BUMBLE BEE DRIFT IN A GREENHOUSE ENVIRONMENT

by

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ABSTRACT

Commercial greenhouses require high densities of managed bumble bee colonies to pollinate crops such as tomatoes. This novel environment contains closely aggregated colonies and a deficit of directional cues which may present orientation challenges to foraging bees, resulting in increased amounts of bee drift, defined as when a bee leaves one colony to join another. I examined orientation and drifting behaviour of *Bombus occidentalis* Greene and *Bombus impatiens* Cresson, the two major bumble bee pollinators of greenhouse tomatoes in British Columbia. The objectives were to establish the extent and frequency of bee drift into foreign colonies, to examine the potential of nest entrance patterns and landmarks to reduce drift in commercial greenhouses, to investigate characteristics of colonies that contained drifting bees, and to determine behavioural and physical characteristics of drifting versus non-drifting bees. On average 28% of marked bumble bees drifted into foreign hives, making up 0.3-34.8% of the population in those colonies. The use of simple black and white patterns and large landmarks did not affect the number of drifting bees, suggesting that disorientation is not a major contributor to drift or to the substantial loss of adult bees from colonies during their first week in a greenhouse. Bees drifted towards the top position when hives were vertically stacked, had decreased foraging times when landmarks were present in the greenhouse, and showed a marginally increased rate of pollen input to colonies. More drifting bees were found in colonies with higher worker and brood populations and greater pollen stores, but increased intra-colony aggressive interactions were not associated with a higher number of drifting bees. Drifting bees had a significantly greater number of mature eggs in their ovaries than did resident worker bees residing in colonies.
hosting drifters, suggesting that drifting could potentially increase the fitness of individual worker bees and may not be solely a function of disorientation and/or nectar robbing. Taken together, our results suggest that drifting of workers into foreign colonies may demonstrate a pre-adaptation to social parasitism.
DEDICATION

This thesis is dedicated to anyone who has worked with and loved something that was potentially deadly. To my parents, who by example led me through a world of discovery and question. To my friends and family, who had to listen until their eyes glazed over about the fascinating behaviours of bees, my thanks for all the bee-related gifts you could find.
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Introduction

Bumble bees have demonstrated global economic importance to pollinate crops in commercial greenhouses and are the only managed pollinators responsible for the commercial production of tomatoes and green peppers (Pressman et al., 1999; Dogterom et al., 1998; Banda & Paxton, 1991; Kevan et al., 1991; Straver & Plowright, 1991). Rearing bumble bees is costly and growers can spend upwards of $35,000 per year to maintain adequate pollination levels. Growers need to manage bumble bees as efficiently as possible, particularly to minimise mortality and disease. Thus, it is important to understand how bumble bees adapt to the greenhouse environment, and how greenhouses impact individual bee behaviours, decisions and colony life cycles.

Bumble bees are social insects, characterised by the presence of altruistic castes, where few individuals (queens) achieve reproductive maturity (Crespi and Yanega, 1995; Hamilton, 1964). Behaviourally distinct castes allow the queen to inhibit egg-laying and influence the actions of worker bees (Cnaani et al., 2000; Duchateau and Velthius, 1989; Gamboa et al., 1987; Hamilton, 1964). The role of a worker bee is to rear siblings, provide resources, guard the nest, and decrease intercolony robbing and disease transfer via nest mate recognition mechanisms (Gamboa et al., 1987).

Bumble bee colonies typify the types of defensive responses found in a structured insect society, and *Bombus* species recognise and frequently attack foreign bees (Plowright and Fuller, 1988; Gamboa et al., 1987; Heinrich, 1979; Free and Butler, 1959; Plath, 1934). However, in commercial greenhouses adults may enter a foreign hive and
remain there. Such drift occurs when individual bees leave one colony and join another (Paar et al., 2002; Pfeiffer and Crailshem, 1998; Jay, 1966; Free, 1958) and may increase the spread of disease between colonies (Fries and Camazine, 2000; Goodwin et al., 1994), and detract from daily foraging activities, and thus cause a decline in colony health and productivity.

The ability to orient back to a natal colony is essential to maintain the population and growth of a social insect colony, and disorientation of bees in greenhouses could inhibit maximal colony growth and survival. Social Hymenoptera have been intensely studied for their ability to travel far distances and return to a specific place (Plowright et al., 1995; Udalova & Karas, 1993; Zeil & Whittman, 1993; Collett, 1992; Cheng et al., 1987; von Frisch, 1967; Tinbergen, 1958). This precision is achieved by a bee utilising a combination of distal and proximal cues and a memory-aided series of vector flight paths. This homing ability is mostly attributed to a path integration system of vectors that may form the basis of a cognitive map, including visual, landmark and olfactory cues, and possibly also magnetic and auditory cues (reviewed in Collett and Collett, 2002 and Capaldi and Dyer, 1999; Wehner et al., 1996; Plowright et al., 1995; Schone et al., 1993a; Schone et al., 1993b; Southwick and Buchmann, 1995). The uniform greenhouse environment presented to a foraging bee is more homogenous than that found in nature, and may promote bee loss and disorientation, potentially increasing bee drift.

Drift also may occur if worker bee reproduction was enhanced in foreign hives. Adult bumble bee workers become more variable in their behaviour at the end of a colony's life cycle and the queen becomes less effective at inhibiting worker ovary development (and egg laying) once she begins producing reproductives (Beekman and
van Stratum, 1998; Duchateau and Veltius, 1989). Adult workers can then develop ovaries and lay mature eggs (Cnaani et al., 2001; Bloch et al., 2000a). In a novel environment where colonies are highly visible and aggregated, drift may present an opportunity for bumble bees to search for a colony where conditions may be optimal for parasitic egg laying.

Bumble bee colonies may be robbed intensively by foreign bees, reducing colony health and fitness (Hamilton, 1964; Free, 1955). Guard bees at a nest entrance decrease such inter-colony robbing and potential disease transfer (Gamboa et al., 1987; Hamilton, 1964; Free, 1957). However, adult bees are more accepting of conspecific foreign bees that arrive with pollen loads (Free and Butler, 1959) and when resources are abundant (Downs and Ratneiks, 2000; Reeve, 1989). Commercially reared colonies arrive at greenhouses with enough sugar solution to sustain the lifetime nectar requirements of the colony, and pollen is abundant in the greenhouse throughout the growing season. Thus, drifters also may enter a colony to rob nectar or pollen.

Bumble bee workers might drift by 1) disorientation; 2) to lay eggs; and 3) to rob nectar and/or pollen. The first objective of this study was to determine whether landscape or hive entrance cues would reduce drifting. The second objective was to determine behavioural and physiological characteristics of drifting bumble bees, and examine if and how they differed from bees not observed to drift. I also examined the dispersal of reproductively developed bees, and explored the idea that the greenhouse environment encourages social parasitism. Drifting to rob resources was not investigated in this study.
TWO:
ORIENTATION AND DRIFTING BEHAVIOUR OF BUMBLE BEES

Introduction

Bumble bees are the sole managed pollinator that sustains the commercial tomato greenhouse industry (*Lycopersicon esculentum* Mill. Solanaceae) world-wide (Dogterom et al., 1998; Kevan et al., 1991), an industry valued at $200 (CDN) million annually in British Columbia, Canada. This relatively new technology has greatly improved pollination (Pressman et al., 1999; Dogterom et al., 1998; Banda and Paxton, 1991; Kevan et al., 1991; Straver and Plowright, 1991), yet satisfactory colony management techniques have not been fully developed. Growers perform little or no bumble bee management, which is surprising because colonies are expensive and inadequate pollination results in decreased fruit set and small fruit. Growers often increase hive numbers to alleviate poor pollination rather than manage existing hives, which may contribute to increased confusion and disorientation of foraging bees.

Bees have impressive learning, memory and navigational capabilities, using distinct features in the surrounding environment to remember nest location (Plowright et al., 1995; Udalova & Karas, 1993; Zeil & Whittman, 1993; Collett, 1992; Cheng et al., 1987; von Frisch, 1967; Tinbergen, 1958). Enriched visual scenes provide honey bees with greater foraging accuracy (Menzel et al., 1998). Honey bee foraging flight paths can be manipulated by the movement of landmarks (Cartwright and Collett, 1983) and the use of simple landmarks increases bumble bee visits to artificial flowers (Redmond and Plowright, 1996). Bumble bees learn the local landscape progressively and return to their nest guided successively by distal cues, then home in on the entrance using proximal cues.
(Plowright et al., 1995). Natural settings provide a bee with orientation landmarks (Plowright et al. 1995; Heinrich 1979), celestial cues (Geiger et al., 1995; Rossel and Wehner, 1984), ephemeral odours (Chittka et al., 1999; Foster and Gamboa, 1989) and variations in flower colour (Gumbert, 2000; Horridge, 1999) and shape (Lehrer et al., 1995), but obvious proximal and distal cues generally are not available in greenhouses.

