and the amount of time spent within flower corollas in order to conform to the assumptions of normality. We also arcsine-transformed the proportions of travel within patches. We used Student's two-sample t-tests to compare male and worker foraging when the two castes had equal variance and

Welch's two-sample t-tests when they did not. We carried out all statistical tests in R (R Development Core Team 2009 version 2.9.2).

Pollen-transfer experiment

We used *Brassica rapa* flowers to examine pollen transfer by male and worker bumble bees because *B. rapa* grows quickly and provides both pollen and nectar rewards. We grew *B. rapa* plants from seed in the lab at room temperature (22–25°C), under continuous fluorescent light. We used a peat and vermiculite potting mix and a wicking system to deliver water with 100 ppm of 20:20:20 NPK fertilizer. Initially, we trained both castes of bee to forage on entire *B. rapa* plants that were placed inside the flight cage. During a second stage of training, we presented bees with single emasculated *B. rapa* flowers that were fixed to 5 x 5 cm yellow cards that provided advertisement and a landing surface.

In the experiment, we used the cards to present an unmodified flower with dehiscent anthers followed by an emasculated flower with a clean stigma to an individual bee and recorded the amount of time the bee spent handling each flower. We considered a bee to be handling a flower when it was manipulating the anthers and stigmas of a flower in an attempt to feed on nectar or collect pollen. We then squashed the stigmas from the emasculated flowers in melted basic fuchsin jelly to count the number of pollen grains transferred to recipient stigmas.

We took the natural logarithms of the number of pollen grains transferred and the handling time of the recipient flower in order to conform to the assumptions of normality. We compared the number of pollen grains transferred and the handling times of workers and males using Student's t-tests. Furthermore, we fit two linear mixed effect models to the data in an attempt to disentangle the effects of male morphology and behaviour on pollen transfer. In the first model, the response variable was the number of pollen grains transferred, the fixed effects were recipient flower handling time and caste, and the random effect was experimental bout. The second, reduced model was the same except that it did not include caste as a fixed effect. We compared these two models using a likelihood ratio test. If a difference in pollen transfer between workers and males is primarily due to a difference in flower handling time, including caste as a fixed effect in the model should not significantly improve the model fit.

RESULTS

Late-season survey

By 20 August in these subalpine-to-alpine habitats, males were more than twice as frequent on flowers than workers were (Tab. 1). The sampling sessions lasted from mid-morning to mid-afternoon. At the beginning of these periods, a few of the males were inactive, and had probably spent the previous night on the flowers in a dormant state. The great majority were actively foraging when caught; however, these counts do not include males that were solely searching for mates.

TABLE I. Caste distribution of complete collections of all bumble bees seen on all flowering plants on three elevational transects from the vicinity of the Rocky Mountain Biological Laboratory, Gothic, Colorado, USA, 20–23 August, 2007. Note that *Bombus insularis* and *B. fernaldae* are social parasites, formerly classified as genus *Psithyrus*, which do not produce workers. On these late-season flowers, males outnumbered workers in nine of 13 species, with an overall ratio of 2.18 males per worker.

<i>Bombus</i> species	Worker	Queen	Male
<i>flavifrons</i>	64	2	121
<i>bifarius</i>	58	0	41
<i>mixtus</i>	11	0	36
<i>appositus</i>	13	3	18
<i>occidentalis</i>	10	0	20
<i>sylvicola</i>	1	7	18
<i>rufocinctus</i>	18	0	5
<i>frigidus</i>	0	0	11
<i>balteatus</i>	2	0	7
<i>melanopygus</i>	1	0	1
<i>insularis</i>	0	0	90
<i>fernaldae</i>	0	1	20
Total	178	13	388

Flight-distance experiment

Workers visited twice as many flowers per minute on average than males did (Tab. 2). The median and mean distance bees travelled between flower patches did not differ significantly between the castes (Tab. 2). However, male bees visited 4.04 fewer flowers per patch than workers and made 12.3% more trips between patches (Tab. 2). The males also spent 7.82 seconds longer within the tubes of flowers they entered (Tab. 2). The results presented here compare 'visited' data between the castes, but all significant statistical comparisons and directions of effects were comparable with the analysis of 'entered' data (Tab. 2).

