

THE UNIVERSITY OF CALGARY

The Economics of Pollen Collection by Bumble Bees

(Hymenoptera: Apidae: *Bombus*)

by

Salman A. Rasheed

A THESIS

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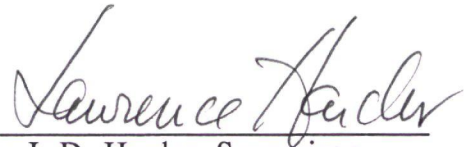
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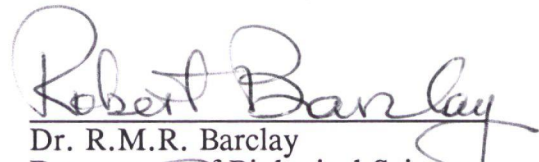


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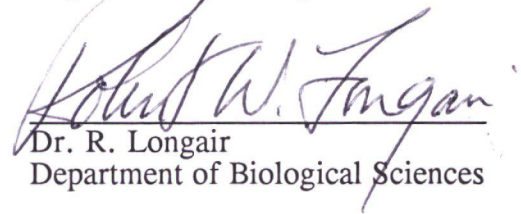
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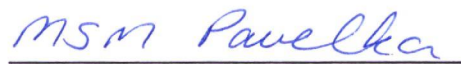
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ABSTRACT

A pollen-collecting bee confronts two problems; which plant species to collect pollen from if several options exist and how to behave to maximize net pollen returns from the chosen species. When collecting pollen from lupines (*Lupinus* spp.) bumble bees (*Bombus* spp.) behave as though they maximize the ratio of pollen collected to metabolic costs (efficiency). Efficiency maximization is probably beneficial because it would maximize pollen collection during a bee's lifetime. When selecting among plant species, bumble bees are sensitive to differences among species in the amount of pollen protein and associated foraging costs, and they preferentially visit plant species that offer the highest efficiency of protein collection within a particular site. Maximization of this currency should enhance delivery of protein-rich pollen to the hive, thereby promoting larval development and reproductive success. Bumble bees consider both foraging benefits and costs when collecting pollen within a single plant species and among different plant species.

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1 Introduction

1.1. Foraging behaviour as an optimization process

Foraging animals repeatedly decide where to feed, how to search for food within a site, and what food to eat. These decisions require animals to measure which food characteristic they value the most and how to treat this characteristic (i.e. maximize, minimize, indifference) (Schoener 1971). In a proximate sense, this value, the foraging "currency", depends on the benefits of resources and associated costs, which can be determined intrinsically (e.g. shore crabs avoid very large mussels because of handling constraints determined by claw size: Elner and Hughes 1978) or extrinsically (e.g. patch use by hoary marmots depends on predation pressure: Holmes 1984). Differences among individuals in their ability to respond to these benefits and costs in foraging behaviour can result in differential individual survival and reproduction (e.g. Blanckenhorn 1991; Scrimgeour 1992). As a result, natural selection can act on foraging behaviour, producing animals that balance benefits and costs to promote their relative lifetime reproductive success. Hence, animals are generally expected to behave optimally in many contexts, including foraging (for review see Pyke *et al.* 1977; Pyke 1984).

As noted above, optimally foraging animals evaluate the various choices they confront according to a particular criterion or "currency", which they maximize or minimize (Schoener 1971). Many animals maximize their rate of net energy intake (DeBenedictis *et al.* 1978; Pyke 1978; Waddington and Holden 1979; Pyke 1980; Houston and Krakauer 1993; Waite and Ydenberg 1994; also see Stephens and Krebs 1986), the ratio of net benefits accrued from a particular behaviour relative to the time spent on that behaviour. In other cases, animals maximize energetic efficiency, the ratio of benefits to costs associated with a particular behaviour (Carlson and Moreno 1982; Schmid-Hempel *et al.* 1985; Kacelnik *et al.* 1986; Schmid-Hempel 1986; Seeley 1986; Dolphin 1988; Welham and Ydenberg 1988; McLaughlin and

Montgomerie 1990; Wolf and Schmid-Hempel 1990; Welham and Ydenberg 1993). Certain ecological conditions may compromise a foraging animal's ability to maximize these currencies. In particular, animals sometimes collect resources that satisfy specific nutritional requirements (Pulliam 1975; Belovsky 1979; Greenstone 1979; Law 1992), or they are unable to collect certain profitable choices because of incomplete information about the foraging environment (Pyke *et al.* 1977; Stephens and Krebs 1986 and references therein).

1.2. Foraging by bees (Hymenoptera, Apoidea)

Honey bees (*Apis mellifera* L.) and bumble bees (*Bombus* spp.) are among the best studied animals from the perspective of foraging economics (e.g. Waddington and Holden 1979; Schmid-Hempel 1986; Seeley 1986; Schmid-Hempel 1987; Varjú and Núñez 1991 for honey bees; Pyke 1979; Pyke 1980; Hodges 1981; Best and Bierzychudek 1982; Hodges 1985; Harder 1988; Pleasants 1989; Cartar and Dill 1990 for bumble bees). As a superfamily bees (Apoidea) are distinguished from their evolutionary ancestors, the sphecoid wasps, by their complete reliance on flowers for energy and nutrition (Michener 1974). Bees (Apoidea) are an extremely diverse assemblage with 9 families consisting of approximately 28 000 species (Michener 1979).

Nectar and pollen are essential resources for bees in that both are necessary for reproductive success and one cannot be substituted for the other because they serve different metabolic functions (Michener 1974). Nectar provides adults with energy for flight and thermoregulation, whereas pollen provides the sole source of protein for egg production by reproductive females and growth of developing larvae (Heinrich 1979a). Foragers collect nectar and transport it internally in their crop: upon returning to the nest, they either mix it with pollen for larval provisioning or some species store it for future use (Michener 1974). In contrast, pollen-collecting

individuals groom pollen from their bodies and pack it externally in scopae (except for Euryglossinae and Hylaeinae in the family Colletidae who ingest pollen along with nectar) and carry it back to the nest to provision larvae (Michener *et al.* 1978). Bee behaviour often differs while collecting each resource. For example, pollen-collecting bees often rapidly vibrate flowers to release pollen, a behaviour never observed when bees collect only nectar (Buchmann 1983). Furthermore, while collecting pollen, bees often visit different plant species than while collecting nectar (e.g. Brian 1957; Liu *et al.* 1975). Hence nectar and pollen comprise distinctly different resources for bees because they satisfy different requirements, require different collection behaviour and are often collected from different plant species.

A foraging bee confronts two general problems: what plant species to visit and how to behave to maximize resource transfer from the chosen plant species to the nest. When deciding which plant species to collect resources from, bee species can restrict their foraging activities to a few plant species (i.e. specialists, oligolecty) or they can forage from a broader array of plant species (i.e. generalists, polylecty) (Fægri and van der Pijl 1979; Eickwort and Ginsberg 1980). However, even polylectic species prefer a restricted number of plant species compared to those available.

The plant species preference of oligolectic bees can be quite strict, and the motivation for plant species choice may be innate or flexible (Linsley 1958; Linsley and MacSwain 1958; Baker and Hurd 1968; Laverty and Plowright 1988; Buchmann and Cane 1989; Cane and Payne 1993). For example, *Hemihalictus lustrans* (Halictidae) gathers pollen exclusively from *Pyrrhopappus carolinianus* (Asteraceae), despite local flowering of other plant species (Estes and Thorp 1975; Barber and Estes 1978). Consequently, *H. lustrans* and *P. carolinianus* share similar seasonal occurrence and geographical distribution. In contrast, *Andrena erythronii* (Andrenidae), an oligolect of *Erythronium* spp. (Liliaceae), uses other pollen sources

in the absence of its preferred host (Michener and Rettenmeyer 1956). Typically, specialists collect a resource more efficiently from their preferred plant species than do generalists (Strickler 1979; Lavery and Plowright 1988, although see Harder and Barrett 1993). For example *Hoplitis anthocopoides* (Megachilidae) collected more pollen per unit handling time from its host species, *Echium vulgare* (Boraginaceae), than did four generalist bee species (Strickler 1979).

In contrast to oligoleges, polylectic bees use taxonomically diverse plant species and their distributions are not limited by specific plant taxa. However, polylectic species prefer a restricted number of plant species from those available. Such preferences can be influenced by time of day (Linsley and Cazier 1970; Linsley 1978), time during the season (Liu *et al.* 1975; Heinrich 1976a) or nectar production (Thomson 1988; Bego *et al.* 1989; Cartar 1991; Dukas and Real 1991). As a result, preferences by polylectic species probably develop as learned responses to variation between plant species in nectar and pollen availability and its influences on foraging returns (Macior 1966; Weaver 1957; Lavery 1980; Lavery 1985; Dukas and Real 1991; Dukas and Real 1993a; Dukas and Real 1993b; Lavery 1994). For example, naive bumble bees take longer to obtain rewards from morphologically complex flowers than do experienced foragers (Lavery 1980). However, learned responses are limited, as bumble bees suffer a reduced ability to discriminate between rewarding and non-rewarding floral types as the number of different floral types increases (Dukas and Real 1993a). The responsiveness of bees to variation in rate of nectar production (Pleasants 1981; Best and Bierzychudek 1982; Dukas and Real 1993b) and pollen availability in individual flowers (Cane and Payne 1988; Buchmann and Cane 1989; Harder 1990a), probably occurs as a result of their learning capabilities. In addition to learning, polylectic preferences may be partially under genetic control because genotypically different family groups of the generalist *Apis mellifera* exhibit

differential preference for nectar and pollen (Robinson and Page 1989; Oldroyd *et al.* 1991).

Nectar collection by bees (especially Apidae) has been well studied and it is clear that bees generally forage economically, measuring benefits and costs. Bee behaviour within resource patches generally maximizes rate of net energy intake (Waddington and Holden 1979; Hodges 1981; Pleasants 1981; Harder and Real 1987); whereas the total nectar load collected during a foraging trip tends to maximize energetic efficiency (Schmid-Hempel *et al.* 1985). Interspecific plant choice by bumble bees typically depends on the interaction between flower structure and bee morphology through their influences on foraging benefits and costs (Harder 1985). In general, flowers with deeper corollas produce more nectar (see Harder and Cruzan 1990 and references therein). However, the rate of nectar ingestion decreases with flower depth, so that flowers of intermediate depth provide the highest rate of net energy intake (Harder 1983; Harder 1986). This optimal flower depth corresponds to the length of a bee's glossa (Harder 1983; Harder 1986; Harder 1988) and, consequently, plant species preferences correlate strongly with bumble-bee glossa length (Heinrich 1976b; Inouye 1978; Morse 1978; Inouye 1980; Ranta and Lundberg 1980; Barrow and Pickard 1984; Harder 1988). When collecting nectar from different plant species, bees are also sensitive to the sugar composition of nectar, although observed preferences differ between studies, including preference for plants with balanced quantities of sucrose, glucose and fructose (Wykes 1952), preference for sucrose-rich nectars (Waller 1972) or no obvious preference for sugar composition (Southwick *et al.* 1981; Wells *et al.* 1992). The behaviour of bees collecting nectar from a single species is also consistent with maximization of rate of net energy intake (Best and Bierzychudek 1982; Pleasants 1989). For example, when visiting *Digitalis purpurea* (Scrophulariaceae) inflorescences, *Bombus flavifrons* foragers begin at the flower with the greatest reward, and leave the inflorescence when the mean reward

from the next flower is lower than the average return from the next plant (Best and Bierzychudek 1982).

Compared to nectar foraging, the economics of pollen collection have received little attention. As indicated in the overview of oligolecty and polylecty, pollen-collecting bees exhibit preferential behaviour for particular plant species. For example, 11 different bee species (Andrenidae) collected pollen from only 32 of the 54 available plant species (Matsumura and Munakata 1969). Matsumura and Munakata (1969) observed that bees collected pollen from plants that were at the peak of their seasonal flowering phenology. Brian (1951) observed that bumble bees collected pollen from only four out of the 27 plant species at her study site and she speculated that this preference was associated with pollen-grain volume, although the exact selection criterion was not identified. Schmidt (1982) showed that honey bees also discriminate among pollen types, although preferences were clearly not related to pH or protein content. In a subsequent experiment Schmidt (1984) found preferences for a mixture of pollen types, rather than a pure diet of the types comprising the mixture. He speculated that preference for a pollen mixture offers a compromise of pollen texture, nutrition, and chemistry. Clearly, bees prefer certain plant species over others; however, the motivation for this preference remains unclear.

When collecting pollen from a single species, bees alter their behaviour in response to the amount of pollen removed from individual flowers. *Habropoda laboriosa* (Anthophoridae), *Bombus* spp. and *Xylocopa virginica* (Xylocopidae) visited pollen-laden *Vaccinium ashei* (Ericaceae) flowers longer than flowers that had been visited previously and contained less pollen (Cane and Payne 1988). Buchmann and Cane (1989) similarly showed that handling time and grooming behaviour of *Bombus sonorus* and *Ptiloglossa arizonensis* (Colletidae) depends on pollen availability of *Solanum elaeagnifolium* (Solanaceae). In addition, bumble bees visited more flowers per inflorescence and groomed significantly more when collecting

pollen from previously unvisited lupine inflorescences (Harder 1990a). Harder (1990a) suggested that bumble bees are responsive to variation in foraging time and metabolic costs while collecting pollen from a single plant species. However, the proximate currency underlying the behaviour of pollen-collecting bees remains to be identified.

1.3. Objectives

In this thesis I address two main objectives: 1) to experimentally determine what economic currency pollen-foraging bumble bees (*Bombus* spp.) maximize when collecting pollen from a particular plant species; and 2) to determine whether pollen abundance and quality influence the role of this currency in determining preference for particular plant species. In chapter two, I address the first objective by deriving different currencies that bees could use when collecting pollen from a single plant species. These currencies all involve the amount of pollen collected during a single foraging trip, but they incorporate foraging times and metabolic costs differently. I compare predictions based on maximization of the candidate currencies with observed behaviour to assess which currency provides the most consistent description of pollen-collecting behaviour. Once I have identified the economic rule that best describes bee behaviour while collecting pollen within a plant species, I consider whether the same currency governs selective foraging between plant species. Specifically, in chapter three, I assess whether selected pollen characteristics (standing crop, pollen volume, protein content) influence plant choice by bumble bees either by themselves, or in the context of net foraging returns. I then compare the rankings of species for these characteristics with the composition of pollen loads collected by bees to assess which characteristics bees use to guide their choice of plant species. Together these chapters demonstrate that bumble bees are sensitive to both foraging benefits and costs when collecting pollen within a single plant species and among different plant species.