A potential consequence of inadequate orientation cues is bee drift, when a bee leaves one colony but returns to another, a phenomenon well-documented for honey bees housed in similar-looking hives kept in close proximity (Free, 1957; Jay, 1965, 1966, 1968) and for alfalfa leaf cutter bees (Goerzen et al., 1995). Feral bumble bee queens do not normally establish nests close together, perhaps because increased disease transfer is a consequence for nests in too-close proximity (Fries and Camazine, 2001; Goodwin et al., 1994; Free and Butler, 1959). Growers managing bumble bees in the novel greenhouse environment have not considered how obscuring hive entrances (Plath, 1934) and aggregating nests (Kearns and Thomson, 2000; Gamboa et al., 1987; Hobbs, 1968) might affect homing ability. Honey bee drift occurs during preliminary orientation flights before they become regular foragers, and their drift can be reduced by the addition of hive entrance colours and landmarks (Fresnaye, 1963; Free, 1958). Drift behaviour has not previously been studied in a greenhouse environment but may be important for management and ensuring the well being of production colonies.

Landmarks also are an essential component of the environment for a foraging bee yet obvious landmarks are not available in a greenhouse environment. Honey bee orientation is the result of context-specific, interdependent, orientation mechanisms (Geiger et al., 1995) as they utilize landmark cues in concert with external and directional
cues (Fry and Wehner, 2002). Bumble bees perceive the environment similarly (Plowright et al., 1995); disoriented bees perform a systematic search until familiar landmarks are encountered (Goulson and Stout, 2001), and they orient to horizontally and vertically striped patterns and associate these patterns with navigation routes from their nest to a reward and back (Colborn et al., 1999). Bees primarily use celestial cues for orientation and landmarks as a reference to fix their navigational position (Wehner et al., 1996) that may lead to improved pollination efficiency by decreasing foraging rates (Plowright et al., 1995). Pollination is most efficient when a foraging bee has adequate information to navigate through its surroundings. Large landmarks in varying colours throughout a greenhouse may provide a contextually stimulating environment, and orientation cues (Redmond and Plowright, 1996), potentially counteracting initial bee loss.

Greenhouse growers report substantial population declines from bumble bee colonies following the first introduction to a greenhouse, but the reasons for this loss are unknown (Whittington, 2003; Morandin et al., 2001). Disorientation may be a key factor, an explanation that may be particularly compelling in homogenous greenhouse environments devoid of landmarks or orientation cues. To test the hypothesis that disorientation contributes to bee loss and drift, we investigated the orientation and drifting behaviour of Bombus occidentalis Greene and Bombus impatiens Cresson, the two major pollinators of greenhouse tomatoes in British Columbia, in three separate experiments. We examined bumble bee orientation ability in a commercial greenhouse when navigation cues such as hive entrance patterns and landmarks were provided, and investigated whether drifting is a consequence of a lack of these cues. We also report on
the extent and direction of bumble bee drift into foreign hives, and foraging time and pollen collection as a consequence of increased contextual landmarks.

Materials and methods

The Extent and Direction of Drift

This study was conducted at Gipaanda Greenhouses Ltd in Delta, B.C., Canada from May 2001 – June 2001. This six ha greenhouse produces tomatoes *(Lycopersicon esculentum* Miller var. Rhapsody) planted in North – South directional rows from a central aisle. Colonies were situated along the centre aisle, in vertical stacks of three hives 3.5 – 4.5 m above the leaf canopy, and were placed on support beams with a 20 cm separation from the top of one colony to the bottom of the next. Each stack of colonies was separated by 5 rows of tomato plants, with each stack alternated North and South along the centre aisle, and with hive entrances facing either East or West. Hive density varied between four and five hives per hectare over the course of this study.

Colonies of *Bombus occidentalis* were supplied by Biobest Biological Systems Ltd and shipped from a rearing facility in Leamington, Ontario, Canada. Bees were contained in 35x25x20 cm plastic boxes inside a Styrofoam insulated cardboard box with a bottom feeder containing a sugar and preservative solution. Colonies arrived at the greenhouse once per week and contained 30 – 100 worker bees. Comb already built by the workers was insulated with cotton wool, which was removed prior to bee marking and not returned to the colony.

All bees in a study colony were marked on their thorax or abdomen, or thorax + abdomen, with a colony-specific colour or combination of colours using Liquid Paper™. During marking, all bees were removed from a colony at one time and kept on ice until
they were slow enough to be handled, marked in succession, and then placed back into
the hive. Hive boxes were marked according to the colour of the bees and week of
introduction to the greenhouse. Placement of hives into the greenhouse was random,
except to ensure that each stack was three colonies high.

A total of 18 colonies were marked over five weeks. For three weeks following
greenhouse introduction, marked hives, all hives in a stack containing an experimental
hive, and the hive in the stack positionally adjacent to a marked hive were assessed.
Numbers of marked bees and unmarked bees were noted for every hive surveyed.

Hive Entrance Orientation

*Bombus occidentalis*

*B. occidentalis* were studied July – August, 2001, tested in the same greenhouse
and supplied by the same company as described in experiment one. A total of 1049 bees
in twelve colonies were marked over five weeks, and introduced to stacks randomly
within the greenhouse. Six colonies had six different hive orientation patterns (Figure 2-
1a) taped underneath the hive entrance opening and covering that entire side of the box.
Black and white patterns were chosen, as bees may prefer one colour to another,
potentially influencing drifting numbers. Colonies were surveyed and assessed following
the same methods as the drift survey mentioned above.

*Bombus impatiens*

This study was conducted at Century Pacific Greenhouses Ltd, in Ladner, B.C.,
Canada, from June – August 2001. This nine ha greenhouse produces tomatoes (var.
Rhapsody) planted in North – South directional rows from a centre aisle. Colonies were
placed in horizontal groups of four, set five m deep from the centre aisle at a height 1.5 m
above the ground (within the leaf canopy). There were five rows of plants between colony groups. Colonies were placed on a shelf with 1-5 cm of space between each colony, with hive entrances facing either East or West. Hive density varied between six and seven hives per hectare over the course of this experiment.

Colonies were supplied by Koppert Industries and shipped from a rearing facility in Romulus, Michigan, U.S.A. Bees were contained in 35x30x20 cm plastic boxes, kept inside a Styrofoam insulated cardboard box with a bottom feeder containing a sugar and preservative solution. Colonies arrived at the greenhouse once per week and contained 30 – 50 worker bees. All 609 workers were marked as in experiment one.

A total of 12 hives were introduced over three weeks, one each to the end of a group of hives. Every other study hive had a black and white striped pattern taped to and covering the entire side of the box where the hive entrance was located and also was placed on the top of the hive (Figure 2-1a). Marked colonies were observed and assessed for three weeks after greenhouse introduction, following the methods described in experiment one, except that colonies surrounding the study hive were not surveyed.

**Landmark Orientation**

*B. occidentalis* were studied April – August 2002 at Gipaanda Greenhouses Ltd. (previously described) and Windset Greenhouses in Ladner, B.C. Windset Greenhouses produces 5.8 ha of tomatoes on the vine (T.O.V.) of which the experimental arena (Phase III) was 2.5 ha. Tomatoes were planted in North – South directional rows from a centre aisle. Hives were positioned in groups of three and stacked two high with a third hive beside the bottom hive. Groups of colonies were placed on a shelf 3.5 m above the leaf canopy, with hive entrances facing either East or West. There were ten rows of plants
Figure 2-1. a) Patterns used on hive entrances of *Bombus occidentalis* and *B. impatiens* (July – August 2001). b) Landmarks used in Windset and Gipaanda greenhouses (April – August 2002).
between stacks. Each set of stacks was directly across the central aisle from another set. Hive density varied between four and five hives per hectare over the course of this study.

Biobest Biological Systems Ltd. supplied the colonies. Workers were marked with coloured and numbered tags (Opalithplattchen, Germany) glued to the thorax. Marked hives, all hives in a stack containing an experimental hive and the hive in the stack positionally adjacent to a marked hive were assessed for two weeks following greenhouse introduction.

Landmarks consisted of large (1 m) shapes of Coroplast placed at random intervals along the centre aisle and in the rows of plants. Sixteen landmarks were used, four of each colour (blue, orange, white, yellow) and four of each shape (Figure 2-1b).