Pollen-transfer experiment

Male bees spent 9.23 seconds longer handling the emasculated recipient flowers than workers (Tab. 2; Fig. 2). Furthermore, males transferred 77.2 more pollen grains to stigmas than workers did. This effect is primarily attributable to differences in handling time between the castes (Fig. 2). Including caste as a fixed effect in the linear mixed effect model did not significantly improve the model fit (df = 6, 4; likelihood ratio = 1.588; p-value = 0.452). There were two male bees that handled the flowers more than four times longer than any of the other bees (Fig. 2). The removal of these outliers did not qualitatively change any of the analyses.

TABLE 2. Summary of results for Student's two sample t-tests and Welch's two sample t-tests (shaded rows) from the flight-distance and pollen-transfer experiments in *B. impatiens*. Square brackets indicate the transformations used.

	t-value	df	p-value	worker mean	worker 95% CI	male mean	male 95% CI
<i>Flight-distance experiment (Visited):</i>							
Visitation rate (flowers/sec)	4.68	22	<.001	0.14	0.11-0.17	0.07	0.048-0.087
Median distance travelled (m) [ln]	-1.72	16.1	0.104	1.49	1.39-1.60	1.70	1.46-1.95
Mean distance travelled (m) [ln]	-1.18	15.8	0.256	1.57	1.49-1.65	1.67	1.50-1.87
Number of flowers per patch [ln]	2.20	22	0.039	9.97	6.6-15.3	5.93	4.3-8.1
Proportion of travel within patch [arcsin√]	3.67	14.6	0.002	0.93	0.91-0.96	0.81	0.72-0.89
<i>Flight-distance experiment (Entered):</i>							
Visitation rate (flowers/sec)	3.47	22	0.002	0.05	0.042-0.057	0.03	0.023-0.040
Median distance travelled (m) [ln]	-1.17	22	0.256	1.57	1.40-1.76	1.70	1.54-1.89
Mean distance travelled (m) [ln]	-0.61	22	0.548	1.67	1.52-1.82	1.72	1.57-1.89
Number of flowers per patch [ln]	4.69	22	<.001	8.76	6.5-11.7	3.10	2.1-4.6
Proportion of travel within patch [arcsin√]	3.53	13.1	0.003	0.90	0.88-0.92	0.75	0.64-0.85
Handling time (sec) [ln]	-3.03	14.5	0.008	8.76	7.4-10.4	16.6	10.8-25.6
<i>Pollen-transfer experiment:</i>							
Number of pollen grains transferred [ln]	-2.82	30	0.008	33	17-63	110	58-207
Handling Time (sec) [ln]	-3.49	30	0.002	4.0	2.6-6.0	13.2	7.2-24.1



Fig. 2. Scatter plot showing the relationship between the time bees spend handling recipient flowers and the number of pollen grains they transfer to those flowers. Solid black line is based on a linear mixed effect model: response variable = $\ln(\text{number of pollen grains transferred})$; fixed effect = $\ln(\text{recipient flower handling time})$; random effect = experimental bout. The means and 95% confidence intervals for the handling time and number of pollen grains transferred by workers (solid black circle) and males (solid black triangle) are also plotted.

DISCUSSION

Our study shows clear differences between male and worker *B. impatiens* foraging behaviour and pollen transfer. Males transferred more *B. rapa* pollen to recipient stigmas than female workers. This could be the result of either behavioural differences, such as handling time, or physical differences in the amount of pollen available on their pile. Pollen transfer tends to correlate with handling time (Thomson 1986) and males had longer handling times in both the foraging and transfer experiments. Because handling time is strongly associated with caste (Fig. 2, Tab. 2), it is difficult to determine the relative effects of handling time and other potential factors such as less grooming, increased electrostatic attraction, or more pile on male pollen transfer. However, a linear mixed effects model suggests that males are better pollen vectors mostly, if not completely, due to increased handling time. It is important to note that increased handling times in males may have other effects, such as increased within-flower self pollination, that were not measured here.

Males visited fewer flowers per patch relative to workers. As a result, flower-to-flower travel by males was more likely to be between patches, suggesting that a higher proportion of male-transported pollen leaves a patch. Such differing patterns of within- and between-patch travel imply that, depending on a plant's reproductive strategy, male and worker pollinators could have very different roles in effective pollen transport. For example, if patches each consist of one individual with many flowers, pollen transport by male bees may reduce geitonogamy, and males may be more efficient pollinators for plants that cannot self-fertilize (de Jong et al. 1993). Similarly, in populations where patches are made up of individuals that are more closely related to each other than to individuals in

different patches, increased between-patch movement could improve outcrossing rates and potentially reduce inbreeding depression (Hauser & Loeschcke 1994). This effect would be reduced in species that are self compatible, if the increased handling times of males also increases within-flower self pollination.