1.4. Bumble bee colony cycle

Behaviour is best understood within the context of natural history and so I will briefly overview the colony cycle of bumble bees (for more details, see Alford 1975; Heinrich 1979a). Bumble bees (Hymenoptera: Apidae: *Bombus*) are primitively eusocial insects with an annual colony cycle. In spring, individual queens that were inseminated during the previous autumn emerge from hibernation, locate a suitable nest site (typically an abandoned small-mammal nest), and lay the first brood of eggs. During development of the first brood, the queen forages to provision the larvae with pollen and nectar. After the first brood of workers ecloses, they forage and maintain the nest and the queen spends all of her time laying eggs. As the number of workers increases with the production of subsequent broods, smaller workers generally remain in the hive performing colony maintenance, whereas larger workers forage. However, individuals will switch tasks, for example forming a larger foraging force if declining colony reserves necessitate (Brian 1952; Free 1955; Inouye 1978; Cartar 1992a). During this ergonomic phase (Oster and Wilson 1978) the colony produces two or more broods of non-reproductive females which increase the colony's workforce (Duchateau and Velthuis 1988). Once the number of workers approximately equals the number of larvae, the colony switches to the reproductive phase, during which unfertilized male eggs are laid and the workers supply sufficient food so that female larvae develop into queen-sized individuals (Cumber 1949; Plowright and Pendrell 1977; Pomeroy and Plowright 1981; Duchateau and Velthuis 1988). Upon emerging, reproductive individuals typically leave the nest and mate with individuals from other nests. With the switch to the reproductive phase, the worker population is not replenished, so that colony productivity eventually declines as workers are lost to various mortality sources (Duchateau and Velthuis 1988). Only fertilized queens of the next generation hibernate through the winter.

2 Collection of non-energetic resources: the economics of pollen collection from a single plant species by bumble bees.

2.1 Introduction

Animals collect different resources to fulfill homeostatic requirements. These resources serve different functions, even though animals probably experience similar costs when collecting these resources. Resource collection may be complicated when the benefits associated with the reward differ from the costs. For example, although bees do not collect pollen for its energetic value, they must expend energy to obtain it. In this chapter, I examine the motivation behind pollen collection by bumble bees from *Lupinus* sp.

2.1.1 Foraging behaviour

Foraging animals often confront diverse alternatives, such as which patch to collect resources from or which prey to include in the diet. These alternatives may have different survival and reproductive consequences for the forager (e.g. Blanckenhorn 1991; Scrimgeour 1992); however foraging animals probably do not consider the lifetime implications of selecting different options. Instead, foragers likely assess alternatives based on more immediate benefits and costs, as determined by prevailing physiological and ecological conditions. Natural selection will favor individuals that make proximate decisions that impart an evolutionary advantage. Such direct criteria for evaluating foraging options are known as currencies (Schoener 1971).

Many foraging decisions imply the use of energy-based currencies. Animals often behave as though they maximize rate of net energy intake during foraging bouts (Werner and Hall 1977; Elner and Hughes 1978; Hodges 1981; Harder and Real 1987; also see Stephens and Krebs 1986; Pyke *et al.* 1977; Pyke 1984; Waite and

Ydenberg 1994). In other instances, animals do not maximize their rate of net energy intake over a foraging bout, but rather maximize energy per volume ingested (Montgomerie *et al.* 1987; Houston and Krakauer 1993) or the ratio of net foraging benefits to metabolic costs (energetic efficiency: Kacelnik *et al.* 1986; Schmid-Hempel 1987). This disparity in behaviour among and within species suggests that even though animals seem to use energy-based currencies, the particular form of energy maximization is context specific.

In contrast to the above examples, some animals behave in manners that are inconsistent with maximization of purely energy-based currencies. Two general circumstances could limit the suitability of energy-based currencies. First, the forager's ability to obtain energy could be compromised by conflicting demands, including: additional nutrient requirements (Pulliam 1975; Belovsky 1979; Greenstone 1979; Law 1992); prey defenses, such as toxic secondary plant compounds (Freeland and Janzen 1974; Farentinos *et al.* 1981; Owen Smith and Novellie 1982; Howard 1987; Schmitz *et al.* 1992); and predator avoidance (Sih 1980; 1982; Lima 1985; Lima *et al.* 1985; Kohler and McPeck 1989; for review see Lima and Dill 1990). Second, in some circumstances animals collect resources whose benefits cannot be reduced to units of energy (e.g. cerumen: Sakagami and Camargo 1964; nesting material: Wimberger 1984; resin: Armbruster 1984; water: Seeley 1986), so that energy maximization is irrelevant. For such resources, foraging benefits are not energy based, even though their procurement involves energy expenditure. Consequently, although foraging for such resources involves an individual's energy budget, the relevant currency cannot be based on energetics alone. The behaviour of animals collecting resources with non-energetic benefits has received little attention.

2.1.2 Pollen collection

Pollen collection by bees (Hymenoptera, Apoidea, 9 families, approximately 28 000 species: Michener 1979) and masarid wasps (Hymenoptera, Vespidae, Masarinae, 220 species: Hicks 1927; Jander 1976; Brothers and Finnamore 1993) is a widespread example of foraging for non-energetic benefits. Pollen provides protein for growth of developing larvae and egg production by reproductive females (for bumble-bee examples see Plowright and Pendrel 1977; Sutcliffe and Plowright 1988), whereas nectar provides the energy for activity and thermoregulation of adults, and moistens the pollen fed to larvae. Although pollen contains energy and trace amounts of vitamins and minerals (Stanley and Linskens 1974), pollen-collecting bees do not value pollen as an energy source. For example, foragers from bumble-bee colonies that are nectar depleted do not rely on pollen as an energy source, rather they switch from pollen to nectar collection (Free 1955; Cartar 1992a). More importantly, pollen and nectar collection require different behaviours (Zimmerman 1982; Galen and Plowright 1985; Buchmann and Shipman 1990), and often involve different plant species (Brian 1957; Liu *et al.* 1975). Therefore, pollen collection can be distinguished from energy-motivated behaviours.

The behaviour of pollen-collecting bees, including the underlying currency, has received little attention. Most nonparasitic bees collect pollen externally (Michener *et al.* 1978) and carry it in specialized structures called scopae or corbiculae, which are typically located on the hind legs. While flying between flowers, a bee grooms pollen from its body and places it in these scopae (Michener *et al.* 1978; Roberts and Vallespir 1978; Thorp 1979). Honeybees (*Apis mellifera* L.), and presumably other bees, monitor the size of the growing pollen load with sensilla on the corbiculae (Ford *et al.* 1981). The ability of bees to assess pollen returns on a per flower basis has been demonstrated (Cane and Payne 1988; Buchmann and Cane 1989; Harder 1990a), and Harder (1990a) suggested that bumble bees forage in a

manner consistent with maximization of the amount of pollen collected per unit of energy expenditure (pollen collection efficiency). However, the proximate rules that bees use to govern their behaviour when pollen foraging have not been explored.

2.1.3 Objectives

This study identifies the foraging currency used by bumble bees when collecting pollen from a single species. I first formulate three alternative currencies, gross pollen load, rate of pollen collection and pollen collection efficiency, which differentially incorporate the amount of pollen collected and the insect's time and energy budgets. I assess the relevance of these alternative currencies by taking advantage of specific features of the interaction between pollen-collecting bumble bees and lupine (*Lupinus* spp., Fabaceae) inflorescences. In particular, the predictable vertical distribution of pollen within lupine inflorescences and the tendency of bees to start low on the inflorescence and work upward, allow me to predict a different starting position along the inflorescence for each currency. By comparing predicted and observed starting positions, I determine which currency best describes pollen collecting behaviour.

2.1.4 Candidate currencies for pollen foraging

I consider three currencies that bees could maximize while collecting pollen: pollen collected per inflorescence, rate of pollen collection and pollen collection efficiency. A bee that maximizes its pollen collection per inflorescence collects as much pollen as it can carry per inflorescence, regardless of how long it takes or how hard it has to work. Although this currency ignores time and energy constraints, it forms a baseline for evaluation of other currencies which incorporate such constraints. A bee maximizing rate of pollen collection (pollen collected/foraging time) collects the maximum amount of pollen per unit time, with corresponding benefits for the

instantaneous rate of colony growth. Nectar-collecting bees often forage as though they maximize rate of net energy intake (Waddington and Holden 1979; Hodges 1981; Pleasants 1981; Harder and Real 1987), and pollen-foraging bees may similarly rate-maximize. Finally, a bee that maximizes its pollen collection efficiency (pollen collected/energetic foraging costs) would maximize both pollen input to the nest and its lifetime. Bee lifespan varies negatively with energetic expenditure (Wolf and Schmid-Hempel 1989), in part because of accumulated wing wear (Carter 1992b), so that bees should be sensitive to increased foraging costs. Indeed, maximization of foraging efficiency explains some aspects of nectar-foraging behaviour by honeybees (Schmid-Hempel *et al.* 1985).

The relevance of these currencies can be assessed by examining responses of pollen-collecting bumble bees (*Bombus* spp.) to variation in pollen availability within flowering stalks (inflorescences) of lupines (*Lupinus* spp., Fabaceae). Lupines do not produce nectar and so bumble bees respond strictly to pollen availability. Pollen availability varies predictably within a lupine inflorescence because flowers are arranged on the inflorescence in whorls and a new whorl opens each day above the currently open flowers. As a result, the highest whorl contains the most pollen and a particular whorl contains more pollen than the one below it because it is younger and has received fewer pollinator visits. In general, the pollen available in the i th open whorl from the top (p_i) follows a negative exponential distribution,

$$p_i = ae^{-bi}$$

where a is the initial pollen production and b is the natural logarithm of the proportional decline in pollen availability between adjacent whorls (Harder 1990a). Because bees start foraging low on inflorescences and move upwards through this distribution (Haynes and Mesler 1984; Harder 1990a), I could estimate how much pollen a bee collected from an inflorescence. If a bee begins its visit to an inflorescence on whorl n , visits a single flower per whorl, removes a proportion, k_i ,

from the i th whorl and moves upward before leaving from the top whorl, it will collect

$$P = \sum_{i=1}^n k_i p_i \quad (1)$$

pollen grains. If k_i does not vary between whorls (i.e. $k_i = k$) then eq. 1 simplifies to

$$P = ka(1 - e^{-bn}) / (e^b - 1) \quad (2)$$

Therefore the optimization problem is to find how many whorls (n) below the top ($n=1$) a bee should begin foraging at to maximize a particular currency.

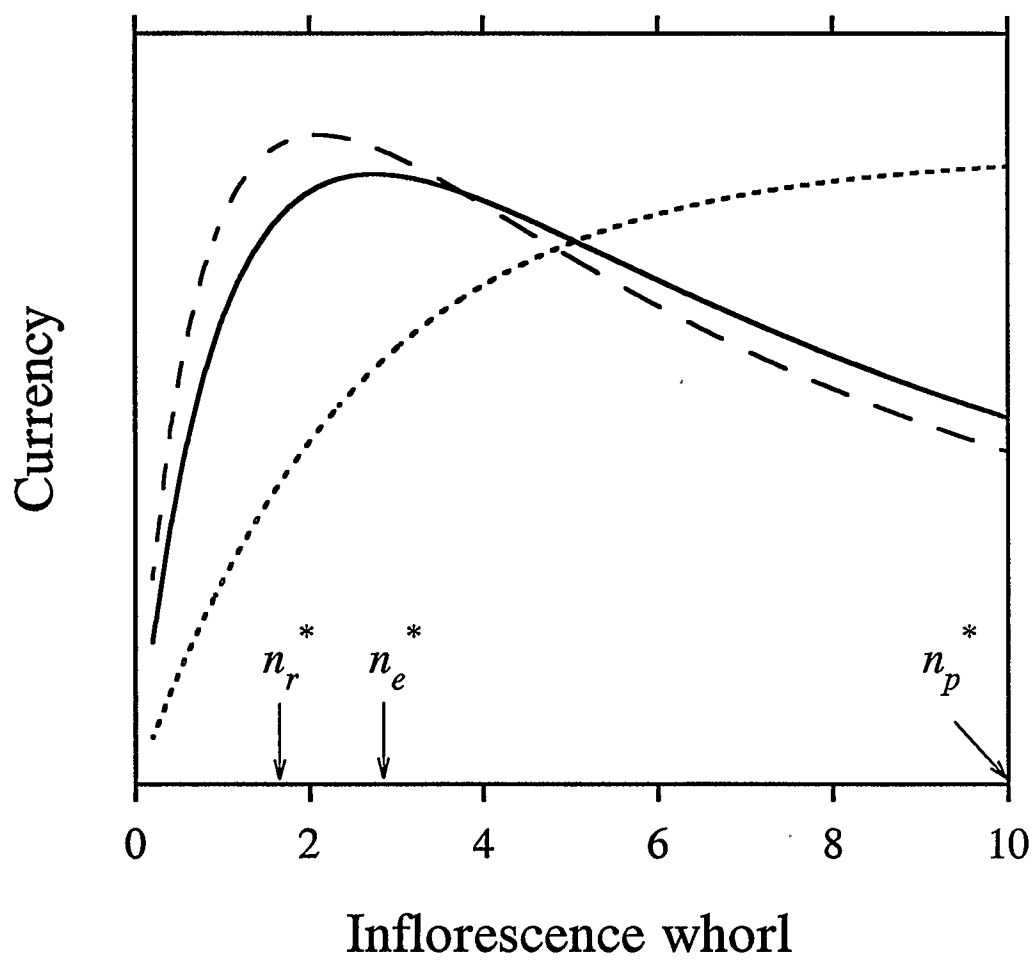
2.1.4.1 Pollen collected per inflorescence

Pollen collected per inflorescence (P) is simply the summation of the function describing the distribution of pollen within an inflorescence (eq. 2). Because P increases monotonically with n (Fig. 2.1), a bee maximizing pollen collected per inflorescence should begin at the lowest open whorl, and visit all whorls above it, before leaving from the top open whorl.

2.1.4.2 Rate of pollen collection

Rate of pollen collection (R) is the amount of pollen collected during a foraging trip divided by the time taken to gather it. The amount of pollen collected equals the number of inflorescences visited (L) multiplied by the amount of pollen collected per inflorescence (P : eq. 2). Collecting time is the sum of the handling times for all flowers visited (Lnt_h , where t_h is per flower handling time), the total flight time between whorls ($L[n-1]t_f$, where t_f is flight time between adjacent whorls) and the total flight time between inflorescences ($[L-1]t_i$, where t_i is flight time between adjacent inflorescences). Therefore,

Figure 2.1 : The relations between pollen collected per inflorescence (dotted line: eq. 1), rate of pollen collection (dashed line: eq. 3) and pollen collection efficiency (solid line: eq. 4), and a bee's starting position on a lupine inflorescence. n_p^* , n_r^* and n_e^* are the respective optimal starting positions (top whorl=1), based on numerical solutions of eq. 2, 6a and 6b, respectively. $L = 10000$ inflorescences, $b = 0.389$, $c_f = 0.435 \text{ J g}^{-1} \text{ s}^{-1}$, $c_h = 0.034 \text{ J g}^{-1} \text{ s}^{-1}$, $t_f = 0.9 \text{ s}$, $t_h = 0.7 \text{ s}$ and $t_i = 2.0 \text{ s}$.



$$R = \frac{L P}{L n t_h + L(n-1)t_f + (L-1)t_i} \quad (3)$$

Practically, it is difficult to count the number of inflorescences a bee visits during a foraging trip. However, if I assume that a bee returns to the nest after collecting some specific load size (M), I can replace L in eq. 3 with M/P , which yields

$$R = \frac{M P}{M n t_h + M(n-1)t_f + (M-P)t_i} \quad (4)$$

Unlike the preceding currency, a bee would maximize its rate of pollen collection by starting to forage in the middle of inflorescences (Fig. 2.1).