Workers in 32 colonies were marked at each greenhouse over 16 weeks totalling 6460 marked bees. Landmarks were placed throughout a greenhouse at the same time as four new colonies and colonies were surveyed for a two week period, after which the landmarks were removed and four new colonies were surveyed for two weeks in a landmark free greenhouse. This schedule was repeated four times. I conducted a landmark and a non-landmark replicate simultaneously; when landmarks were present in one greenhouse they were not present in the other.

Foraging bouts of marked bees were observed with and without the presence of landmarks one week after colony introduction to Windset. Bee numbers, colour, size and time of foraging bout were recorded as they left the hive and when they returned. Bee pollen load size was recorded for returning bees, using an index from one to five, with five being the largest load size observed. Analyses that incorporate pollen load size were blocked by observed bee size because the index was subjective and bee size may
confound the result. Observations were recorded one week apart on days with similar weather and greenhouse conditions, to ensure foraging bout duration was not a consequence of differing weather conditions, as bee activity can be positively correlated with increasing greenhouse temperatures (Morandin et al., 2001).

Data Analysis

All data was analysed in JMP IN 4.0.3 (Academic) using ANOVA Tukey-Kramer HSD and bivariate comparisons. Results are reported with the mean and 95% confidence interval.

Results

The Extent and Direction of Drift

Over all experiments, only 12% of marked bees were found in their original hives one week after marking, and 28% of the originally marked bees were observed in foreign colonies. Thus, high adult bee mortality occurred during their first week in the greenhouse, with 60% of marked bees unaccounted for a week after marking (Figure 2-2). *B. impatiens* colonies demonstrated the greatest marked bee loss, but their unmarked worker populations increased slightly but not significantly over a two week period (45±4 worker bees in week one to 56±14 worker bees in week two). Populations of *B. occidentalis* in 2001 declined from an average of 110±16 bees, (range of 60 – 199) in the first week prior to introduction to an average of 48±14 bees (range of 37 - 66) surveyed over the next three weeks. *B. occidentalis* populations sustained a similar decline during their first week in the greenhouse in 2002 (95±16 bees in week one to 58±12 in the following weeks). The proportion of marked bees that remained in *B. occidentalis* colonies was similar during the pattern and landmark experiments (Figure 2-2).
Figure 2-2. Mean percentage amount of *Bombus occidentalis* (B.occ) and *B. impatiens* (B.imp) drifting out of a marked colony that were not seen again (■), found elsewhere (■), or remained in their original colony (□), for all colonies assessed from all greenhouses studied during May – August 2001 and April – August 2002. The percentages (+ 95% confidence intervals) reveal no differences in the amount of bee drift and bee return when hive entrance patterns and landmarks were present.
Overall, 7.2±1.8% of all bees in foreign colonies were drifters from originally marked colonies, and all hives surveyed had at least one drifting bee a week after marking. The proportion of *B. occidentalis* found in foreign hives ranged from 0.3-34.8% (2001) and 0.5-12.4% (2002), and 0.1-12.2% for *B. impatiens*. Fewer marked *B. impatiens* were seen in foreign colonies during the pattern experiment, partially because the colonies surrounding the marked *B. impatiens* colonies were not surveyed as they were in greenhouses containing *B. occidentalis*.

Significantly more drifters were found in the top hives of vertical stacks compared to bottom locations, with middle colonies not different from top or bottom locations (df=68, F=4.61, p=0.01; Figure 2-3). The middle location had significantly higher worker populations (df=2, F=5.04, p=0.009) than bottom locations, with top hives intermediate. There was no difference in the mean number of marked bees remaining in their original hive based on hive location ($\bar{x}_{\text{BOTTOM}}=10.4\pm4.0$, $\bar{x}_{\text{MIDDLE}}=11.7\pm4.0$, $\bar{x}_{\text{TOP}}=10.3\pm4.0$; df=2, F=0.155, p=0.86).

**Hive Entrance Orientation**

Hives with and without patterns on their entrances showed no significant differences between both the numbers of drifting bees and marked resident bees for

*B. occidentalis* (drift: $\bar{x}_{\text{PATTERN}}=2.0\pm0.8$, $\bar{x}_{\text{NO PATTERN}}=1.7\pm1.0$, $t$-test=-0.88, df=10, p=0.40; return: $\bar{x}_{\text{PATTERN}}=25.8\pm9.0$, $\bar{x}_{\text{NO PATTERN}}=21.8\pm8.8$, $t$-test=-0.84, df=10, p=0.42) and *B. impatiens* (drift: $\bar{x}_{\text{PATTERN}}=1.4\pm0.42$, $\bar{x}_{\text{NO PATTERN}}=2.1\pm0.68$; $t$-test=0.80, df=10, p=0.44; return: $\bar{x}_{\text{PATTERN}}=3.7\pm2.4$, $\bar{x}_{\text{NO PATTERN}}=5.8\pm2.4$, $t$-test=1.48, df=10, p=0.17) (Figure 2-2).
Figure 2-3. More bees (*Bombus occidentalis*) drifted into top hives of vertical stacks compared to bottom hive locations, and colony populations in the middle locations were higher than the bottom locations. Bars with the same letter were not significantly different (Tukey-Kramer HSD test, $p<0.05$).
Landmark Orientation

The mean number of Bombus occidentalis drifters present in colonies did not differ significantly at either Gipaanda or Windset greenhouses with and without the presence of landmarks ($\bar{x}_{\text{LANDMARKS}} = 3.3 \pm 0.6$; $\bar{x}_{\text{NO LANDMARKS}} = 2.7 \pm 0.6$; df=1,30; $F=2.32$, $p=0.13$) (Figure 2-2). The mean number of marked bees returning to their hive of origin with the presence of landmarks (19.8±4.3 bees) also was not significantly different (df=1,30; $F=0.214$, $p=0.65$) when landmarks were not present (18.7±4.3 bees). Returning marked resident bees were 44% of hive populations at Gipaanda and 46% at Windset, when surveyed after the first week of marked bee introduction.

When landmark and non-landmark treatments were pooled, colonies consisted of an average of 16% drifting bees (2.3±1.7) per hive in the first week. These foreign bees traveled a mean distance of 6.6±1.7 aisles to their destinations. At both greenhouse locations, most bees drifted into hives that were in close proximity to their original hive (df=1,41; $F=7.1$, $p=0.01$), staying mostly on the same side of the central aisle from where they originated (Figure 2-4).

Drifters observed residing in a colony on more than one week composed 31% of the total drifting population; 69% of drifters were not seen the second week or subsequently. Of that population, observations revealed three different types of drifters: transients, residents, and voyeurs. The transient drifters constituted 11.3% of the total drifters, traveled an average distance of 5.5±2.4 aisles on a weekly/daily basis, and were found in different hives week after week. Resident drifters constituted 11.4% of the drifting population, traveled 4.2±1.0 aisles, and then remained in the same colony they drifted into originally. Voyeurs were 8.2% of the drifting population, traveled an
Figure 2-4. Distance histogram indicating the frequency of *Bombus occidentalis* that drifted after their first week in the greenhouse from their original colony to a foreign colony a) on the same side of the central aisle; b) across the central aisle (Gipaanda and Windset Greenhouses, Ladner, BC). A row distance of zero indicates bees that drifted within their home stack of hives.
Mean Percentage of Bees Drifting Within the Central Aisle (+95% C.I.)

Mean Percentage of Bees Drifting Across the Central Aisle (+95% C.I.)

Distance (aisles)
Figure 2-5. Bumble bees at Windset greenhouse had shorter foraging times when landmarks were present (p=0.002), and returned with marginally but not significantly increased rates of pollen loads when bees were blocked by size (p=0.06; Tukey-Kramer HSD test). The gray circle indicates the mean foraging time and pollen index for all bees (± 95% confidence interval).
The graph shows the relationship between pollen index and time foraging (s) for two categories: Landmark (●) and No Landmark (○). The data points indicate a trend where individuals foraging near landmarks spend less time foraging compared to those without landmarks. The error bars suggest variability in the data.
average of 5.6±1.9 aisles but returning to their original hive after being found in a foreign colony. Since the remaining 69% of drifters were seen only once, we did not assign these individuals to these categories.