The confined area in which the experiments were conducted prevented the observation of large-scale pollen transfer patterns. The tendency of males to fly longer distances may be stronger than could be detected in our flight cage. On the other hand, there are a number of potential behaviours that may limit a male's foraging range in the field--site fidelity, traplining, or territory guarding--causing them to remain in a particular area, much as workers remain in the area around their colony (Ackerman et al. 1982).

The combination of increased patch switching and increased pollen transfer could cause very different patterns of pollen dispersal by male and worker bees. *B. impatiens* males may transfer greater proportions of pollen long distances, potentially resulting in higher quality pollination services. However, the contribution of a pollinator to plant fitness is a complex thing to measure: it depends not only on the amount of compatible pollen transferred (quality) and the number of floral visits (quantity) by a particular pollinator (Ivey et al. 2003; Mayfield et al. 2001; Stebbins 1970), but also on what other pollinators are visiting (Thomson & Thomson 1992). Males in our experiments show a lower overall foraging rate, suggesting that males probably facilitate fewer successful pollination events than workers. The importance of quality versus quantity to pollinator effectiveness is specific to each plant species, so males may be more effective pollinators of some species while female workers are more effective for others.

Because males left patches after visiting fewer flowers, we infer that they might cause less geitonogamy when visiting real plants with multiple flowers. We cannot extrapolate from our lab experiments to estimate how effectively male visitation reduces geitonogamy in nature: departure decisions probably hinge on situation-specific details of inflorescence architecture, reward, schedules, and probably attempts by males to combine foraging with mate-finding. Our experiments do suggest an intrinsic caste difference in patch tenacity that would be worth studying in the field.

As a result of differences in pollination effectiveness between the castes, flowering plants may have adapted to recruit a particular pollinator caste in order to meet reproductive needs. For example, a plant species that experiences fitness costs with increased geitonogamy may evolve to increase its proportion of male pollinators by flowering later in the season, much as competition for pollinators can lead to shifts in flowering phenology (Mosquin 1971). Several species of Gentianaceae flower late enough in the season at the Rocky Mountain Biological Laboratory for male bumble bees to outnumber female workers. For example, *Gentiana parryi* started to flower after male bumble bees usually outnumbered female workers in 2010 (J. Ogilvie pers. comm.), though we have no evidence that the predominance of males is the adaptive explanation for late flowering. The results

of our experiment hint at the possibility that this kind of specialization may be possible for bumble bees. However, given that males have reduced foraging rates, this specialization may be limited to plant species that receive abundant visitation and show severe costs of inbreeding. Further studies are needed to determine whether there is selective pressure for attracting *Bombus* pollinators of different castes, or whether sex differences in pollination efficiency may have contributed to the evolution of pollination systems that involve predominantly male bees.

Research on bumble bee pollination has a long-standing bias towards the study of female workers, in part because workers are obviously assiduous *foragers* focused on flower-feeding, while males are considered slow-moving, possibly short-lived "*drones*" focused on mate-finding. However, male bumble bees have a longer lifespan than males of most other social insect species, with life expectancies similar to those of workers (Baer & Schmid-Hempel 2006), and many populations of *Bombus* species are actually male biased in the late summer (Tab. I; Bourke 1997). Furthermore, a bee need not be an efficient social forager for a colony in order for it to be an important pollinator. For example, individuals of numerous non-social species, such as solitary and euglossine bees, are important pollinators (Williams & Dodson 1972; Ayasse et al. 2000; Spaethe et al. 2007).

The contribution of male bumble bees to pollination and their potential role in the evolution of flowers has been largely overlooked. Caste differences in bumble bees will cause males to visit fewer flowers than workers, but their slower pace and less systematic foraging produce compensation in the form of less pollen loss and greater pollen-transfer distances. How this trade-off between visit quality and quantity works out for plants will require more study. Expanding research to include caste-based variation in pollinators will allow for a more comprehensive understanding of plant-pollinator interactions throughout the flowering season.

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