2.1.4.3 Pollen collection efficiency

Pollen collection efficiency (E) is similar to collection rate (eq. 4), except that handling and flight times are multiplied by the metabolic costs of handling (c_h) and flight (c_f), respectively. Pollen collection efficiency is therefore,

$$E = \frac{M P}{M n t_h c_h + M(n-1)t_f c_f + (M-P)t_i c_f}, \quad (5)$$

which is also maximized by the bee beginning foraging in the middle of an inflorescence (Fig. 2.1).

The optimal number of whorls visited for each currency is obtained by differentiating equations 4 and 5 and optimizing with respect to the number of whorls visited (n^*), producing the following equalities,

$$\text{RATE} \quad e^{b n^*} - b n^* = 1 - b(t_f - t_i)/(t_h + t_i) \quad (6a)$$

$$\text{EFFICIENCY} \quad e^{b n^*} - b n^* = 1 - b(t_f c_f - t_i c_f)/(t_h c_h + t_i c_f) \quad (6b)$$

which must be solved numerically (see Appendix 2.1 for descriptions of the optimal starting positions for these currencies when k_i decreases as the bee moves up the inflorescence). Note that a flower's initial pollen production (a), the proportion of pollen that the bee removes from each flower (k) and the bee's maximum pollen load

(M) have cancelled, and therefore should not affect the optimal starting position. In general, a bee maximizing its efficiency of pollen collection will always visit more whorls per inflorescence (i.e., start lower) than a bee maximizing its pollen collection rate. This lower starting position reduces total flight costs because flight between whorls involves shorter flights on average than flight between inflorescences (Fig. 2.1). Moreover, a bee maximizing either efficiency or rate of pollen collection will always visit fewer whorls than a bee maximizing pollen collected per inflorescence. Consideration of foraging time and costs results in avoiding unprofitable lower flowers.

Numerical solutions of eq. 6a and 6b illustrate the effects of specific parameters on optimal starting position. Generally, increases in the coefficient describing the decay in pollen distribution within an inflorescence (b) decrease the expected optimal number of whorls visited (Fig. 2.2). More specifically, when the distribution of pollen along the inflorescence changes slowly (i.e., when b is < 0.1), there is a marked difference in n^* between rate and efficiency maximization. In contrast, increases in flight time between inflorescences (t_i) increase the optimal number of whorls visited, so that long flights between inflorescences (> 8 s) produce a two-whorl difference between n_e^* and n_r^* (Fig. 2.3). Hence, by studying pollen collection by different bee species over a range of conditions (i.e. different lupine species, different plant densities) I should be able to determine which currency provides the most consistent description of observed behaviour.

2.2 Methods

To determine which currency best describes bumble-bee pollen-collection behaviour, I observed foraging bees at seven sites in south-western Alberta and south-eastern British Columbia during the summers of 1991 and 1992. I studied bee

Figure 2.2 : The effect of the distribution of pollen within an inflorescence (b) on the optimal number of whorls visited (top whorl=1) based on maximization of rate of pollen collection (n_r^*) and pollen collection efficiency (n_e^*). The dashed and solid lines represent n_r^* (eq. 6a) and n_e^* (eq. 6b) respectively, when a bee removes a fixed proportion of pollen from each flower. The dotted line illustrates n_e^* when this proportion declines exponentially up the inflorescence (eq. 8b). Symbols along the upper abscissa indicate the values of b for the seven samples; Burnell Lake (B), Creston (C), Chain Lakes Provincial Park (H), Porcupine Hills (P), Stimson Creek (S), Stimson Creek - second visit - day 1 (T_I), Stimson Creek - second visit - day 3 (T_{II}), Waterton Lakes National Park (W). See Fig. 2.1 for parameter values.

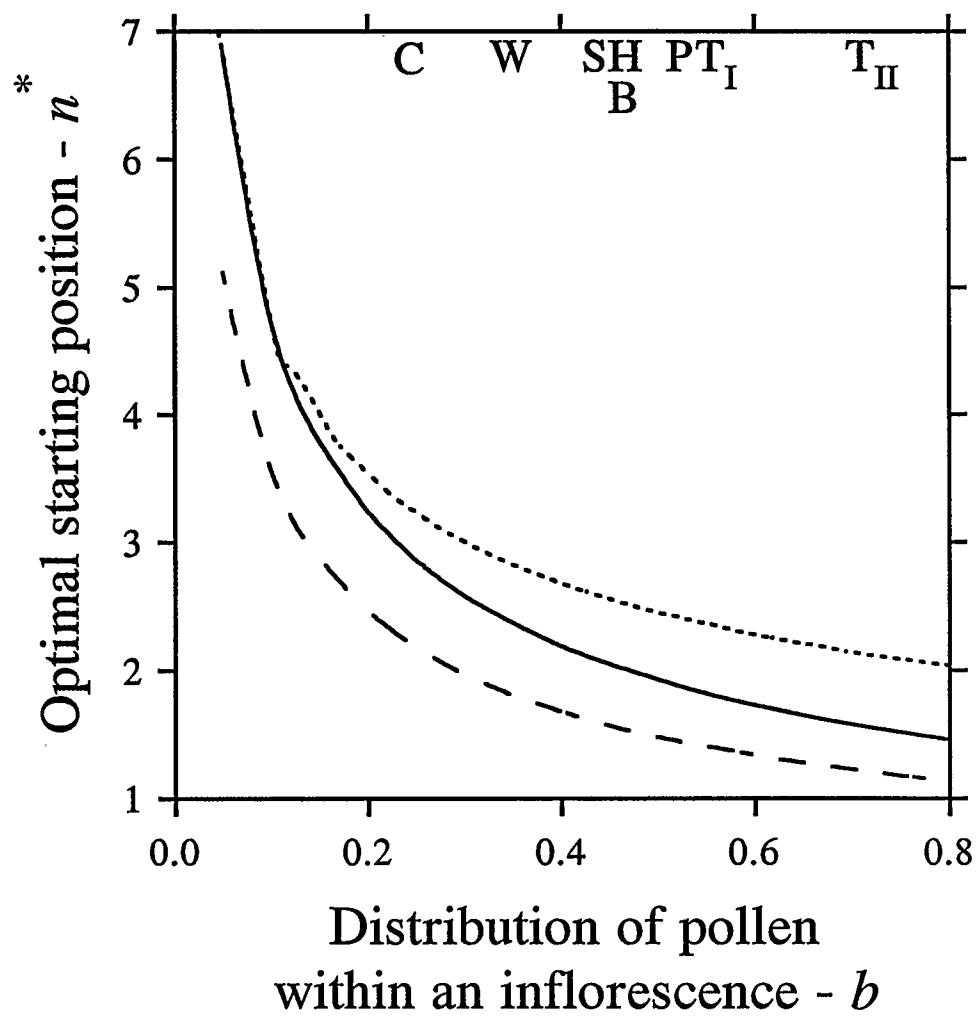
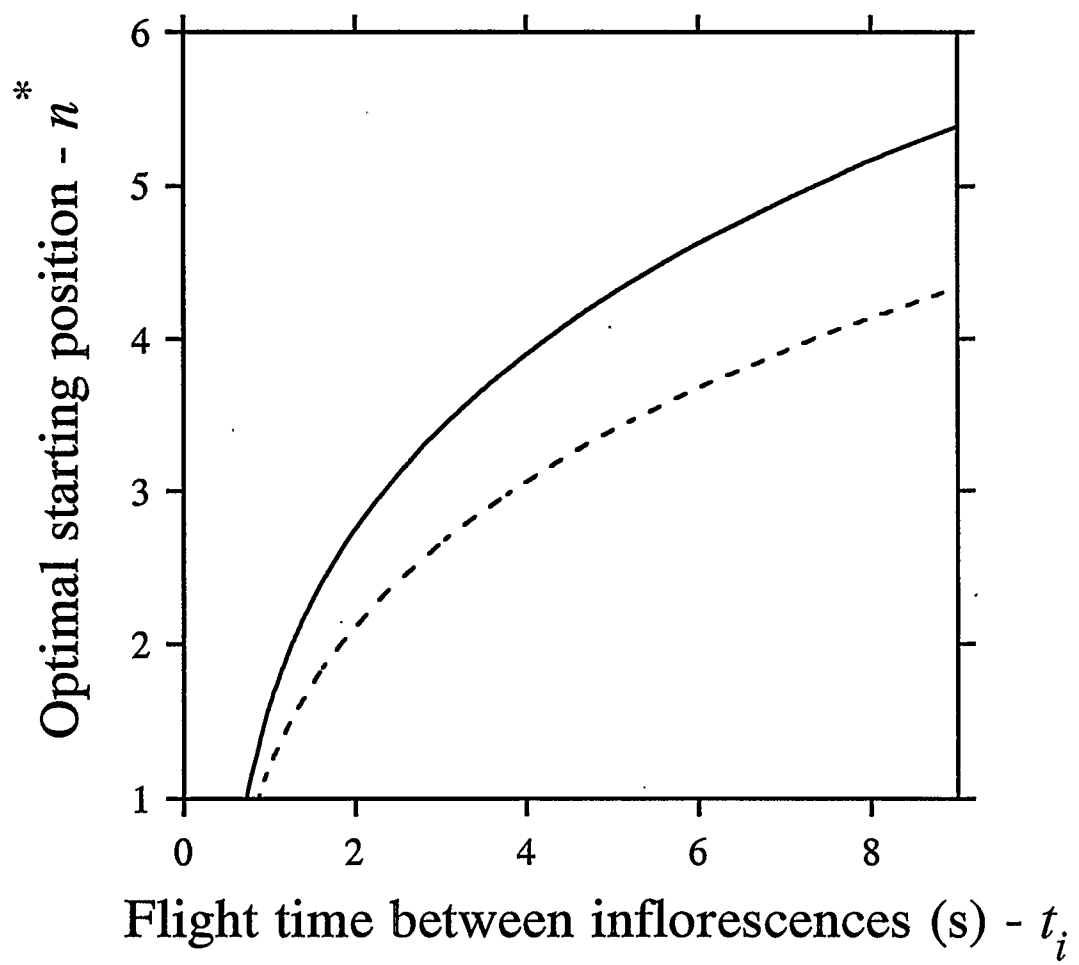


Figure 2.3 : The effect of flight time between inflorescences (t_i) on the optimal number of whorls visited (top whorl=1) based on maximization of rate of pollen collection (n_r^* : dashed line) and pollen collection efficiency (n_e^* : solid line). Based on eq. 6a and 6b with other parameters as in Fig. 2.1.



behaviour on four different lupine species over a variety of different environmental conditions (see Appendix 2.2 for information on each site).

To assess the relevance of the described currencies to bee behaviour, I compared observed starting positions within inflorescences to predicted positions based on the prevailing foraging environment. Prediction of optimal starting position requires estimates of the distribution of pollen within inflorescences and the time and energy spent on flight time between whorls, handling time, and flight time between inflorescences. I measured these parameters at each of the study sites, except for metabolic rates, which were obtained from published values (see Heinrich 1975a). These values were substituted into equations 6a and 6b and numerically solved for the optimum number of whorls visited. The predicted starting positions for each currency were compared to the mean observed positions for the bees in each sample by a paired *t*-test. I judged the currency that resulted in the most non-significant *t*-tests to be the most consistent description of the economic motivation underlying bumble-bee pollen foraging.

2.2.1 Parameter estimates

2.2.1.1 Pollen distribution within inflorescences

To quantify the pattern of pollen availability within inflorescences (*b*) during each day that I observed bee behaviour at a site, I collected one flower per whorl from 20 inflorescences (two flowers from each whorl of ten inflorescences at the Creston, British Columbia site). These flowers were preserved separately in 75% ethanol until they could be dissected and sonicated for 5 min to dislodge pollen trapped in the anthers or other floral parts. Pollen was counted with a Particle Data®, Elzone 180XY particle counter, which assigned each particle to one of 128 logarithmic diameter classes and counted the number of particles in each size class

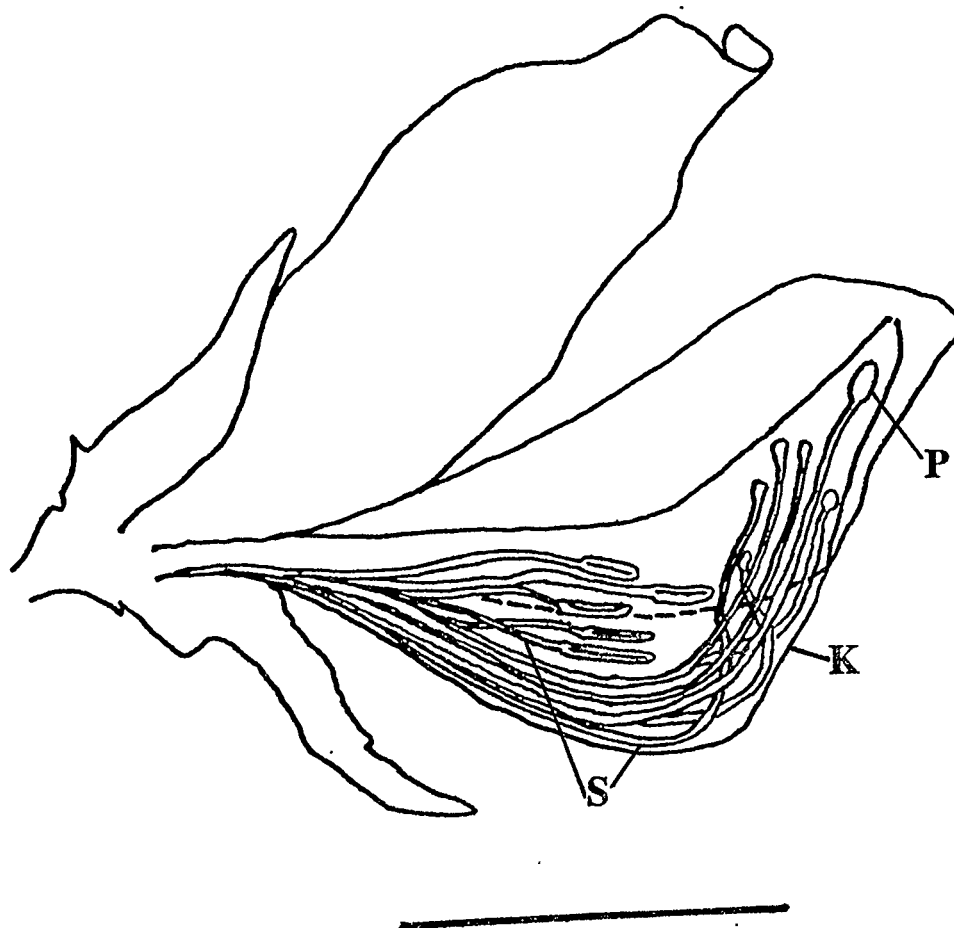
(see Harder 1990b for details). Each estimate of pollen availability was based on the average count for three subsamples, representing a total of 10% of a flower's pollen.