Bees blocked by size showed decreased pollen foraging times when landmarks were present (df = 10; p = 0.002; Figure 2-5). Foraging bees returned with the same quantities of pollen whether landmarks were present or not (\(\bar{x}_{\text{LANDMARK}} = 4.3\pm0.99\), \(\bar{x}_{\text{NO LANDMARK}} = 3.8\pm0.99\), F = 0.18, df = 10, p = 0.51). There was no relationship between the size of the bee and the amount of pollen brought back to the hive (\(\bar{x}_{\text{SMALL}} = 3.0\pm2.0\), \(\bar{x}_{\text{MEDIUM}} = 4.7\pm0.78\), \(\bar{x}_{\text{LARGE}} = 3.3\pm0.99\), F = 0.80; df = 2, p = 0.10). The duration of time spent foraging was not correlated with a larger (indexed) quantity of pollen on bees returning to the hive (\(r^2 = 0.0070\), df = 12, p = 0.80). The rate of pollen returned to hives expressed as pollen index load per time foraging and blocked by bee size was marginally increased when landmarks were present (\(r^2 = 0.26\); df = 10; p = 0.06; Figure 2-5).

**Discussion**

Our results indicate that an average of 28% of bumble bees in greenhouses drift into foreign colonies and remain there, a phenomenon not previously explored in this novel agricultural setting. Drifting *B. occidentalis* and *B. impatiens* were found in every hive surveyed, with 0.3-34.8% of adult bees in foreign colonies composed of drifters. This proportion may be an underestimate because hives we did not survey also may have contained drifting marked or unmarked bees. The slight species differences we observed in the numbers of drifting bees may have been mostly the results of methodological variation, as only marked *B. impatiens* colonies were assessed, but we examined both marked and unmarked *B. occidentalis* colonies. The higher mortality seen in the
landmark experiments than the survey and hive entrance pattern experiments with *B. occidentalis* may reflect seasonal changes in bee mortality, as the former experiments were conducted over a longer period.

Drift was directed towards the top hive position when hives were vertically stacked. Hymenoptera tend to climb up to higher vantage points to gain direction (i.e. see Baarends, 1941 for digger wasps), and bumble bees might then enter the nearest hive.

Most bees did not drift further than six aisles (30 m) away from their original hive, similar to distances traveled by drifting honey bees (Pfeiffer and Crailsheim, 1998; Jay, 1966), and drift was not skewed East or West. The close proximity of bumble bee hives in greenhouses may contribute to increased levels of drift, as honey bee drift depends on the distance between colonies (Pfeiffer and Crailsheim, 1998; Jay, 1966), and feral bumble bee colonies are not normally aggregated (Kearns and Thomson, 2000; Gamboa et al., 1987; Hobbs, 1968).

Surprisingly, the use of simple black and white hive entrance patterns or large landmarks did not have any significant effect on reducing the numbers of drifting bees, contrary to what we hypothesized from other learning and orientation studies of bees in laboratory environments. The patterns and landmark shapes we used were chosen from the literature demonstrating that bumble bees orient to black and white contrasting edges (Colborn et al., 1999; Horridge, 1999), recognize and prefer the same colors we used for our landmarks (Gumbert, 2000), and use similar landmarks for homeward orientation when foraging (Fry and Wehner, 2002; Redmond and Plowright, 1996; Geiger et al., 1995; Plowright et al., 1995; Zeil and Whittmann, 1993; Collett, 1992; Cheng et al., 1987; von Frisch, 1967; Tinbergen, 1958). The greenhouse environment has many
factors that are not as easily controlled as in laboratory studies, such as celestial cues, access to outside forage, and a central aisle that is described as a “highway” for bee travel by greenhouse workers. Also, none of the greenhouses studied had fluctuations of their internal environments, dissimilar to field conditions.

Laboratory findings demonstrate the potential for homing orientation but this potential was not realized in the greenhouse environment. Greenhouse colonies reared in a commercial facility may arrive with an inflated population because workers have never left the colony; therefore some bee loss through age is expected. The large proportion of bees lost after their first week in the greenhouse may be explained by their lack of foraging experience (Capaldi and Dyer, 1999), great variability in their learning ability (Guirfa et al., 2001; Free, 1958) or their drift into hives that were not surveyed.

Bees can learn specific objects and their visible boundaries, and are adept at distinguishing abstract interrelationships like sameness and difference, possibly to improve their foraging ability (Guirfa et al., 2001). The number of bees that drifted and the distribution of their distance traveled were not different with and without landmarks or patterns, suggesting that other factors may influence drift. For example, bees in tomato greenhouses forage exclusively for pollen, as tomato flowers offer no nectar reward, and bees may enter a foreign hive to find sugar from a known source for the return trip home, and either remain or subsequently depart to return to their home nest. Drifting bees may enter foreign hives at the end the day, reside there over-night, and continue home in the morning, similar to honey bee foragers that will spend the night away from the hive (Southwick and Buchmann, 1995; Heinrich, 1979). Hive conditions such as nutrition, age, and population size may be important factors governing drift, and
bees may drift for biologically significant reasons such as increasing their individual fitness, a topic I will discuss in the next chapter.

Other orientation cues such as colony odours may be diluted when colonies are in close proximity, particularly in a greenhouse where similar types of pollen and sucrose solution are present in all hives. Olfactory cues at the nest entrance exist for nest recognition purposes (Foster and Gamboa, 1989; Hefetz et al., 1993), and are the predominant cues when visual cues are unavailable (Chittka et al., 1999). Genetic similarity of commercial bumble bees may further diminish nest recognition cues and increase drift. Microsatellite analysis of workers, drones and their queen in future studies might provide insights about hive-fidelity.

The definition of drift, “bees that leave their original hive to join another”, needs to be expanded. Our observations revealed three distinct types of drifters: 1) **Transient** drifters found in more than one foreign hive over a four week period, 2) **Resident** drifters that drifted once and then remained in their new colony, and 3) **Voyeur** drifters that drifted into a foreign hive but later returned to their original hive. Transient drifters may be searching for their original hive or an optimal colony situation that they can exploit either by achieving a higher dominance ranking, by laying their own eggs, or by robbing nectar. Resident drifters may have originally drifted into a hive due to disorientation and found a position where they might reproduce. Voyeur drifters may have been lost originally, but then returned to their home colony. The behaviours we have observed suggest that bees have high behavioural plasticity, and the ability to learn and process information to flexibly adapt to their environment (Guirfa et al., 2001).
Drifting bees represented close to one tenth of hive populations and almost a third of the bees we marked, potentially transferring disease, disrupting colony interactions, robbing nectar, or laying eggs. These actions may effectively diminish pollinator productivity and potentially increase costs to the greenhouse grower. Honey bee drift in managed colonies has been linked with proximity of hive entrances, bee loss through immigration (Free, 1958, 1961; Jay, 1965, 1966, 1968, 1969), and the spread of disease (Goodwin et al., 1994; Fries and Camazine, 2001). Managed bumble bee colonies do not seem to exclude foreign bees, and in captivity have accepted forced introductions even of different species (Free and Butler 1959) as well as foreign bees that return with loads of pollen (Heinrich, 1979).

Foraging times were reduced when landmarks were present, and pollen foraging rates were marginally increased, suggesting landmarks contributed to increased foraging and potentially greater efficiency for individual bees. Bumble bees previously showed decreased foraging times when landmarks were present (Chittka et al., 1999; Redmond and Plowright, 1996), but our observations were limited to only two weeks of the growing season in one greenhouse, and should be investigated further. Decreased foraging time for a similar load might increase foraging proficiency, and for that reason greenhouse growers might include large landmarks within greenhouses. Further experiments on the foraging efficiency of bees in this novel environment might focus on this potentially useful management tool.

Our studies determined that orientation cues are not useful management options to reduce drift and potential bee loss, although landmarks may decrease foraging times. We quantified drift but not the fundamental impact of drifting, such as the amount of disease
transfer. Also, additional studies of bumble bee hive placement in an irregular or non-repetitive layout might lead to decreased drift. In the next chapter I will discuss behavioural characteristics and colony-level biological factors that influence which colonies bees are most likely to drift into.
THREE:
"GIRLS GONE WILD": SOCIAL IMPLICATIONS OF DRIFT IN THE GREENHOUSE ENVIRONMENT

Introduction

Bumble bees are the primary managed pollinator of commercial greenhouse tomatoes (Dogterom et al., 1998; Banda and Paxton, 1991; Kevan et al., 1991). Techniques to establish and maintain colonies have been successful, but substantial adult mortality can occur in greenhouse environments (Whittington, 2003; Morandin et al., 2000), resulting in colony population declines and decreased pollination efficiency, which is costly for growers. Management research has focused on pollination effectiveness, optimal colony density, the effects of nutrition provided by tomato pollen, interspecific interactions among bees and the benefits of glass versus plastic greenhouse coverings (Whittington, 2003; Morandin et al., 2000; Pressman et al., 1999; Dogterom et al., 1998). However, conspecific behavioural interactions have not been well-studied in this environment.