For each site, analysis of covariance was used to determine whether the pollen standing crop (log-transformed) differed between whorls (covariate), between sampling days (fixed effect) and between plants within days (random effect). This analysis provided an estimate of the slope of the relationship describing pollen distribution (b) and initial pollen production (a), for each sampled inflorescence. For every site and sampling day, a test for heterogeneous slopes determined whether the standing crop of pollen declined similarly over the open whorls, among the 20 sampled inflorescences.

2.2.1.2 Proportion of pollen removed from a flower

Equations 6a and 6b are based on the assumption that the proportion of pollen removed from a flower does not vary between whorls. To assess this assumption I took advantage of the unusual pollen-dispensing mechanism of lupines (Dunn 1956; Wainwright 1978; Juncosa and Webster 1989). Lupine flowers present pollen to pollinators on a stigmatic brush, rather than on the anthers. During flower development the anthers shed their pollen and push it into the apex of the fused keel petals (Fig. 2.4). While visiting a lupine flower a bee depresses the keel petals, forcing the stigma through the pollen mass and out a hole in the petals. The bee then rakes the pollen from the stigma with its prothoracic legs and leaves the flower, allowing the stigma to resume its original position, resetting the dispensing mechanism. To simulate a single bee visit, I manipulated the dispensing mechanism once and collected the expelled pollen in a microcentrifuge tube with 70% ethanol. The flower and remaining pollen were collected separately and stored similarly. Pollen samples were prepared and pollen counted as described above. The proportion of pollen removed from a particular flower was determined by dividing the pollen

Figure 2.4 : An exposed lupine flower revealing the keel petals (K), the pistil (P) terminating with the stigma, and two sets of stamens within the keel (S). The scale bar represents 5 mm in the scale of the exposed flower.



removed by the total pollen available before manipulation (i.e., removed + remaining). This manipulation was performed for one flower from each whorl on 20 inflorescences during the first visit to Stimson Creek and at Chain Lakes. I derived an empirical relationship for proportion of pollen removed (k) based on this pollen manipulation experiment.

2.2.1.3 Foraging times and observed starting position

I quantified the different components of foraging time for two groups of bees at each site. For the first group of bees, I videotaped within-inflorescence behaviour with a Panasonic® WV-5000 camera equipped with a 12X zoom lens. The video-tape was viewed at 1/6 original speed to facilitate measurement of flight time between whorls (t_f) and handling time per flower (t_h). For the second set of bees I recorded the starting whorl and number of open whorls for a series of inflorescences and flight time between inflorescences (t_i). This behaviour was recorded onto a voice-activated tape recorder and the times were immediately transcribed using stopwatches. All observed bees were captured after visiting several inflorescences, slightly anesthetized with ethyl acetate and weighed. The pollen loads were also removed and later weighed to the nearest milligram. These masses allow assessment of the effects of bee mass or pollen load mass on associated aspects of foraging behaviour.

2.2.2 Optimal starting position

If the proportion of pollen removed from a flower (k) did not vary between whorls, I could use eq. 6a and 6b to calculate optimal starting positions for pollen collection rate and efficiency respectively. However, the proportion of pollen removed varied predictably with flower position along the inflorescence (see section 2.3.1.1). I therefore modified eq. 4 and 5 to incorporate the observed relation

between k and flower position and then varied the value of whorl number (n) to find the starting position that maximized each currency.

Calculation of the optimal starting position incorporated site-specific estimates of the distribution of pollen within inflorescences and foraging parameters. If pollen distribution within an inflorescence (b) did not differ between days I used estimates averaged over all sampling days at a site; otherwise I used daily estimates for b . Also, I derived an empirical relationship for proportion of pollen removed (k) from a manipulation experiment at Stimson Creek and Chain Lakes and substituted this relationship at the other sites. I used site-specific averages for flight time between whorls (t_f) and handling time (t_h) because these parameters were estimated for a different group of bees than the bees for which I recorded starting position. In contrast, prediction of optimal starting position incorporated the average flight time between inflorescences (t_i) for each bee. At every site, except Porcupine Hills, nonsignificant variation between bee species in all aspects of flight allowed me to consolidate bee species.

2.2.3 Variation in foraging conditions

Equation 6a and 6b present a deterministic view of pollen collection from lupines; however, all parameters incorporated in that model are subject to variation. To determine whether such variation affects predictions, I simulated pollen collection after incorporating the variance associated with the slope of the distribution describing the relationship between pollen availability and whorl (b), the flight time between inflorescences (t_i), the flight time between whorls (t_f) and handling time (t_h). An individual simulation involved predicting starting position with eq. 6a and 6b based on a value for a particular parameter randomly chosen from a normal distribution with mean and variance as observed in the field. Each simulation was run 100 times before the average optimal starting position was calculated. As for the deterministic

analysis, the average predicted starting position was compared to the observed starting position. For all sites, conclusions regarding which currency is a better indicator of observed behaviour was unaffected by stochastic variation in foraging parameters, therefore I do not present these results.

2.3 Results

2.3.1 Parameter estimates

2.3.1.1 Pollen distribution within inflorescences

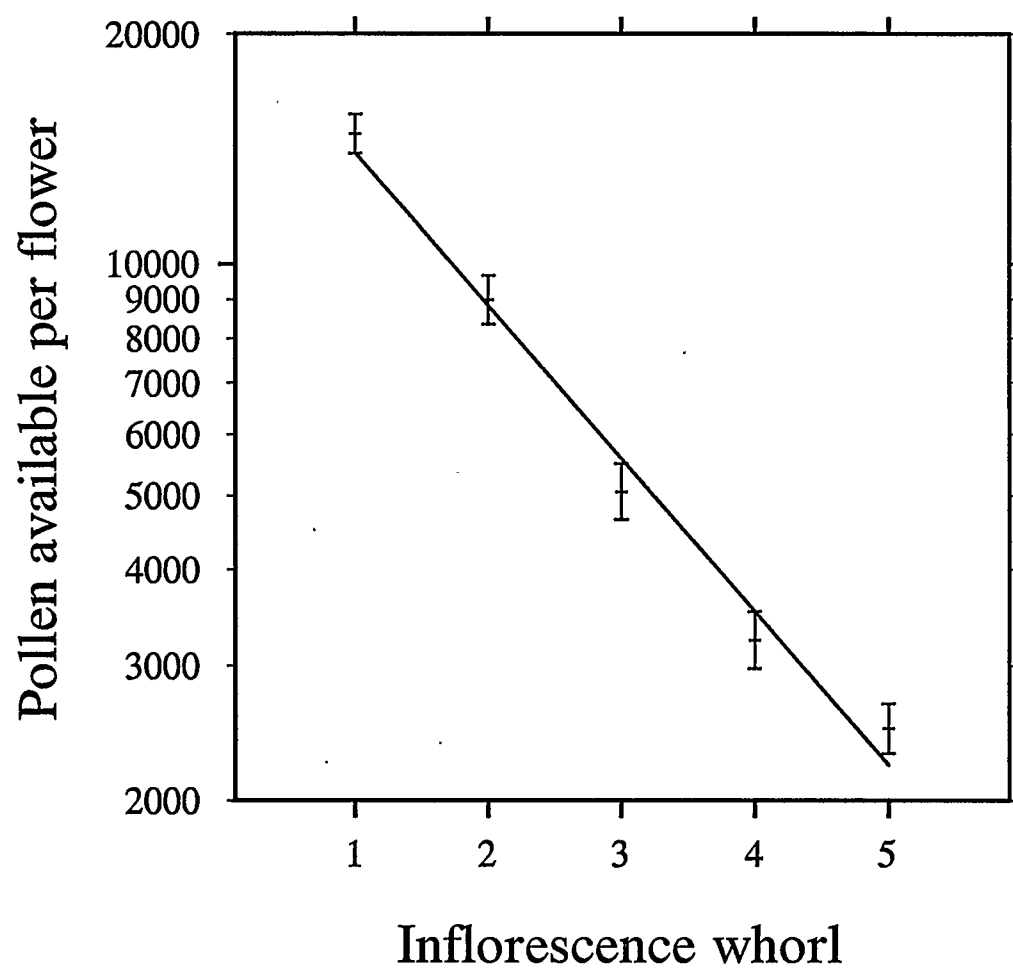
As required by my model of pollen collection (eq. 1), pollen availability in lupines declined exponentially from the top whorl down at all six sites (Table 2.1: whorl effect; Fig. 2.5). For example, for *L. sericeus* at Chain Lakes mean pollen availability (p) varied with position (i : $i=1$ for flowers in the top whorl) as $p = 22026e^{-0.440i}$ ($F_{4,214} = 2.04$, $P < 0.05$), indicating that a given flower contains 64% ($e^{-0.440}$) as much pollen on average as flowers in the next higher whorl (Fig. 2.5). Pollen availability differed between every location and on two separate occasions at Stimson Creek (Fig. 2.2 and Appendix 2.2). Between sites, the slope of the relationship describing pollen distribution (b) generally decreased with average number of open whorls per inflorescence ($R^2 = 0.77$, $P < 0.05$). With one exception, the slope of the pollen distribution at a site did not differ between sampling days (Table 2.1: whorl $\times$ day effect), so I typically estimated a common function for all days at a site (see Appendix 2.2 for parameter estimates). During the second visit to Stimson Creek, the distribution of pollen within inflorescences differed between the first and last observation days so daily descriptions of pollen distribution were necessary. The standing crop of pollen declined similarly within inflorescences for all plants (test for heterogeneous slopes among plants: whorl $\times$ plant(day) effect: $P > 0.05$ in all cases), over all observation days, at all sites except Waterton Lakes.

Table 2.1. Analysis of within-inflorescence pollen distribution for lupines during seven samples of pollen-collection behaviour

Study site	Effect				
	whorl	day	whorl×day	plant(day)	whorl×plant(day)
Burnell Lake	$F_{1,240}=350.16^{***}$	$F_{2,63}=1.09$	$F_{2,240}=0.11$	$F_{77,240}=0.43$	$F_{77,240}=0.32$
Chain Lakes	$F_{1,140}=567.38^{***}$	$F_{1,39}=0.78$	$F_{1,140}=0.086$	$F_{38,140}=1.15$	$F_{38,140}=0.87$
Creston	$F_{1,105}=129.28^{***}$	$F_{2,25}=2.10$	$F_{2,105}=2.57$	$F_{24,105}=0.73$	$F_{24,105}=1.29$
Porcupine Hills	$F_{1,80}=312.66^{***}$	$F_{1,38}=0.29$	$F_{1,80}=0.07$	$F_{38,80}=0.91$	$F_{38,80}=0.76$
Stimson Creek (first visit)	$F_{1,120}=470.96^{***}$	$F_{1,38}=8.42^{**}$	$F_{11,120}=3.78$	$F_{38,120}=1.01$	$F_{38,120}=1.67$
Stimson Creek (second visit)	$F_{1,60}=436.86^{***}$	$F_{1,42}=0.59$	$F_{1,60}=11.31^{**}$	$F_{38,60}=0.92$	$F_{38,60}=1.27$
Waterton Lakes	$F_{1,175}=769.66^{***}$	$F_{2,57}=0.18$	$F_{2,175}=0.96$	$F_{57,175}=2.22^{***}$	$F_{57,175}=2.01^{**}$

** $P < 0.01$, *** $P < 0.001$

Figure 2.5 : The relationship between mean ($\pm$ SE) pollen available per *L. sericeus* flower and flower position (top whorl=1) at Chain Lakes. Based on a sample of 40 inflorescences.



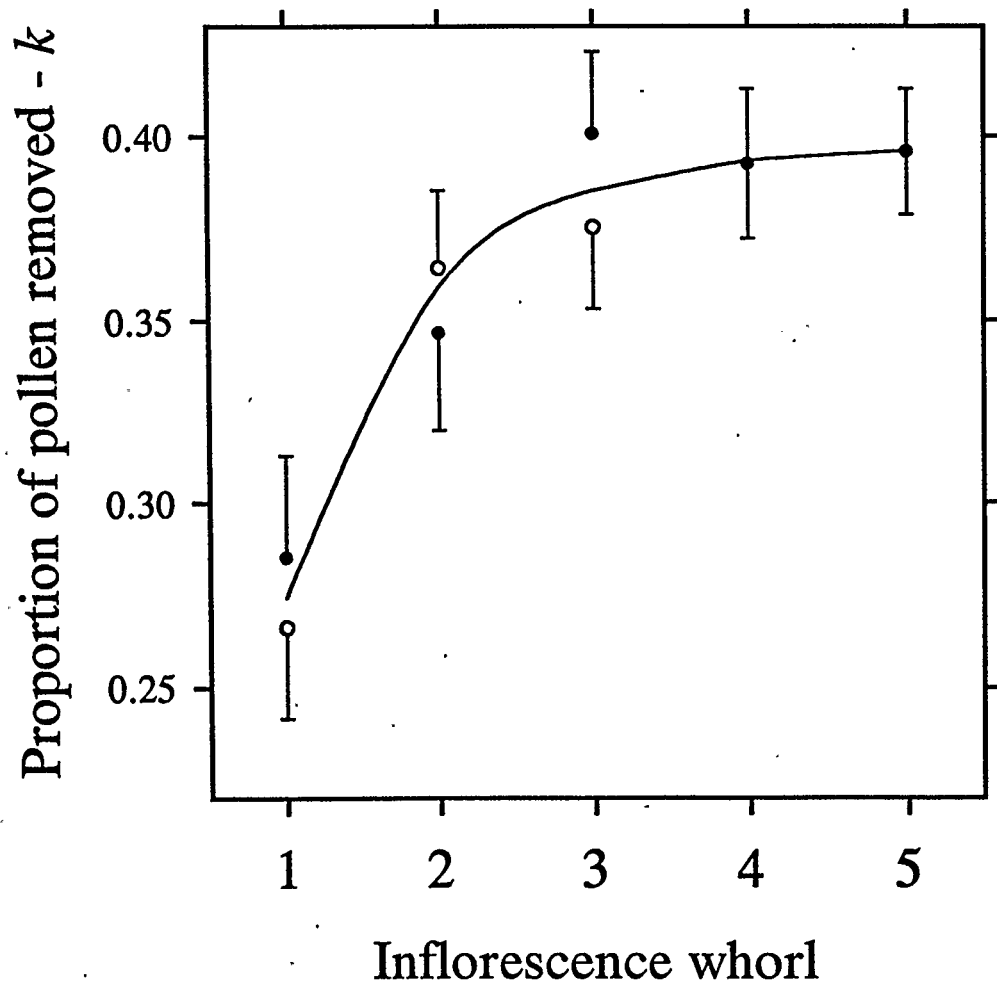
The proportion of pollen removed from flowers during a single manipulation (k), increased asymptotically down the inflorescence ($k = 0.397[1 - e^{-1.174i}]$, $F_{2,6} = 4328.72$, $P < 0.001$, $r = 0.98$, Fig. 2.6). I incorporated this relation of removal proportion to flower position when estimating optimal starting position for all sites. Although this complication alters the specific relation of optimal starting position to the foraging parameters (see Appendix 2.1), the qualitative relations remain unchanged (see Fig. 2.2).

2.3.1.2 Foraging times

Average handling time (t_h) per bee ranged from 0.2-1.6 s over all sites (mean $\pm$ SD = 0.7 ± 0.12 s, 160 bees, Appendix 2.2). Handling time differed between sites (overall site effect: $F_{6,153} = 19.49$, $P < 0.001$), in particular, bees at Creston handled flowers fastest, whereas bees at Waterton Lakes handled flowers slowest. Differences in handling time cannot be attributed to variation between lupine species (lupine species effect: $F_{3,3} = 2.01$, $P > 0.05$). Rather, variation in handling time seems to originate from site-specific characteristics, because bees exhibit different handling times when collecting pollen from the same lupine species at different sites (site within lupine species effect: $F_{3,153} = 16.42$, $P < 0.001$). Handling time did not differ between bee species at a site ($P > 0.05$ in all cases), except at Chain Lakes, where *B. bifarius* handled flowers longer than *B. occidentalis* and *B. rufocinctus* ($F_{2,167} = 7.57$, $P < 0.001$). Differences between bees in handling time relate primarily to mass, as bigger bees ($F_{1,157} = 9.43$, $P < 0.05$: based on log-transformed data), and bees carrying heavier pollen loads ($F_{1,157} = 4.98$, $P < 0.05$) typically handled flowers faster. Hence heavier bees manipulate the lupine dispensing mechanism with less difficulty than lighter bees.

Mean flight time between whorls within an inflorescence per bee (t_f) ranged between 0.4-3.0 s over all sites (mean $\pm$ SD = 1.0 ± 0.12 s, 160 bees, Appendix 2.2).

Figure 2.6 : The relationship between mean ($\pm$ SE) proportion of pollen removed during a manipulation (k) of a *L. sericeus* flower and inflorescence whorl at Stimson Creek (first visit: hollow circles) and Chain Lakes (filled circles). Based on 20 inflorescences.



This component of flight time differed significantly between different sites (overall site effect: $F_{6,153} = 10.29$, $P < 0.001$) due to two influences. First, bees differed in flight duration between whorls of different lupine species (lupine species effect: $F_{3,4} = 7.90$, $P < 0.05$). For example, bees at Waterton Lakes collecting pollen from *L. lepidus* spent the least time flying between whorls, whereas bees at Creston on *L. burkeii* spent the most. Second, bees collecting pollen from the same lupine species at different sites had different flight times between whorls (site within species effect: $F_{3,153} = 2.83$, $P < 0.05$). Neither bee mass ($F_{1,157} = 0.11$, $P > 0.05$: based on log-transformed data) nor pollen load mass ($F_{1,157} = 2.13$, $P > 0.05$) significantly affected flight time between whorls, suggesting that mass does not restrict maneuverability within an inflorescence. Differences between bees within a site cannot be attributed to variation among bee species ($P > 0.05$ in all cases) and therefore resulted from unidentified individual differences.

Average flight time between inflorescences (t_i) per bee varied considerably (C.V.=86.5%), ranging between 0.4-11.1s (mean $\pm$ SD = 1.9 ± 1.4 s, 178 bees, Appendix 2.2) over all sites. Average flight time per bee did not vary consistently between sites (overall site effect: $F_{5,157} = 1.23$, $P > 0.05$). Individuals within sites differed in their flight times between inflorescences (bee within site effect: $F_{157,652} = 1.35$, $P < 0.05$); however, neither bee mass ($F_{1,176} = 1.71$, $P > 0.05$: based on log-transformed data) nor pollen load mass ($F_{1,176} = 0.69$, $P > 0.05$) explained individual differences. Moreover, differences in flight time between inflorescences could not be attributed to differences between bee species ($F_{4,173} = 0.17$, $P > 0.05$). Most of the variation in between-inflorescence flight time probably resulted from local variation in inflorescence density (pers. obs.).

2.3.2 Starting position

Mean starting position per bee varied significantly among sites ($F_{7,169} = 61.62$, $P < 0.001$: considering the two days during the second visit to Stimson Creek as separate samples, Table 2.2). Trend analysis (Kirk 1982) of differences between samples indicated a significant linear influence of the mean slope of the distribution of pollen within inflorescences ($F_{1,169} = 204.95$, $P < 0.001$). Between-bee variation in flight time between inflorescences weakly affected mean starting position (regression, $F_{1,176} = 3.41$, $P < 0.05$), but this influence disappeared when differences between sites were incorporated (ANCOVA $F_{1,168} = 0.78$, $P > 0.35$). These results indicate that pollen-collecting bees behave flexibly and respond to their immediate foraging environment. In addition, it seems that the distribution of pollen within inflorescences influences bee behavior more strongly than variation in plant density and its effects on flight time between inflorescences.

In addition to the preceding extrinsic factors, characteristics of the bees themselves affected their starting position on lupine inflorescences. Based on an ANCOVA with site as the categorical variable and masses of the bee and its pollen load as covariates, heavier bees visited significantly more whorls than smaller bees (partial regression coefficient $\pm$ SE = 1.03 ± 0.346 , $F_{1,163} = 8.88$, $P < 0.001$). The effect of pollen load mass on starting position differed among sites (test for heterogeneous slopes, $F_{6,163} = 3.01$, $P < 0.01$). At Stimson Creek (both samples), Porcupine Hills and Burnell Lake, pollen load had no significant effect ($P > 0.25$ in all cases). In contrast, at Waterton Lakes (partial regression coefficient $\pm$ SE = 22.17 ± 9.11) and Creston (38.92 ± 17.25), bees with large loads started lower on inflorescences, whereas the reverse was true at Chain Lakes (-12.56 ± 5.10). Together these results indicate that foraging costs significantly influence the behaviour of pollen-collecting bees.

Table 2.2. Comparison of mean ($\pm$ SE) observed and mean ($\pm$ SE) expected starting positions for pollen collected per inflorescence, rate of pollen collection and pollen-collection efficiency, for each site. The predicted starting position for pollen collected per inflorescence represents the total available whorls per inflorescence. *t*-values represent the outcomes of paired-sample *t*-tests comparing observed and predicted starting positions

Study site	Number of bees	Observed starting position	Pollen collected per inflorescence		Rate of pollen collection		Pollen-collection efficiency	
			Predicted starting position	<i>t</i>	Predicted starting position	<i>t</i>	Predicted starting position	<i>t</i>
Burnell Lake	13	1.8 $\pm$ 0.1	3.5 $\pm$ 0.1	13.29***	1.6 $\pm$ 0.1	-2.51*	1.9 $\pm$ 0.1	0.87
Chain Lakes	22	3.0 $\pm$ 0.1	5.0 $\pm$ 0.0	17.78***	2.5 $\pm$ 0.1	-3.45**	2.7 $\pm$ 0.1	-1.98
Creston	10	3.6 $\pm$ 0.2	7.0 $\pm$ 0.0	14.41***	2.8 $\pm$ 0.1	-2.42*	3.1 $\pm$ 0.2	-1.19
Porcupine Hills	30	1.3 $\pm$ 0.1	2.2 $\pm$ 0.1	9.86***	1.0 $\pm$ 0.1	-4.00***	1.4 $\pm$ 0.1	0.18
Stimson Creek (first visit)	42	2.6 $\pm$ 0.1	5.0 $\pm$ 0.0	34.60***	2.2 $\pm$ 0.0	-4.85***	2.4 $\pm$ 0.1	-2.28
Stimson Creek (second visit)	24	1.5 $\pm$ 0.1	2.1 $\pm$ 0.1	5.96***	1.7 $\pm$ 0.1	3.54	1.7 $\pm$ 0.2	1.91
Waterton Lakes	30	2.0 $\pm$ 0.1	3.2 $\pm$ 0.2	8.50***	1.2 $\pm$ 0.1	-7.25***	1.4 $\pm$ 0.1	-5.06**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Comparison of observed and predicted starting positions clearly distinguish which of the three currencies is most closely associated with pollen collection. In all cases, bees started foraging above the lowest whorl on an inflorescence (Table 2.2), so that predictions based on total pollen collected per inflorescence fail to describe bee behaviour adequately. Maximization of rate of pollen collection adequately described bumble-bee behaviour at only one of the seven sites (Table 2.2, Fig. 2.7), as bees typically began foraging slightly lower on the inflorescence than predicted. In contrast, maximization of pollen-collection efficiency correctly predicted average starting position at six of the seven sites (Table 2.2, Fig. 2.7), with only the bees at Waterton Lakes behaving decidedly different than expected. Therefore, of the currencies assessed pollen-collection efficiency provides the most consistent explanation for the behaviour of pollen-collecting bumble bees.

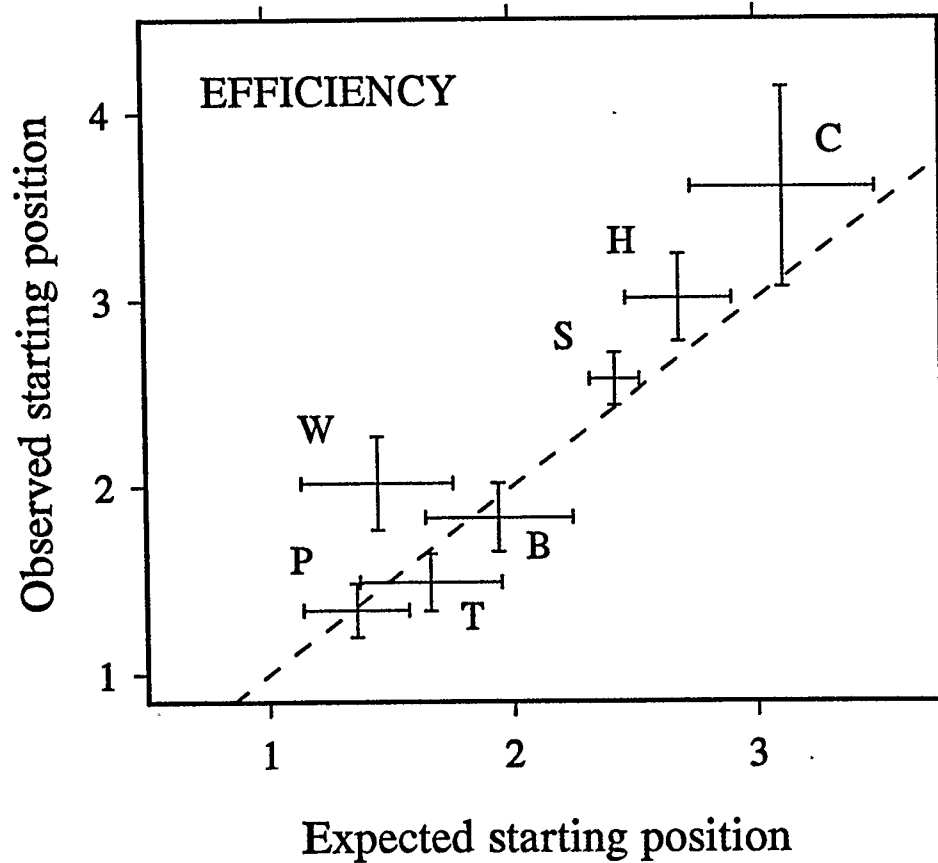
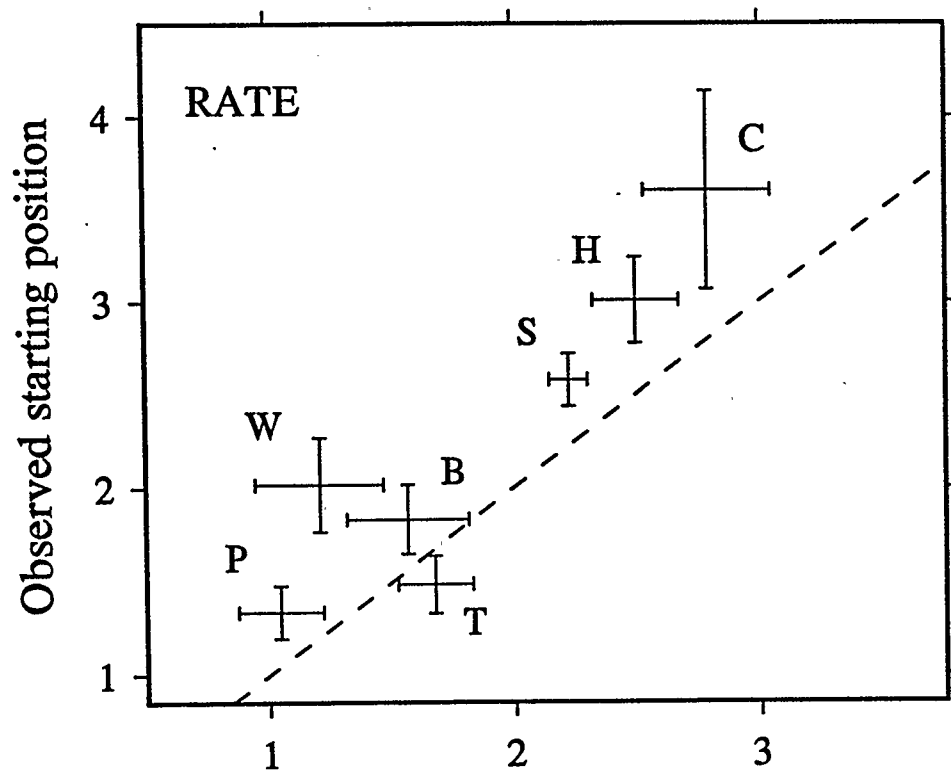
2.4 Discussion

2.4.1 Pollen collecting currency

Early studies of pollen-collecting behaviour suggested that bumble bees cannot determine the amount of pollen they collect from single flowers (Hodges and Miller 1981; Haynes and Mesler 1984), even though bees can monitor their pollen loads with sensilla on the corbiculae (Ford *et al.* 1981). More recent studies demonstrate that bees adjust handling time and grooming behaviour according to the amount of pollen removed from single flowers (Cane and Payne 1988; Buchmann and Cane 1989; Harder 1990a). My study corroborates these latter findings because observed starting position differed between sites and between dates at the same site (e.g. Stimson Creek) in association with differences in the distribution of pollen within an inflorescence and foraging costs.