Bee drift, when a bee leaves one colony to join another, generally has been associated with orientation errors (Paar et al., 2002; Pfeiffer and Crailshem, 1998; Jay, 1966) and could be a factor contributing to bumble bee loss. Drift is a well-documented phenomenon for honey bees housed in similar-looking hives kept in close proximity in apiaries (Pfeiffer and Crailshem, 1998; Jay, 1965, 1966; Free, 1958), and for alfalfa leaf cutter bees (Goerzen et al., 1995). Beekeepers attempt to minimise drift because of the potential for disease transfer (Fries and Camazine, 2000; Goodwin et al., 1994) nectar robbing, and adult mortality (Jay, 1966, 1968; Free and Butler, 1959). Drifting out of colonies may increase individual worker fitness but likely decreases natal colony fitness.
Goodwin et al., 1994; Jay, 1968), and nest mate recognition is important in this context to minimise the extent of drifting (Downs and Ratnieks, 2000). Aggressive interactions from foreign bees entering a hive could lead to less time spent foraging and the early development of reproductives, resulting in a smaller foraging work force and a decrease in the amount of pollination achieved by each colony.

Orientation cues such as nest entrance patterns and spatially non-uniform apiary layouts are usually employed to decrease the amount of honey bee drift (Goerzen et al., 1995; Jay, 1966). Bumble bees nest in the ground in pre-existing burrows, commonly disguise their hive entrances (Free and Butler, 1959), and normally do not aggregate their nests (Kearns and Thomson, 2000; Gamboa et al., 1987), whereas in greenhouses colonies are highly visible and are located in one central area. Commercial producers provide nest boxes with identical outward appearances, and hive entrances are not cryptic. A typical commercial greenhouse contains a homogenous distribution of tomato plants repeated in regularly spaced rows, providing worker bees with clear visual access to a large number of similar-looking hives. The uniformity of a greenhouse environment may further promote bee disorientation and loss, leading to increased bee drift, subsequent pollination decline and colony expenditure increase. However, when bumble bees were provided with nest entrance patterns or large landmarks scattered throughout the greenhouse, the amount of bee loss and drift was not reduced (Birmingham and Winston, in prep.), suggesting that alternate biologically important motives may affect the propensity for worker bees to drift.

Bumble bee queens exert reproductive dominance over workers through pheromones and aggression, resulting in reduced or absent development of worker
ovaries (Cnaani et al., 2000; Duchateau and Velthius, 1989; van der Blom, 1986). Social interactions also influence ovary development (Duchateau and Velthius, 1989) and some dominant workers develop ovaries and lay eggs (Bloch et al., 2000a). This occurs mostly in the final phase of a colony's life cycle when worker populations are high (Cnaani et al., 2000; Duchateau and Velthius, 1989). Workers perceive the onset of larval queen development, signifying the end of a cycle, and often begin to lay unfertilized male eggs (Cnaani et al., 2000). Since greenhouses contain many colonies at varying stages in their life cycles, worker bees might have unusual opportunities to drift into foreign colonies to achieve a higher dominance ranking via agonistic acts (Duchateau and Velthius, 1989) and/or lay eggs.

Social parasitism, when a parasite benefits from brood care or resources of a host, is common in *Bombus* species (Schmid-Hempel, 1998). *Bombus occidentalis*, the primary pollinator of greenhouses in British Columbia, recognises and attacks foreign bees and other intruders, as its nests are commonly usurped by the closely related social parasite *Psythirus* sp. in nature (Kupper and Schwammberger, 1995; Free and Butler, 1959). *B. occidentalis* should therefore have strong kin and colony recognition mechanisms (Plowright and Fuller, 1988; Gamboa et al., 1987) to minimise such social parasitism. Conspecific reproduction of foreign bees entering a colony may represent an incipient stage of such social parasitism.

In this study we report biological characteristics of colonies and of drifting bees that suggest commercial greenhouse environments encourage a predisposition for parasitic behaviour through drifting, rather than drift being only a consequence of disorientation or other errors. We predicted that 1) drifting workers would drift into more
populous late-stage colonies with good pollen stores as they would provide more likely opportunities for worker reproduction, 2) drifting bees would have more developed ovaries than resident bees in colonies hosting drifters, and 3) aggressive behaviour would be higher in colonies hosting more drifters because drifters would need to defend themselves and assert their dominance.

**Materials and methods**

Data were gathered from three different greenhouses: Gipaanda Greenhouses Ltd, Century Pacific Greenhouses Ltd., and Windset Greenhouse, in Delta, B.C., Canada. Data were collected from Gipaanda during May 2001 – June 2001 and May 2002 – August 2002, from Century Pacific during June 2001 – August 2001, and from Windset during April 2002 – August 2002.

**Greenhouse Descriptions**

**Gipaanda Greenhouses Ltd.**

The six ha greenhouse produced tomatoes (var. Rhapsody) planted in North – South directional rows from a central aisle. Colonies were situated along the centre aisle, in vertical stacks of three hives 3.5 – 4.5 m above the leaf canopy and were placed on support beams with a 20 cm separation from the top of one colony to the bottom of the next. Each stack of colonies was separated by five rows of tomato plants, with each stack alternated North and South along the centre aisle and with hive entrances facing either East or West.

Colonies of *Bombus occidentalis* were supplied by Biobest Biological Systems Ltd and shipped from a rearing facility in Leamington, Ontario, Canada. Bees were contained in 35x25x20 cm plastic boxes inside a Styrofoam insulated cardboard box with
a bottom feeder containing a sugar and preservative solution. Colonies arrived at the greenhouse once per week and each contained 30 – 100 worker bees. Comb already built by the workers had been insulated with cotton wool, which was removed prior to bee marking and not returned to the colonies.

**Century Pacific Greenhouses Ltd.**

The nine ha greenhouse produced tomatoes (var. Rhapsody) planted in North–South directional rows from a centre aisle. Colonies were stacked in horizontal groups of four, set 5 m deep from the centre aisle at a height of 1.5 m above the ground (within the leaf canopy). There were five rows of plants between stacks. Colonies were placed on a shelf with 1-5 cm of space between each colony, with hive entrances facing either East or West.

Colonies of *B. impatiens* were supplied by Koppert Industries and shipped from a rearing facility in Romulus, Michigan, U.S.A. Bees were contained in 35x30x20 cm plastic boxes, kept inside a Styrofoam insulated cardboard box with a bottom feeder containing a sugar and preservative solution. Colonies arrived at the greenhouse once per week and contained 30 – 50 worker bees. Comb built by the workers prior to shipping had been insulated with cotton wool, which was removed prior to bee marking and not returned to the colonies.

**Windset Greenhouse Ltd.**

Windset Greenhouses produced 5.8 ha of tomatoes on the vine of which the experimental arena (Phase III) was 15 acres. Tomatoes were planted in North–South directional rows from a centre aisle. Hives were positioned in groups of three and stacked two high with a third hive beside the bottom hive. Groups of colonies were
placed on a shelf 3.5m above the leaf canopy, with hive entrances facing either East or West. There were ten rows of plants between stacks. Each set of stacks was directly across the central aisle from another set.

Biobest supplied the *B. occidentalis* colonies.

**Marking Procedure**

All bees in a study colony from Gipaanda and Century Pacific (2001) were marked on their thorax or abdomen, or thorax + abdomen, with a colony-specific colour or combination of colours using Liquid Paper™. Bees from Gipaanda and Windset studied during 2002 were marked with coloured numbered tags glued to the thorax supplied by Opalithplattchen (Germany). During marking, all bees were removed from a colony at one time and kept on ice until they were sluggish enough to be handled, marked in succession, and then placed back into their hive. Hive boxes were marked according to the colour of the bee tags and week of introduction to the greenhouse. Placement of hives into the greenhouse was random with respect to possible hive locations available.

**Colony Assessments**

The colour and/or number of all marked bees were noted for every hive surveyed. Data were collected on the number of marked workers, unmarked workers, queens, drones, brood (the number of pupae, open pupae, larval masses and egg masses), honey pots and pollen pots. Drifters were defined as marked bees that were found in a colony from which they did not originate.

*Gipaanda (2001)* - Eighteen *B. occidentalis* colonies were marked over seven weeks starting in May. For three weeks following greenhouse introduction, hives with marked bees, all hives in a stack containing an experimental hive and the hive in the stack
positionally adjacent to a marked hive were assessed. From July onward an additional 12 colonies were marked over six weeks.

*Century Pacific (2001)* - A total of 12 *B. impatiens* hives were introduced over three weeks, one each to the end of a row of hives that were already established in the greenhouse. Marked colonies were observed and assessed for three weeks after greenhouse introduction, but colonies surrounding the study hive were not surveyed.

*Gipaanda and Windset (2002)* – A total of 32 *B. occidentalis* colonies were marked over 16 weeks at each greenhouse. Hives were assessed as for Gipaanda 2001 for two weeks following greenhouse introduction.

**Aggression Survey**

Behavioural surveys of colonies of *B. occidentalis* were conducted at Gipaanda and Windset greenhouses in 2002. Data were collected for 60 seconds prior to colony assessments, and again five minutes later. Colonies were assigned an aggression index value from one to five when they were first opened with five being the highest aggression value. Specific behaviours recorded included the number of bees seen buzzing, running, flying and posturing. Posturing was defined as when a bee remained still except to raise one or more legs in a defensive manner.

**Bee Collection and Dissection Procedure**

Marked *B. occidentalis* were collected from Gipaanda and Windset greenhouses during May – August 2002. Five marked drifters and five marked original resident bees were selected randomly from on top of the brood and removed from hives two weeks after their introduction to the greenhouse. Drifter and original resident bees were placed
in separate plastic Petri dishes and stored frozen prior to dissection, which occurred within three months.

*B. occidentalis* were removed from the freezer and allowed to thaw for a minimum of five minutes. Bee tag colour and number were noted and then removed and the bee’s fresh weight was recorded. The distance between the eyes of each bee also was measured to indicate size (Wilson, 1971). An index from one to three of wing wear was used to approximate the age of the bee, with three indicating the greatest amount of wear as wing wear is considered a reasonable measure to compare bee ages (Cartar, 1992). All measurements were taken using an ocular micrometer.

Bees were dissected in 70% ethanol under a dissecting microscope. The basal oocyte length of the terminal oocyte and ovary length to the last nutritive cell excluding the membrane was measured from both the left and right ovary. The distinction between mature eggs and oocytes was determined using a descriptive index (Duchateau and Velthius, 1989). The number of mature eggs and the total number of oocytes were counted. The left and right ovaries were weighed separately then discarded.

**Data Analysis**

Square root transformations ($\sqrt{x+3/8}$) were performed when the data were non-normally distributed because the small counts formed a Poisson distribution (Zar, 1984). Regressions were examined in JMP IN 4.0.3 (Academic) and ANOVA comparisons were analysed with SAS (SAS Institute, 1988). Site-specific differences and interactions between greenhouses were accounted for in the statistical models. Mean results are reported with 95% confidence intervals.
When the number of drifters was positively correlated with increased worker populations, worker relationships to the amount of queens, drones, brood, honey and pollen pots were determined. Where the worker relationship to other colony factors was significantly positive, a drifter to worker ratio was used to remove the covarying effect that all colony variables increase as the worker population increases.

**Results**

**Colony Assessments**

For *B. impatiens* 2001, a positive relationship was found between the mean number of drifters and the size of the adult worker ($r^2=0.36$, df=1, $p=0.04$; Figure 3-1) and drone populations ($r^2=0.38$, df=1, $p=0.03$; Figure 3-2). There was no relationship between the mean number of drifters and queens ($r^2=0.0020$, df=1, $p=0.89$; Figure 3-2), brood ($r^2=0.089$, df=1, $p=0.35$; Figure 3-1), honey ($r^2=0.20$, df=1, $p=0.14$; Figure 3-3) or pollen pots ($r^2=0.073$, df=1, $p=0.39$; Figure 3-3).

For *B. occidentalis* in 2001, a positive relationship also was found between the number of drifters and adult workers ($r^2=0.070$, df=1, $p=0.005$; Figure 3-1). Worker populations ($\bar{x} = 48.0 \pm 5.9$) increased significantly with the number of drones ($\bar{x} = 2.58 \pm 1.2$, $F=16.7$, df=1,16, $p=0.0003$), brood ($\bar{x} = 84.8 \pm 12$, $F=31.7$, df=1,16, $p<0.0001$) and pollen ($\bar{x} = 0.67 \pm 0.30$, $F=4.67$, df=1,16, $p=0.04$) but there was no relationship between the number of drifters and the number of drones ($r^2=0.039$, df=1, $p=0.68$; Figure 3-2), the amount of brood ($r^2=0.059$; $p=0.42$; Figure 3-1) or pollen ($r^2=0.13$, df=1, $p=0.30$; Figure 3-3), when the number of workers was added as a covariate to the statistical model. The amount of honey pots ($r^2=0.23$, df=1, $p=0.10$;
Figure 3-3) and the number of queens also did not have an effect on the number of drifters ($r^2=0.018$, $df=1$, $p=0.53$; Figure 3-2).

During 2002, *B. occidentalis* worker populations ($\bar{x}=44.8\pm2.8$) increased significantly with brood populations ($\bar{x}=60.1\pm3.6$, $F=35.5$, $df=1,30$, $p<0.0001$) and honey pots ($\bar{x}=33.0\pm2.2$, $F=17.1$, $df=1,30$, $p<0.0001$), and was therefore added as a covariate to the statistical model. The number of drifters also increased positively with brood ($r^2=0.23$, $df=1,30$, $p<0.0001$; Figure 3-1), but there was no relationship with the amount of honey pots ($r^2=0.093$, $df=1,30$, $p=0.10$; Figure 3-3). The number of *B. occidentalis* drifters increased positively with increasing numbers of workers ($r^2=0.13$, $df=1$, $p<0.0001$; Figure 3-1), drones ($r^2=0.034$, $df=1$, $p=0.006$; Figure 3-2) and pollen pots ($r^2=0.17$, $df=1$, $p<0.0001$; Figure 3-3), but not with the numbers of queens ($r^2=0.0026$, $df=1$, $p=0.45$; Figure 3-2).

In 2002, more *B. occidentalis* drifters were observed in hives that had been in the greenhouse longer than 5 weeks, but less than 11 weeks ($N=12$; $\bar{y}_{\text{DRIFTERS}}=1.55+0.124x$; $df=1$, $r^2=0.53$, $p=0.008$; Figure 3-4). Greenhouse growers did not normally keep hives in the greenhouse longer than 13 weeks. Satellite colonies (small auxiliary colonies of mostly pupae and egg masses separate from the main colony area) and egg cannibalism by workers were observed during assessments for both bee species in both years.

**Ovary Dissections**

Dissected drifting bees (*B. occidentalis*) had a greater number of mature ($F=5.64$, $df=1,125$, $p=0.02$) and immature ($F=4.41$, $df=1,125$, $p=0.04$) eggs in their ovaries than did resident marked bees of the colony they drifted into (Figure 3-5; 41% of drifting bees versus 22% of resident bees had mature eggs). Head width and wing wear measurements
of drifters ($\bar{x}_{\text{HEAD WIDTH}}=6.2\pm0.16$ mm, $\bar{x}_{\text{WING WEAR}}=0.82\pm0.24$) and residents ($\bar{x}_{\text{HEAD WIDTH}}=6.1\pm0.18$ mm, $\bar{x}_{\text{WING WEAR}}=0.78\pm0.24$) were not significantly different (df=125, $F=0.00$, $p_{\text{HEAD WIDTH}}=0.97$; df=125, $F=0.09$, $p_{\text{WING WEAR}}=0.77$), suggesting they were of similar size and age.

Colony assessment data of 16 *B. occidentalis* drifters with mature eggs in their ovaries revealed they left hives with smaller worker populations and entered hives with larger worker populations ($F=7.46$, df=1,14, $p=0.02$), greater numbers of queens (df=1,14, $F=19.9$, $p=0.0006$), larger amounts of brood (df=1, $F=18.4$, $p=0.0009$) and less pollen (df=1,14, $F=4.58$, $p=0.05$; Figure 3-6). The number of drifters (df=1,14, $F=3.70$; $p=0.08$), remaining marked bees (df=1,14, $F=2.14$; $p=0.17$), drones (df=1,14, $F=1.58$; $p=0.23$) and honey (df=1,14, $F=3.38$; $p=0.09$) had no effect on colony choice for drifters with egg-laying potential (Figure 3-6). Drifters without mature eggs in their ovaries were found in hives where colony characteristics were not significantly different than the colonies they left (df=1,14; $F_{\text{DRIFTERS}}=0.0012$, $p_{\text{DRIFTERS}}=0.97$; $F_{\text{WORKERS}}=0.00220$, $p_{\text{WORKERS}}=0.963$; $F_{\text{QUEENS}}=0.348$, $p_{\text{QUEENS}}=0.56$; $F_{\text{DRONES}}=0.407$, $p_{\text{DRONES}}=0.53$; $F_{\text{BROOD}}=0.0347$, $p_{\text{BROOD}}=0.85$; $F_{\text{POLLEN}}=2.33$, $p_{\text{POLLEN}}=0.14$; $F_{\text{HONEY}}=0.786$, $p_{\text{HONEY}}=0.39$; Figure 3-6).