Pollen collection by bumble bees involves evaluation of a variety of environmental influences. Bumble bees do not base their behaviour solely on pollen

Figure 2.7 : Comparison of observed and expected mean ($\pm 95\%$ CI) starting positions for rate of pollen collection and pollen collection efficiency. The dashed line through each graph represents equality of observed and expected starting positions. Burnell Lake (B), Creston (C), Chain Lakes Provincial Park (H), Porcupine Hills (P), Stimson Creek (S), Stimson Creek-second visit (T), Waterton Lakes National Park (W).



collected per inflorescence, because in all cases they started foraging above the lowest whorl (Table 2.2). Overall, bumble bees collected pollen as though they maximized collection efficiency rather than collection rate. Hence, both time and energy costs play an important role in an individual's behavioural decisions, as has also been demonstrated for other animal species in different contexts (Seeley 1986; Dolphin 1988; Welham and Ydenberg 1988; McLaughlin and Montgomerie 1990; Wolf and Schmid-Hempel 1990; Welham and Ydenberg 1993).

Although bees at most sites began foraging near the whorl predicted by efficiency maximization, at Waterton Lakes observed behaviour was inconsistent with predictions based on this currency. However, this apparent failure may represent the "exception that proves the rule". Predictions may have failed at Waterton Lakes because in contrast to other sites, pollen production varied between plants for a given day, even though the slope of the relation between pollen availability and flower position (*b*) remained consistent (Table 2.1). Consequently, bees may have encountered difficulties in assessing pollen availability and so foraging behaviour may have been compromised. A more likely reason that predictions based on pollen-collection efficiency failed at Waterton Lakes involves inclement foraging conditions. The Waterton Lakes area of southwestern Alberta is notorious for frequent strong and gusty winds (Salmon *et al.* 1993). During my observations of bee behaviour at this site, conditions were qualitatively more severe than any other site and bees generally had difficulty orienting and landing because of gusty winds and moving inflorescences (pers. obs.). High wind detrimentally affects efficiency of both bumble bee flight and landing on a moving inflorescence (Eisikowitch and Woodell 1975; Teräs 1976; Woodell 1978). As a result, bees probably experienced higher foraging costs at Waterton Lakes than the costs incorporated in the prediction of starting position. With increased costs, a bee maximizing its pollen-collection efficiency should start lower on inflorescences to reduce the time and effort spent in longer, costly flights

between inflorescences. Indeed, bumble bees at Waterton Lakes spent less time flying between whorls and more time handling flowers than bees at other sites. This increased handling time did not result from collection of more pollen, as the pollen-dispensing mechanism of lupines limits the pollen that can be removed during a single flower visit (Harder 1990a). Rather, prolonged handling time probably resulted because under these extreme wind conditions, pollen loads that protrude from a bee's side may affect aerodynamics and increase flight costs. Waterton Lakes was one of the two sites at which bees with large loads visited more whorls per inflorescence. Overall, these considerations imply that bees at Waterton Lakes may have maximized their pollen-collection efficiency, but the predictions of their behaviour did not account for all relevant costs.

Foraging time and metabolic costs are probably important influences on foraging by bumble bees because foragers live for only a few weeks (Garófalo 1978; Rodd et al. 1980; Goldblatt and Fell 1986), a period representing a considerable portion of the lifespan of temperate bumble-bee colonies. Such colonies include relatively few individuals (Hobbs 1966a; Hobbs 1966b; Husband 1977), so that individual foragers are valuable. Individuals that work harder and harvest more pollen per workday suffer a shorter median life expectancy (Wille *et al.* 1985). Indeed, bumble bees that maintain the colony and seldom forage live longer than foragers (Brian 1952), and bumble bees do not always work as hard as possible when foraging (Cartar and Dill 1990; Plowright *et al.* 1993).

These considerations imply that foragers should collect pollen in a manner that reduces metabolic costs, thereby prolonging individual lifespan and increasing their net lifetime contribution to the colony. Houston *et al.* (1988) modified Macevicz and Oster's (1976) model for optimal allocation of resources during colony development to assess how foraging strategy (rate versus efficiency maximization) affects reproductive success. They showed that if the likelihood of mortality depends on

foraging performance and increases over an individual's life, then rate maximization leads to overly intensive foraging behaviour. Under these conditions, efficiency maximization allows a forager to maximize both lifespan and the lifetime contribution of resources to the colony. Furthermore, Ydenberg *et al.* (1994) predicted that rate and efficiency maximization were context specific, depending on whether an individual was feeding itself or provisioning for others. Assuming that foragers maximize total daily delivery when gathering food for others, subject to meeting their own energetic requirements, maximizing efficiency ensures the highest total daily delivery (Ydenberg *et al.* 1994). The findings from this study seem to concur with these predictions.

2.4.2 Differences between pollen and nectar collection

Pollen and nectar are very different resources, so that pollen collection differs in several ways from nectar collection. First, although pollen sometimes functions as a pollinator attractant, it contains male gametes which, from a plant's perspective, are much more valuable than any nectar constituents. As a result, plants probably exercise considerably more control over the dispensing of pollen, than they do when dispensing nectar. For example, lupines limit pollen removal by individual pollinators through staggered flower maturation and a pollen dispensing mechanism (Harder and Thomson 1989; Harder and Wilson in press, for other examples see Macior 1964 and 1973; Buchmann 1983; Armstrong 1992; Harder and Barclay in press). Dispensing mechanisms in particular, probably increase foraging costs because of the additional complexity involved in handling the flower. Moreover, not only do plants limit pollen removal, but foragers also face diminishing returns when collecting pollen from plants with dispensing mechanisms (Harder and Barclay, in press). Consequently, pollen acquisition may be complex because some pollen sources have relatively complicated methods to limit pollen removal.

Second, although pollen and nectar are both essential resources for bumble bees, collection of these resources may be different because larvae are fed different proportions of pollen and nectar. Larval food consists of pollen that is slightly moistened with nectar and so larvae receive considerably more pollen in their diet. Pollen limitation can lengthen larval development and result in smaller workers: severe limitation can halt larval development completely (Plowright and Pendrel 1977; Sutcliffe and Plowright 1988; Sutcliffe and Plowright 1990). In contrast, such effects on offspring growth are unlikely immediate results when nectar is limited. Differences between the amount of pollen and nectar consumed may motivate foragers to evaluate pollen collection differently.

Finally, pollen collection generally involves grooming, with vigorous leg movements over the body to move the pollen off the body and onto the legs, and additional manipulation to pack the pollen into the corbiculae (Michener *et al.* 1978). Pollen-collecting individuals groom extensively both when flying between flowers and inflorescences, as well as before returning to the nest. Bumble bees are sensitive to the amount of pollen they accumulate on their body, because they intensify grooming when they encounter previously unvisited pollen-laden flowers (Harder 1990a). Grooming may increase the costs of pollen collection, especially if it prolongs flights between flowers. Nectar-collecting bees groom less frequently and do not pack pollen into their corbiculae, so grooming probably complicates pollen collection.

2.4.3 Collection of non-energetic resources

Collection of non-energetic resources is seemingly more complex than collection of energetic resources because the proximate benefits derived from such resources cannot be directly equated with the time and energy costs of obtaining them. However, it seems that collection of non-energetic resources may in fact be similar to collection of energetic resources because animals collecting energetic resources also

maximize energetic efficiency in certain contexts (Schmid-Hempel *et al.* 1985; Seeley 1986; Schmid-Hempel 1987; Wolf and Schmid-Hempel 1990). As a result, animals often seem to maximize the ratio of benefits to costs, regardless of characteristics of the benefits.

3 Economic motivation for the preferences of pollen-collecting bumble bees for plant species

3.1 Introduction

Foraging behaviour is an integral component of an animal's behavioural repertoire and foraging animals typically include only particular items in their feeding and provisioning behaviour. Particular food items are commonly included in the diet for two reasons. First, to satisfy their energy budgets animals often prefer larger food items that contain more energy, as long as they are not associated with excessive handling costs (e.g. Werner and Hall 1974; Elner and Hughes 1978; Bence and Murdoch 1986). Second, animals often prefer foods that satisfy specific nutritional requirements (e.g. Belovsky 1979; Sweeney *et al.* 1986) as supplements to energy-rich, but nutrient-poor foods. Regardless of the criterion, preferential foraging often promotes an animal's fitness (Johnson *et al.* 1980; Hughes and Chiment 1988; Krischik and Denno 1990; Minkenberg and Ottenheim 1990).

Animals also collect resources without energy equivalents (e.g. cerumen, Sakagami and Camargo 1964; nesting material, Wimberger 1984; resin, Armbruster 1984; water, Seeley 1986; floral oil, Buchmann 1988). When collecting these resources animals must use and be able to discriminate different criteria for evaluating the available choices. However, the motivation for preference among such non-energy based resources remains relatively unclear.

3.1.1 Pollen preferences

Bees (Hymenoptera: Apoidea) collect two food resources: nectar, which provides energy, and pollen, which fulfills the protein requirement necessary for individual growth. Pollen and nectar are essential resources for bees because both are required for survival, and one cannot be substituted for the other. Pollen collection also requires different behaviours than nectar collection. For example, pollen-

collecting bumble bees move shorter distances between plants, visit more flowers per inflorescence and revisit flowers more often than nectar-collecting bees (Zimmerman 1982). Additionally, pollen-collecting bumble bees visiting *Epibolium angustifolium* tend to start higher up the inflorescence than nectar-collecting individuals because lower flowers have ceased presenting pollen (Galen and Plowright 1985). Pollen-collecting bees also often visit different plant species than when collecting only nectar (Brian 1957; Liu *et al.* 1975). Such behavioural differences suggest that bees collecting pollen employ different criteria for plant species choice than nectar-collecting bees.

Although bees can collect pollen from many plant species, pollen loads typically consist of relatively few species (Brian 1951; Brian 1954; Free 1963). Pollen preference is advantageous because honey-bee (Fewell and Winston 1992; Camazine 1993) and bumble-bee (Sutcliffe and Plowright 1988; Sutcliffe and Plowright 1990) colonies are pollen limited, and larvae obtain essential amino acids from certain pollen (De Groot 1953; Campana and Moeller 1977; Herbert *et al.* 1970). Although it is clear that bees prefer pollen from particular plant species (Vivino and Palmer 1944; Synge 1947; Brain 1951; Free 1970; Mackensen and Tucker 1973; Schmidt 1982; Schmidt 1984; Schmidt and Johnson 1984; Cripps and Rust 1989), the basis for these preferences is unclear.

Preference for particular plants, in spite of the diversity of available alternatives, suggests the maximization of some currency. When collecting pollen from a chosen species, bumble bees behave as though they maximize the ratio of foraging benefits to total costs (efficiency) (Chapter 2). If pollen-collecting bees generally maximize foraging efficiency, then preferences for particular plant species could arise for two nonexclusive reasons. First, bees may be able to harvest pollen more efficiently from a particular species, so that pollen collection from that species may be less costly. Specialization increases foraging gains because individuals do not

have to pay the learning costs associated with switching between plant species (Lavery 1994). Second, bees may consistently collect pollen from a particular plant because its pollen provides some specific benefit such as the concentration of adequate nutrients for growth (Levin and Haydak 1956; Standifer 1967; Loper and Berdel 1980; Schmidt *et al.* 1987) and digestibility (Barker and Lehner 1972; Peng *et al.* 1985). The collection of beneficial pollen could occur only if bees recognize pollen characteristics that enable discrimination. As of yet, the criteria that motivate preferences for particular plant species remain unclear.

Plant species differ considerably in many pollen characteristics which may influence the selective behaviour of pollen-collecting bees, including standing crop, grain size, and protein content (Wodehouse 1935; Todd and Bretherick 1942; Bell 1959; Lee 1978). Bees are responsive to variation in the amount of pollen available per plant (Cane and Payne 1988; Buchmann and Cane 1989; Harder 1990a) and can be expected to adjust their behaviour to collect pollen from plants with the highest standing crop. Pollen-grain size could also affect pollen value because bees use only the protoplasmic nutrients found in pollen and discard the indigestible pollen wall (exine) in their faeces (Peng *et al.* 1985). Finally, the availability of certain essential amino acids found in pollen protein limits bee larval development (Standifer *et al.* 1960; Standifer 1967), so that protein content may also be an important determinant of pollen quality.

3.1.2 Objectives

In this chapter I assess whether pollen standing crop, grain volume, protein content and foraging costs influence the choice of plant species by pollen-collecting bees. To allow me to distinguish influences of standing crop and currency on foraging behaviour, I consider pollen volume and protein content from three perspectives, 1/ intrafloral estimates, 2/ estimates that incorporate the standing crop of pollen and 3/

estimates that account for foraging time and metabolic costs. The first two perspectives are plant specific, whereas the third perspective additionally incorporates bee characteristics. To identify which of these perspectives explains bee preferences most completely, I rank the plant species available at a site based on pollen volume and protein content for each pollen-quality perspective and compare these rankings with the composition of pollen loads from individual bumble-bee foragers.

3.2 Methods

3.2.1 Study Sites

I studied pollen collection at three sites which included a variety of plant species as potential pollen sources. The Hailstone Butte I site consisted of a wet meadow and grassy slope, separated by a gravel road, near Hailstone Butte, Alberta (50°11'N; 114°26'W). The gravel road was rarely used and did not affect movement of pollinators between the field and adjacent slope. The species in flower at this site included *Hedysarum alpinum* L., *Hedysarum sulphurescens* Rydb., *Oxytropis splendens* Dougl., *D. conjugens* Greene and *P. groenlandica* Retz. Both *Hedysarum* species and *O. splendens* grew densely interspersed in a 40 × 40 m area on a gentle, dry, grassy slope on the north side of the road. This patch of plants had fairly distinct boundaries and no other flowering plants occurred in the neighboring area. Bumble bees can collect both nectar and pollen from *H. alpinum*, *H. sulphurescens* and *O. splendens*. The 20 × 50 m wet field on the south side of road contained *D. conjugens* and *P. groenlandica*, neither of which produce nectar. Although I did not specifically measure flowering phenology, both *D. conjugens* and *P. groenlandica* were past peak flowering during this study.

Hailstone Butte II, also located near Hailstone Butte, Alberta (50°11'N; 114°24'W), consisted of a steep hillside on which *Hedysarum sulphurescens* and *Lupinus sericeus* Pursh flowered simultaneously. Both plant species grew together in

a 30 × 30 m area, and no other plants flowered in the vicinity. *Lupinus sericeus* produces only pollen, whereas *H. sulphurens* produces both pollen and nectar as pollinator attractants.