Drifting bees that were observed more than once comprised 31% of the total drifting population (leaving 69% of all marked drifting bees that were not seen in colonies after the first week they were described as drifters). The drifters seen on more than one occasion displayed three distinct patterns of drift: transient (found in $3.2\pm1.6$ foreign hives over a four week period), immigrant (drifted once and then remained in the
new colony) and voyeur (drifted into a foreign hive but later returned to their original hive). See Chapter Two for further information.
Figure 3-1. The number of drifters in a colony for both bee species increased significantly with increasing colony population. Drifting *B. occidentalis* increased significantly with the amount of brood in both 2001 and 2002. As worker and brood populations increased during April to August (2002), the number of *B. occidentalis* drifters increased (worker $r^2=0.13$, $p<0.0001$; brood $r^2=0.23$, $p<0.0001$; $n=221$).
B. impatiens 2001

No. Workers Amount of Brood

B. occidentalis 2001

No. Workers Amount of Brood

B. occidentalis 2002

No. Workers Amount of Brood
Figure 3-2. Drifting *B. impatiens* increased significantly with the numbers of drones, but was not significantly affected by queen number (n=12). *B. occidentalis* drifters increased with the number of drones only in 2002, and not with increasing queen populations.
Figure 3-3. Colonies with more pollen pots had an increased number of *B. occidentalis* drifters in 2002 (n=221). There was no observed relationship between the amount of honey and drifters.
Figure 3-4. A greater number of *Bombus occidentalis* drifters entered older hives ($n=12$, $r^2=0.56$, $p=0.008$), but their numbers declined once the colony was past the age of 11 weeks. The numbers of hives at each age are in brackets.
Mean No. Drifters (+95% C.I.)

\[ y = 1.55 + 0.124x \]

Colony duration in greenhouse (weeks)
Figure 3-5. *Bombus occidentalis* drifters had more mature (df=1,125, F=5.64, p=0.02) and immature eggs (df=1,125, F=4.41, p=0.04) in their ovaries than resident marked bees of the same colony. Letters indicate significantly different results.
Figure 3-6. a) Colony composition of the home (from) and the destination colonies (to) of 16 Bombus occidentalis drifters with mature eggs in their ovaries. Destination colonies had significantly more queens (F=19.9; p=0.0006), workers (F=7.46; p=0.02), brood (F=18.4; p=0.0009) but fewer pollen pots (F=4.58; p=0.05). The number of drifters (F=3.70; p=0.08), drones (F=1.58; p=0.23) and honey (F=3.38; p=0.09) did not differ. b) Colony composition of the home (from) and the destination colonies (to) of 22 B. occidentalis drifters without mature eggs in their ovaries. Destination colonies did not differ in their composition from home colonies. Bars with an asterix indicate means that are significantly different (Tukey-Kramer HSD).
Aggression

Indices of aggression for *B. occidentalis* were not positively correlated with the number of drifter when the number of workers was used as a covariate in the statistical model (n=51; df=2,50; $\bar{x}_{\text{INDEX}} = 1.79\pm0.22$, $F_{\text{INDEX}} = 2.47$, $p_{\text{INDEX}} = 0.12$; $\bar{x}_{\text{BUZZING}} = 2.79\pm0.65$, $F_{\text{BUZZING}} = 0.08$, $p_{\text{BUZZING}} = 0.78$; $\bar{x}_{\text{RUNNING}} = 1.71\pm0.71$, $F_{\text{RUNNING}} = 2.99$, $p_{\text{RUNNING}} = 0.09$; $\bar{x}_{\text{FLIERS}} = 0.91\pm0.39$, $F_{\text{FLIERS}} = 0.325$, $p_{\text{FLIERS}} = 0.57$; $\bar{x}_{\text{POSTURING}} = 0.90\pm0.37$, $F_{\text{POSTURING}} = 0.373$, $p_{\text{POSTURING}} = 0.54$), indicating that the number of foreign bees was not a predictor of the levels of aggression in a colony. Indices of aggression increased significantly with increasing worker population (n=51; df=2,50; $F_{\text{INDEX}} = 3.95$, $p_{\text{INDEX}} = 0.05$; $F_{\text{BUZZING}} = 6.50$, $p_{\text{BUZZING}} = 0.01$; $F_{\text{RUNNING}} = 5.03$, $p_{\text{RUNNING}} = 0.03$; $F_{\text{FLIERS}} = 4.87$, $p_{\text{FLIERS}} = 0.03$; $F_{\text{POSTURING}} = 7.51$, $p_{\text{POSTURING}} = 0.008$), indicating that larger colonies were more aggressive.

Discussion

Drifting bumble bees (*Bombus occidentalis*) often were found in older hives with greater numbers of adult workers, brood, pollen and drones. Further, drifting *B. occidentalis* had more developed eggs in their ovaries than resident non-drifting marked bees. Results for drifting *B. impatiens* were not as extensive but we found significant positive relationships between increasing numbers of drifters and adult worker and drone populations. Together, these results suggest that drifting may be a biologically meaningful strategy by workers to increase their individual fitness.

Aspects of these data provide evidence that drifting bumble bees act as opportunistic social parasites when in the greenhouse environment. Drifters entered hives with increased numbers of workers, greater pollen resources and potentially less
queen control due to their higher population, age and onset of drone production, colony attributes that would enhance the likelihood of successful egg production. The extent of ovary development was not dependent on the age or size of dissected drifters versus resident bees. Drifters with egg-laying potential left significantly smaller colonies to enter older, larger colonies with a greater amount of brood and where more reproductives had been produced, a point in colony cycles when other workers are less likely to eat worker laid eggs (Ratnieks, 1988; van der Blom, 1986). Drifters without egg-laying potential did not demonstrate the same pattern of dispersal. Queen reproductive control over workers is reduced in colonies where reproductives are being produced, normally near the end of a colony's cycle (Cnaani et al., 2000; Bloch and Hefetz, 1999; Duchateau and Velthius, 1989). These factors taken together suggest that drifters with reproductive potential did not randomly choose which hives to enter, but selected colonies where their individual fitness would be enhanced.

Colony aggression increased with worker population, but higher numbers of drifting bees were not found in more aggressive colonies. However, we only observed colonies with smaller than average greenhouse worker populations and aggression is normally associated with large colonies that are producing reproductives (Bloch et al., 2000b; Duchateau and Velthius, 1989; Plowright and Fuller, 1988). Dissected drifters were not larger than dissected resident bees, suggesting that drifters with reproductive capabilities were not always aggressive or dominant within the hives they entered. Potentially, drifters with mature eggs in their ovaries are entering colonies that are less aggressive and more accepting of foreign bees, thereby evading possible conflict. An
individual bee may trade-off the risk of attack and potential death when entering a colony with mature eggs in her ovaries for individual fitness gain.

Drifting behaviour may involve disorientation, but our data suggest drifting can represent a possible early stage in the evolution of a parasitic species, somewhere between the social bumble bee parasite *Psythirus* and a colony’s own reproducing workers. *Psythirus* are obligatory social parasites of *Bombus* species that have lost the worker caste (Schmid-Hempel, 1998). Their queens establish nests by either killing or evading the queen, and behaviourally and chemically blend into the hive to allow workers to become accustomed to their presence (Kearns and Thomson, 2000). *Psythirus* queens will then reproduce instead of or alongside the host *Bombus* queen as the *Bombus* workers continue bringing nectar and pollen back to the hive (Kupper and Schwammberger, 1995). Worker bumble bees also lay eggs in the presence of the queen at the end of the colony life cycle (Bloch et al., 2000a; Duchateau and Velthius, 1989; Owen and Plowright, 1982; Roseler, 1974), and drifting greenhouse bees may take advantage of the unrelated workers in older colonies, using the food brought back to the hive to rear their brood. Social parasites often are derived from species that share an immediate ancestry with their hosts (Emory’s Rule) and molecular evidence suggests a close relationship between *Psythirus* and *Bombus* (Koulianos et al., 1999). Commercially reared colonies have similar nesting types, which also should facilitate social parasitism (Schmid-Hempel, 1998).