The third study site, located near Stimson Creek, Alberta (50°16'N; 114°15'W), consisted of a gently sloping meadow. Potential pollen sources for bumble bees at this site included *Lupinus sericeus*, *Geum triflorum* Pursh, *Geranium viscosissimum* Fisch.&Mey., *Vicia americana* Muhl. and *Oxytropis monticola* A. Gray. These plants were scattered over a 60 × 60 m area. Except for *L. sericeus*, all plants studied at this site produce both pollen and nectar.

3.2.2 Pollen characteristics

I determined plant density by transect sampling. At every site, I established 1-m wide transects at 10-m intervals, so that the sampled area represented 10% of the site. For each species within the transect I counted the number of stems and the total number of open flowers per stem. Transects were sampled every day during June 25 to June 27/92 (Hailstone Butte I), Aug 5 to Aug 7/91 (Hailstone Butte II) and June 4/91 (Stimson Creek).

To quantify pollen availability, I randomly collected 20 flowers in the morning from each plant species and placed them in separate microcentrifuge tubes containing 70% ethanol. I dissected the flowers in the laboratory and counted the pollen using a Particle Data® Elzone 180XY particle counter (see Harder 1990b for details). I estimated pollen standing crop per m² for each species by the product of the number of pollen grains per flower, the number of open flowers per stem and the number of flowering stems per m². To assure that the estimates of standing crop incorporated variation in all three of its components, each of the 20 observations of standing crop involved a selected value from the samples of floral pollen content, flower number

per inflorescence and inflorescence density (similar methods applied to the other composite variables described below).

To measure pollen volume and establish a library of known grains for identification of bee-collected pollen I randomly collected five flowers from each species and stored them separately in microcentrifuge tubes with 70% ethanol. I later acetolyzed the pollen and anthers (Fægri and Iverson 1989) to digest both floral tissue and pollen contents, leaving pollen exines intact. I permanently mounted the acetolyzed pollen grains in silicon oil and viewed them under a light microscope. Although acetolysis enables species identification of pollen grains based on exine characteristics, this detail was not necessary in this study as all species could be unequivocally identified by pollen size and shape. I used a Wild® M11 light microscope to measure pollen grain diameter (circular grains) or lengths of long and short axes (elliptical grains). Grain volume was calculated according to $4\pi ab^2/3$, where a is grain length and b is grain width (for circular grains $a=b$). I also estimated pollen volume standing crop for each plant species by multiplying grain volume by the estimated number of grains at the entire site.

To estimate pollen protein content for each species, I collected 5 flowers from each species and stored them in microcentrifuge tubes with 70% ethanol. Later, I removed all floral tissue except pollen, which I then ground in the original microcentrifuge tube with a glass pestle. I estimated protein concentration (protein/g) using the Technicon Auto-Analyzer® technique (Schuman *et al.* 1973). I favoured this less complicated procedure over the standard micro-Kjeldahl technique because it provides equally reliable results, but permits faster analysis of the digested tissue and involves less opportunity for analytical error. I estimated protein standing crop by dividing the amount of protein per gram of pollen by the number of grains per gram of pollen (see below) and multiplying the product by pollen standing crop.

3.2.3 Bumble-bee pollen loads

I assessed pollen preferences by bumble bees at each site by analysis of the pollen loads that they carried on their corbiculae. Pollen loads from bees allowed me to address two questions: from which plant species did a bee collect pollen and what is the general relationship between number of grains and pollen mass? Each day during the study period, I captured as many bees with pollen loads as possible using a fine-mesh insect net. After lightly anesthetizing a bee with ethyl acetate, I weighed her and removed the pollen loads from both corbiculae with a scalpel. The pollen loads were stored dry in microcentrifuge tubes until dry mass was weighed in the laboratory. Bees were released after they revived from the anesthetic.

The two pollen loads from each bee were combined and weighed before processing. I then placed the pollen in 1.5 ml 0.63% NaCl solution and sonicated it for 5 min to break up the load. The resulting pollen slurry was diluted with an additional 48.5 ml of NaCl solution and vortexed and two samples were removed. To determine bumble bee pollen foraging preference, I took a 5-ml subsample from the 50-ml pollen suspension and placed it in the cylindrical counting chamber of a Wild® M40 inverted microscope. After the pollen grains settled to the bottom of the chamber, I counted and identified 1000 grains. For all sites, pollen loads contained either at least 85% of a preferred plant species, or 2 or 3 plant species were equally represented in the pollen load. As a result, I considered a bee to have preferred a particular plant species if that species represented more than 85% of the bee's pollen load.

To convert measures of protein concentration into protein standing crop I required the relationship between number of grains and pollen mass. To quantify this relation, I used the second subsample from pollen loads for Hailstone Butte I because bees at this site collected pollen from three species with a range of grain sizes. I took a 10-ml subsample from the 50-ml pollen suspension and sonicated it for another 5

min to break up any remaining clumps of pollen. Then I counted the number of grains in three 1-ml subsamples using a Particle Data® Elzone 180XY particle counter, and averaged three counts for each subsample. The particle counter assigns each of the pollen grains into one of 128 logarithmic size classes. Multiple regression revealed that pollen mass depends on the number (n) and average size of pollen grains (s : μm) that comprise the load ($F_{1,15}=35.09$, $P<0.001$, $R^2 = 0.86$, $\log[\text{pollen mass}] = -10.29 + 0.0000099n + 0.16s$). I used this relation to calculate the mass of the standing crop of pollen for each species given the number of available grains and their average diameter.

3.2.4 Foraging efficiency and foraging parameter estimates

The behaviour of bumble bees while collecting pollen from a single plant species depends on foraging time and metabolic costs in a manner that is consistent with maximization of pollen-collection efficiency (Chapter 2). Efficiency is the ratio of foraging benefits to foraging costs, or more specifically

$$E = \frac{MP}{Mnt_h c_h + M(n-1)t_f c_f + (M-P)t_i c_f}, \quad (1)$$

where: P is the per-flower availability of the pollen characteristic valued by bees (e.g. number of grains or protein content), M is the bee's maximum pollen load, n is the average number of flowers visited per inflorescence, t_h is the handling time per flower, t_f and t_i are the flight time between flowers within an inflorescence and between inflorescences, respectively; and c_h and c_f are the bee's rates of energy expenditure of handling and flight, respectively. If bees maximize this currency while foraging then the plant species offering the largest mean efficiency should be preferred.

Determination of efficiency for each available plant species requires plant-specific parameter estimates; however, the bees at a site typically limited their pollen

collection to a single species, and I did not observe bumble bees foraging on all available species. As a result, although pollen standing crop, volume and protein content could be readily quantified for each available plant species (see above), bee parameters had to be estimated indirectly for plant species that the bees did not visit. For the species visited by bees, I recorded flight time between flowers within an inflorescence (t_f) and handling time (t_h) with a voice-activated tape recorder and immediately transcribed the times using stopwatches. For the unvisited species, I used the corresponding times for bees visiting lupine inflorescences. I estimated mean flight between inflorescences (t_i) for all species based on Harder's (1985) equation relating flight time to distance and a bee's wing length. To calculate average expected flight distance, I measured the distance between 10 arbitrarily selected pairs of plants for each species. Because I measured bee mass, but not wing length, I calculated regressions between wing length and mass from 36 previously collected *B. bifarius*, *B. melanopygus* and *B. occidentalis* workers and used these relations to predict wing length for the bees whose pollen collection had been observed. Wing length (W) depends on body mass (M) similarly for *B. bifarius* and *B. melanopygus*, therefore I calculated a pooled regression equation for these species ($W = 6.47 + 24.41M$, $F_{1,27}=213.65$, $P<0.001$, $R^2=0.89$). The corresponding relation for *B. occidentalis* is $W = 8.52 + 13.73M$ ($F_{1,7}=6.24$, $P<0.05$, $R^2=0.47$).

For each plant species at a site, I determined four estimates of mean efficiency based on pollen volume and protein content, unadjusted and adjusted for standing crop. For these four cases, I calculated individual efficiency values according to eq. 1 by randomly choosing an observation for flight time, handling time, and the per-flower availability of the pollen characteristic from a normal distribution with mean and variance as observed in the field for each plant species at a site. I repeated this process to generate a sample of 50 observations. This allowed me to determine

not only a mean efficiency value, but also to address whether variation influenced predicted foraging preferences.

Finally, for each measure of pollen quality I ranked the plant species at a site. All pollen characteristics were compared with single-factor analysis of variance, and significant differences between plant species were determined with Tukey's multiple pairwise comparisons. Species that did not differ significantly were considered to be of equal rank.

3.3 Results

3.3.1 Hailstone Butte I

The five plant species at this site differed significantly in all measured pollen characteristics (Table 3.1). Because I expect bees to select plant species that are most valuable according to the bees' selection criterion, I will highlight the highest ranked species for each pollen characteristic (see Table 3.1 and 3.2). In this context, *D. conjugens* could be distinguished from all other species by the standing crop of pollen per flower, a bee's efficiency of collecting a given volume of pollen from a flower and from the site as a whole, as well as a bee's efficiency of collecting protein per flower. In contrast, *P. groenlandica* ranked highest for volume per grain, volume of pollen per flower and volume of pollen from the site. Additionally, *D. conjugens* and *P. groenlandica* were equally the most rewarding species in terms of protein standing crop and the efficiency of pollen collection based on protein standing crop (Table 3.1 and 3.2). Pollen protein content and the standing crop of pollen in the entire site provided the least opportunity for distinguishing high-ranking plant species, as in both cases three species were equivalently highly ranked.

I captured 17 bumble bees of two species, *B. bifarius* and *B. occidentalis*, at Hailstone Butte I. Pollen loads carried by these bees imply heterogeneous preferences (Table 3.3): except for two bees that collected *H. alpinum* pollen, all bees collected

Table 3.1. Summary of pollen characteristics (mean, lower SE, upper SE) at Hailstone Butte I. Included are intrafloral pollen characteristics, density-adjusted pollen characteristics and collection efficiency estimates for the available plant species. Values are based on log-transformed data, hence the asymmetrical standard errors. Values in a given row followed by the same letter for a particular site do not differ significantly, whereas values with dissimilar letters differ based on Tukey's multiple comparisons with $\alpha=0.05$. For each characteristic, the letter "a" always denotes the most profitable plant species, whereas subsequent letters denote progressively less profitable plant species.

	Plant species				
	<i>D. conjugens</i>	<i>H. alpinum</i>	<i>H. sulphurescens</i>	<i>O. splendens</i>	<i>P. groenlandica</i>
Intrafloral characteristics					
Floral standing crop (grains/flower $\times 10^3$, $n=18$)	156.89 a 123.55-199.23	13.52 b 11.56-15.82	22.01 b 19.36-25.04	12.22 b 11.23-13.30	12.74 b 11.90-13.65
Pollen grain volume (mm ³ /grain $\times 10^{-6}$, $n=20$)	1.36 d 1.30-1.42	1.81 cd 1.77-1.84	2.23 c 2.18-2.28	3.77 b 3.60-3.95	6.67 a 6.47-6.87
Floral pollen volume (mm ³ /flower, $n=20$)	0.32 b 0.30-0.33	0.03 b 0.029-0.031	0.06 b 0.055-0.058	0.05 b 0.047-0.051	0.09 a 0.086-0.091
Pollen protein content (mg protein/g pollen, $n=20$)	10.72 b 8.83-13.02	10.46 b 9.54-11.47	14.23 ab 13.16-15.39	13.73 a 12.66-14.88	18.11 a 17.45-18.79

....continued

	Plant species				
	<i>D. conjugens</i>	<i>H. alpinum</i>	<i>H. sulphurescens</i>	<i>O. splendens</i>	<i>P. groenlandica</i>
Density characteristics					
Pollen standing crop (grains/m ² ×10 ⁴ , n=20)	6.60 a 5.19-8.38	3.02 ab 2.46-3.72	0.84 c 0.70-1.01	1.96 bc 1.70-2.27	4.15 ab 3.09-5.58
Volume standing crop (mm ³ /m ² , n=20)	0.14 b 0.11-0.17	0.024 c 0.019-0.030	0.086 b 0.071-0.11	0.10 b 0.09-0.12	0.71 a 0.53-0.87
Protein standing crop (mg protein/m ² , n=20)	5.31 a 4.30-6.56	0.35 b 0.28-0.43	0.55 b 0.39-0.80	0.49 b 0.40-0.58	2.09 a 1.68-2.59
Efficiency characteristics					
Floral pollen volume (mm ³ /flower/J, n=50)	0.33 a 0.32-0.34	0.0096 e 0.0095-0.0097	0.015 c 0.014-0.015	0.013 d 0.012-0.013	0.038 b 0.037-0.039
Volume standing crop (mm ³ /m ² /J, n=50)	1.42 a 1.23-1.64	0.40 b 0.33-0.48	0.60 b 0.50-0.73	0.17 c 0.14-0.20	0.58 b 0.50-0.67
Floral pollen protein (mg protein/flower/J, n=50)	0.32 a 0.30-0.33	0.066 e 0.065-0.067	0.22 c 0.21-0.23	0.082 d 0.081-0.083	0.28 b 0.27-0.29
Protein standing crop (mg protein/m ² /J, n=50)	3.57 a 3.33-3.85	0.45 c 0.39-0.52	0.89 b 0.76-1.03	0.37 c 0.32-0.44	2.60 a 2.21-3.06

Table 3.2. Plant species rankings based on pollen characteristics, including intrafloral characteristics, density-adjusted characteristics and collection efficiency estimates, for the two sites at Hailstone Butte and Stimson Creek. Based on results of Tukey's multiple comparisons presented in Tables 3.1, 3.4 and 3.5 (top rank=1).

	Hailstone Butte I					Hailstone Butte II		Stimson Creek				
	<i>D. con.</i>	<i>H. alp.</i>	<i>H. sul.</i>	<i>O. spl.</i>	<i>P. gro.</i>	<i>H. sul.</i>	<i>L. ser.</i>	<i>G. tri.</i>	<i>G. vis.</i>	<i>L. ser.</i>	<i>O. mon.</i>	<i>V. ame.</i>
Intrafloral characteristics												
Floral standing crop	1	2	2	2	2	1	2	1	2	2	2	2
Pollen grain volume	4	3,4	3	2	1	2	1	2	1	2	2	2
Floral pollen volume	2	2	2	2	1	2	1	2	1	3	3	3
Pollen protein content	2	2	1,2	1	1	1	1	3	3	1	1,2	1
Density characteristics												
Pollen standing crop	1	1,2	3	2,3	1,2	1	2	1	4	1	2	3
Volume standing crop	2	3	2	2	1	2	1	1	2	1	2,3	3
Protein standing crop	1	2	2	2	1	1	1	2	4	1	3	4
Efficiency characteristics												
Floral pollen volume	1	5	3	4	2	2	1	2	1	3	5	4
Volume standing crop	1	2	2	3	2	2	1	2	1	2	3	2
Floral pollen protein	1	5	3	4	2	2	1	2	1	3	4	4
Protein standing crop	1	3	2	3	1	2	1	2	1	1	3	2

Table 3.3. Pollen-load composition for the two sites at Hailstone Butte, Alta. and at Stimson Creek, Alta. Values represent the number of bumble bees whose pollen loads contained pollen from predominantly one plant species.