Not all drifting bees had reproductive development, and some may have drifted for non-reproductive reasons, such as disorientation or nectar robbing. The transient, resident and voyeur drifting behaviours observed here may reflect all three reasons why
bumble bees might drift. Foraging bees might drift into foreign colonies where there is an abundant energy supply to fuel their foraging trips, and are accepted because of the pollen loads they carry (Downs and Ratnieks, 2000; Free and Butler, 1959). It is possible that drifters did not recognise they were in a foreign colony, and/or were not recognised as foreign by guard bees due to similar environmental conditions they may have been raised in (Foster and Gamboa, 1989), and the constant supply of similar pollen close to the nest. Foraging bees with large pollen loads were observed entering and then leaving foreign colonies with pollen loads intact after a brief (4 second) stay. Further behavioural observations might determine how much drift could be attributed to disorientation, nectar robbing or social parasitism.

Results for *B. impatiens* were less extensive than for *B. occidentalis*, since fewer *B. impatiens* colonies were studied, surrounding hives were not surveyed, bees were not individually marked and smaller proportions of bees were seen a subsequent time than for *B. occidentalis*. *B. impatiens* were observed to be more aggressive than *B. occidentalis* and therefore may have been more successful at excluding drifting bees, but at this point it would be premature to speculate whether differences between *B. occidentalis* and *B. impatiens* were due to biological differences or to a less intensive experimental effort for *B. impatiens*.

The novel greenhouse environment increases the potential for worker reproduction because bees can drift into foreign, highly visible hives, or search for a hive where egg-laying conditions may be optimal. The higher brood populations associated with drifting could have been due to worker reproduction, but this hypothesis cannot be explored further by the present study, as we did not take samples to determine maternity.
However, commercially reared *B. occidentalis* have the same low level of isozyme variability as wild populations (Mullen and Rust, 1994) suggesting that any lack of nest mate recognition was not due to inbreeding at commercial rearing facilities. Commercially reared populations genetically mimic wild populations, suggesting drifting behaviour is mostly a consequence of the greenhouse environment.

Drifting bumble bees in a novel environment exhibit important pre-adaptations for social parasitism. Their drift behaviour could be an active dispersal to establish themselves in nests where egg laying was more likely than in natal nests, and to survive adult worker aggression and evade egg removal, as found in the parasitic Cape honey bee *Apis mellifera capensis* (Neumann and Hepburn, 2002). By drifting into foreign colonies, workers may have their male offspring reared by unrelated workers, simultaneously avoiding competition with siblings also trying to rear male offspring, and increasing the total male production by members of their natal colony. These drifters might accumulate both indirect fitness, by helping at the nest, and direct fitness, by laying reproductives, much like *Polistes* wasps (O’Donnell, 1996). Our study did not determine whether bees with developed ovaries were successful in laying and/or rearing male eggs, but Bloch et al. (2000a) and Duchateau and Velthius (1989) found that adult *B. terrestris* with developed ovaries could successfully lay eggs, provided they have adequate amounts of protein, as bees without access to pollen will not develop ovaries (Duchateau and Velthius, 1989). Resources are not limited in a greenhouse, where colonies are provided with sugar solution and pollen is readily available and not expected to be a limiting factor. Greenhouse colonies may also be less aggressive and more accepting of foreign bees because resources are abundant (Downs and Ratnieks, 2000; Reeve, 1989).
Reproductively developed drifting bumble bees were found in more populous, late stage colonies with greater pollen stores, indicating that bumble bee drift in this novel environment may provide opportunities to increase individual fitness. Bumble bees adapt well to the greenhouse environment, demonstrating a high degree of behavioural plasticity (Guirfa et al., 2001) expected from a species whose natural habitat ranges from the Arctic to the equator. Future studies might focus on frequency and motives for bumble bee drift, and whether this phenomenon is common in wild habitats, and the degree of success in egg laying by drifting workers, as the greenhouse environment may encourage a natural drifting behaviour.
Conclusion

The frequency of drift was extensive within the commercial greenhouse environment. Bumble bees drifted in all directions and their distribution was concentrated close to their original hive. Landmarks and hive entrance patterns did not decrease the amount of drift or bumble bee loss during the first week colonies were placed in greenhouses. However, landmarks did marginally improve the foraging rate of worker bees, potentially resulting in greater foraging efficiency (Redmond and Plowright, 1996). Further experimentation might examine the effects of hive entrance patterns and landmarks placed concurrently in greenhouses and how different hive placements might obscure nest entrances and provide a more natural setting.

The high amount of drift observed in the greenhouse may create a different social environment than that found in a more natural setting. Drifters had significantly greater amounts of mature and immature eggs in their ovaries when compared to resident adult workers of similar size and age in the colonies the drifters joined. Drifting bees also had a greater number of mature eggs in their ovaries than did bees that did not drift, and entered hives that contained significantly more workers, queens and brood, and less pollen than drifters that did not have mature eggs in their ovaries. Drifters entering less aggressive hives that are larger and potentially under less queen control due to their size and age (Cnaani et al., 2000; Duchateau and Velthius, 1989) may increase their individual fitness by laying eggs in a colony where they can evade queen control and worker policing (Ratneiks, 1988; van der Blom, 1986), producing their own male
offspring in colonies where queens are already producing males (Beekman and van Stratum, 1998; O'Donnell, 1996). Further experiments could focus on whether drifting workers actually lay eggs that survive and produce drones.

There are many other examples of social systems where workers evade reproductive queen control. Gall-forming aphids of the *Pemphigus* species have individuals that drift for selfish or parasitic reasons (Abbot et al., 2001). These societies are clonal, with workers that are asexual daughters of the foundress and whose function is to defend the nest. Individuals that drift within this society enter a neighbouring gall to reproduce and do not defend their original nest or the one they have entered. These aphids leave the nest as first-instar nymphs, continuing their development after foreign colony intrusion. Anarchistic honey bees (*Apis mellifera*) evade worker policing of their eggs, a worker behaviour that helps the queen maintain worker sterility, and an increased threshold to ovary inhibiting pheromones, to successfully rear unfertilized eggs (Barron et al., 2001). *Polistes* wasps accumulate indirect and direct fitness gains by helping at the colony then later reproducing (O'Donnell, 1996).

Does the managed greenhouse environment magnify a naturally occurring behaviour? Little is known about drifting in feral bumble bees and alien workers found in hives of the large, aggressive species *Bombus hypnorum* have been attributed to an usurpation event (Paxton et al., 2001). Heterospecific bumble bees are accepted in feral colonies when the introduction is forced (Free and Butler, 1959) even though bumble bees do recognise nestmates and attack foreign bees as its nests commonly are usurped by the parasitic bumble bee *Psythirus* in nature (Foster and Gamboa, 1989; Plowright and Fuller, 1988; Gamboa et al., 1987; Free and Butler, 1959). Feral honey bee colonies of
Apis dorsata nest in dense aggregations and are not subject to the same frequency of drift as managed honey bees (Paar et al., 2002). Ecology certainly can alter the behaviour of an organism. For example the social roles of Polistes biglumis bimaculatus are modified due to their ecology, a mountainous environment lacking in resource which causes the queen to continue to forage after workers and gynes emerge (Lorenzi and Turillazzi, 1986).

The impact of a unique environment on the social structure of bumble bee colonies has not been considered by greenhouse growers. Greenhouses provide worker bees with clear access to enter a wide range of hives, providing the opportunity for an adaptive response that might have an impact on intra and inter-colony interactions and pollination effectiveness. Growers normally increase the numbers of hives when pollination levels decline, although obscuring nests entrances or scattering colonies throughout the greenhouse may increase worker hive-fidelity and reduce the incidence of drift.

Drift traditionally has been associated with a negative impact on a colony’s fitness, such as increased disease, loss of resources from robbing, and the possible addition of worker-laid eggs from another colony. Bees might drift due to 1) disorientation, 2) to lay eggs, and/or 3) to rob resource. Disorientation may contribute to bumble bee drift as inexperienced foragers are not always able to orient properly and find their colony (Capaldi and Dyer, 1999; Rodd et al., 1980). Bumble bee foragers have access to abundant resources throughout the greenhouse and within their own colony and may not need to rob other colonies. However robbing may persist when resources are abundant, as robbing may still require less energy than foraging (Downs and Ratnieks,
2000; Reeve, 1989). The third explanation for drift in a greenhouse reflects a pre-adaptation to social parasitism by evading queen control and potentially laying eggs in the colonies into which bees drift. Bumble bees are essential pollinators of wild and managed ecosystems and drifting may have important consequences for the structure of bumble bee societies in more natural environments, and may provide an alternate strategy for colony living and gene dispersal.
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