Individuals carrying loads with > 85% pollen			
Site - Bumble bee species - caste	Plant species		
Hailstone Butte I	<i>Dodecatheon conjugens</i>	<i>Pedicularis groenlandica</i>	<i>Hedysarum alpinum</i>
<i>Bombus bifarius</i> - queen	3	0	0
<i>Bombus bifarius</i> - worker	3	4	0
<i>Bombus occidentalis</i> - queen	0	3	0
<i>Bombus occidentalis</i> - worker	3	1	2
Hailstone Butte II	<i>Lupinus sericeus</i>	<i>Hedysarum sulphurescens</i>	
<i>Bombus bifarius</i> - worker	16	3	
<i>Bombus melanopygus</i> - worker	5	4	
<i>Bombus occidentalis</i> - worker	32	0	
Stimson Creek	<i>Lupinus sericeus</i>		
<i>Bombus bifarius</i> - worker	12		
<i>Bombus melanopygus</i> - worker	5		
<i>Bombus occidentalis</i> - worker	5		

either *D. conjugens* or *P. groenlandica* pollen. These differences between individual bees could have resulted for two reasons. Individuals may have based their collection on different criteria, and so the motivation for pollen collection from *D. conjugens* or *P. groenlandica* differs from the perspectives examined in this study. Alternatively, *D. conjugens* and *P. groenlandica* may have been equally valuable, but could not be profitably harvested simultaneously. This latter explanation seems most likely because these plant species were spatially separated and their morphologically different flowers required different handling techniques to extract pollen (Lavery 1980; Lavery 1994). Furthermore, bees that predominantly collected either *D. conjugens* or *P. groenlandica* pollen typically had both types of pollen present in their load (however, one species was considerably more abundant, see Methods), along with some grains of *H. alpinum*.

As outlined above, *D. conjugens* and *P. groenlandica* were equivalently ranked for only two pollen characteristics, protein standing crop and the efficiency of pollen collection based on protein standing crop. As a result, intrafloral characteristics seem to be inadequate predictors of plant species preference by bumble bees at this site. In contrast, foragers seem to be sensitive to species-specific protein availability within the site as well as the foraging costs associated with collecting protein from the site.

3.3.2 Hailstone Butte II

Only two plant species were available at this site and they differed considerably in their pollen characteristics. *Hedysarum sulphurescens* was the best candidate for pollen collection by bumble bees at this site based on only two characteristics, pollen standing crop per flower and over the entire site. On the other hand, *L. sericeus* produces relatively large pollen grains (Table 3.4) so that it ranked higher than *H. sulphurescens* for pollen grain volume, pollen volume per flower,

Table 3.4. Summary of pollen characteristics (mean, lower SE, upper SE) at Hailstone Butte II. Included are intrafloral pollen characteristics, density-adjusted pollen characteristics and collection efficiency estimates for the available plant species. Values are based on log-transformed data, hence the asymmetrical standard errors. Values in a given row followed by the same letter for a particular site do not differ significantly, whereas values with dissimilar letters differ significantly ($P < 0.05$). For each characteristic, the letter "a" denotes the most profitable plant species whereas the letter "b" denotes the least profitable plant species.

	Plant species	
	<i>H. sulphurens</i>	<i>L. sericeus</i>
Intrafloral characteristics		
Floral standing crop (grains/flower $\times 10^3$, $n=18$)	12.84 a 11.59 - 14.23	8.03 b 7.29 - 8.85
Pollen grain volume (mm ³ /grain $\times 10^{-6}$, $n=20$)	2.23 b 2.16 - 2.30	10.36 a 9.97 - 10.70
Floral pollen volume (mm ³ /flower, $n=20$)	0.031 b 0.030 - 0.032	0.09 a 0.087 - 0.093
Pollen protein content (mg protein/g pollen, $n=20$)	13.78 a 12.77 - 14.88	15.19 a 13.82 - 16.70
Density characteristics		
Pollen standing crop (grains/m ² $\times 10^4$, $n=20$)	77.73 a 69.50 - 86.94	32.04 b 27.68 - 37.08
Volume standing crop (mm ³ /m ² , $n=20$)	1.71 b 1.53 - 1.87	3.56 a 3.07 - 4.16
Protein standing crop (mg protein/m ² , $n=20$)	8.00 a 6.77 - 9.45	11.52 a 9.86 - 13.46
Efficiency characteristics		
Floral pollen volume (mm ³ /flower/J, $n=50$)	0.012 b 0.011-0.012	0.047 a 0.047-0.048
Volume standing crop (mm ³ /m ² /J, $n=50$)	0.42 b 0.37-0.47	1.66 a 1.54-1.79
Floral pollen protein (mg protein/flower/J, $n=50$)	0.080 b 0.079-0.081	0.095 a 0.094-0.096
Protein standing crop (mg protein/m ² /J, $n=50$)	2.89 b 2.81-2.98	5.86 a 5.74-5.98

volume of pollen at the site, and all aspects of a bee's pollen-collection efficiency. Both plant species at this site ranked equally according to protein per pollen grain and protein standing crop (Table 3.4 and 3.2).

I collected pollen loads from 60 workers at this site, including 19 *B. bifarius*, 9 *B. melanopygus*, 32 *B. occidentalis*. The pollen loads of 53 of these bees contained mainly *L. sericeus* pollen (Table 3.3), whereas the remaining seven pollen loads consisted of *H. sulphurescens* (Table 3.3). These results suggest that most bumble bees at Hailstone Butte II preferred *L. sericeus*; however, in isolation these preferences cannot be clearly associated with a specific pollen characteristic.

3.3.3 Stimson Creek

At Stimson Creek, bees encountered five plant species that differed markedly in all measured pollen characteristics (Table 3.5). Unlike the Hailstone Butte sites, there was more variation in the highest ranked plant species among the different measures of pollen quality. From an intrafloral perspective every plant species shared the highest rank at least once. For example, *Geum triflorum* flowers had the most pollen, whereas *Geranium viscosissimum* had pollen grains three times the volume of the next largest grain, and most pollen volume per flower (Table 3.5). *Lupinus sericeus* and *O. monticola* pollen had equally high protein content (Table 3.5). From a density perspective, *L. sericeus* and *G. triflorum* shared the highest ranking for pollen standing crop and volume standing crop, and *L. sericeus* ranked highest for protein standing crop. Based on a collection efficiency perspective, *G. viscosissimum*, with its large grains, ranked highest for volume per flower and volume at the site, as well as floral protein content. However, bees could have collected pollen equally efficiently from *G. viscosissimum* and *L. sericeus* based on protein standing-crop.

Table 3.5. Summary of pollen characteristics (mean, lower SE, upper SE) at Stimson Creek. Included are intrafloral pollen characteristics, density-adjusted pollen characteristics and collection efficiency estimates for the available plant species. Values are based on log-transformed data, hence the asymmetrical standard errors. Values in a given row followed by the same letter for a particular site do not differ significantly, whereas values with dissimilar letters differ based on Tukey's multiple comparisons with $\alpha=0.05$. For each characteristic, the letter "a" denotes the most profitable plant species whereas subsequent letters denote progressively less profitable plant species.

	Plant species				
	<i>G. triflorum</i>	<i>G. viscosissimum</i>	<i>L. sericeus</i>	<i>O. monticola</i>	<i>V. americana</i>
Intrafloral characteristics					
Floral standing crop	43.76 a	2.75 b	17.34 b	10.45 b	7.98 b
(grains/flower $\times 10^3$, n=18)	33.34-57.43	2.49-3.05	16.09-18.68	9.41-11.59	7.27-8.75
Pollen grain volume	17.42 b	54.01 a	11.28 b	8.14 b	15.67 b
(mm ³ /grain $\times 10^{-6}$, n=20)	16.48-18.33	51.32-56.84	10.52-11.98	7.92-8.34	14.58-16.05
Floral pollen volume	1.01 b	1.56 a	0.20 c	0.089 c	0.13 c
(mm ³ /flower, n=20)	0.96-1.07	1.48-1.64	0.19-0.21	0.087-0.090	0.12-0.14
Pollen protein content	6.20 c	7.19 c	15.19 a	12.34 ab	11.23 b
(mg protein/g pollen, n=20)	6.00-6.40	6.61-7.60	13.82-16.70	11.89-12.81	10.66-11.83

....continued

	Plant species				
	<i>G. triflorum</i>	<i>G. viscosissimum</i>	<i>L. sericeus</i>	<i>O. monticola</i>	<i>V. americana</i>
Density characteristics					
Pollen standing crop (grains/m ² x10 ⁴ , n=20)	8.69 a 7.07-10.69	0.06 d 0.04-0.07	16.38 a 14.21-18.89	1.57 b 1.38-1.79	0.44 c 0.36-0.53
Volume standing crop (mm ³ /m ² , n=20)	2.23 a 1.81-2.67	0.23 b 0.17-0.32	1.79 a 1.55-2.12	0.20 bc 0.18-0.24	0.08 c 0.07-0.10
Protein standing crop (mg protein/m ² , n=20)	0.77 b 0.65-0.91	0.05 d 0.04-0.07	3.10 a 2.66-3.61	0.25 c 0.22-0.28	0.07 d 0.06-0.09
Efficiency characteristics					
Floral pollen volume (mm ³ /flower/J, n=50)	0.40 b 0.36-0.45	1.05 a 1.03-1.08	0.11 c 0.10-0.11	0.026 e 0.026-0.027	0.065 d 0.064-0.066
Volume standing crop (mm ³ /m ² /J, n=50)	1.11 b 0.95-1.30	3.21 a 2.60-3.97	0.95 b 0.84-1.07	0.26 c 0.21-0.32	0.82 b 0.70-0.95
Floral pollen protein (mg protein/flower/J, n=50)	0.33 b 0.32-0.35	1.20 a 1.18-1.22	0.081 c 0.080-0.081	0.054 d 0.053-0.055	0.057 d 0.056-0.057
Protein standing crop (mg protein/m ² /J, n=50)	0.60 b 0.51-0.71	2.00 a 1.74-2.29	1.83 a 1.56-2.15	0.22 c 0.18-0.26	0.48 b 0.42-0.56

I captured 22 workers at Stimson Creek, represented by *B. bifarius*, *B. melanopygus* and *B. occidentalis*. Interestingly, even though five potential pollen sources occurred at this site, all bees carried loads that consisted exclusively of *L. sericeus* pollen (Table 3.3). This outcome indicates that bees at Stimson Creek, regardless of species, homogeneously preferred to collect pollen from *L. sericeus*.

Lupinus sericeus offers the single most profitable choice for bees at Stimson Creek from only one measured characteristic, protein standing-crop. In addition, *L. sericeus* shared an equally high rank with one other plant species for pollen protein content, pollen standing crop, volume standing crop, and a bee's efficiency at collecting protein from the site. Bee behaviour at this site indicates that bumble bees consider *L. sericeus* markedly better than other plant species because all bees collected only *L. sericeus* pollen and no evidence suggested that bees even sampled other plant species.

3.4 Discussion

3.4.1 Pollen preference criteria

At all sites bumble bees exhibited obvious preferences, as has been observed in other studies (Brian 1951; Matsumura and Munakata 1969; Schmidt 1982).

Comparison of observed preferences at the three sites with species rankings of the measured pollen characteristics reveal several features about pollen selection: bumble bees do not assess plant species solely on intrafloral characteristics; they seem to be sensitive to plant density and its effects on the standing crop of pollen at a site; and they consider protein availability at the site as a whole. In addition, bumble bee behaviour suggests that individuals may be sensitive to foraging costs.

Although there is general agreement among the three sites, some results are somewhat contradictory in the pollen characteristics most closely associated with bee preferences. Only one measured pollen characteristic explains bee preferences when

the two Hailstone Butte sites are considered together: a bee's efficiency at collecting protein from the site. In contrast, at Stimson Creek, *G. viscosissimum* and *L. sericeus* were equally profitable based on this currency, but all bees collected only *L. sericeus* pollen. The apparent disagreement between the pollen-collection criteria at Hailstone Butte and Stimson Creek could have arisen for three reasons. First, bees may maximize different currencies at the different sites. This explanation seems unlikely because pollen-collecting bumble bees presumably experience similar nutritional and energetic demands at all sites. Second, bees behave similarly at all the sites, but they maximize a currency not measured during this study. For example, *Geranium* pollen contains relatively high amounts of starch (Baker and Baker 1979), and pollen-collecting bees may attempt to limit their dietary starch intake. It is not possible to assess this explanation directly with the available data. Third, bees behave similarly at all sites and maximize a measured currency, but some pollen characteristics were estimated inaccurately for one or more plant species. This explanation is quite possible because foraging costs could not be measured for plant species on which bees were not observed foraging. In particular, substitution of handling times from lupines as surrogates for other species at Stimson Creek may be inappropriate, especially for *G. viscosissimum*. The structure of lupine flowers allows bees to extract pollen in a single, quick action (mean $\pm$ SE handling time = 0.7 ± 0.02 s). In contrast, the 10 anthers in a *Geranium* flower are widely separated, so that a pollen-collecting bee would have to move from anther to anther, which would greatly increase handling time per flower. Consequently, protein standing crop efficiency was probably overestimated for *Geranium viscosissimum*, so that this species was less profitable than the preferred species, *L. sericeus*. If this explanation is correct, then one criterion consistently explains observed bee behaviour at all locations: a bee's efficiency at collecting protein from the site.

To maximize pollen-collection efficiency, bumble bees must assess pollen standing crop at a site. The lifespan of a temperate bumble bee colony typically overlaps the flowering periods of many plant species and so bees confront a changing variety of potential pollen sources (Heinrich 1976a; Pleasants 1981). Additionally, bees encounter seasonal and yearly changes in the density of individual plant species (Pojar 1974; Heinrich 1975b; Heinrich 1976a; Pleasants 1981). Consequently, sensitivity to standing crop allows foragers to reliably assess variation in foraging benefits.

Changes in the density of flowering inflorescences also affect foraging costs through variation in the distance between inflorescences and the associated flight costs. Flight is energetically expensive (Heinrich 1975a; Ellington *et al.* 1990) and is the major cost component of foraging. Bumble bees seem to reduce such costs by not foraging at maximum intensity (Cartar and Dill 1990; Plowright *et al.* 1993). Foraging costs are probably important because they affect the longevity of individual workers (Wille *et al.* 1985; Schmid-Hempel and Wolf 1988; Wolf and Schmid-Hempel 1989; Cartar 1992b) and, therefore their contribution to the colony during their lifetime. Even though bumble bee workers live only about two weeks (Rodd *et al.* 1980; Goldblatt and Fell 1986), their lifespan makes up a significant portion of the duration of a temperate bumble-bee colony. Because temperate bumble-bee colonies consist of relatively few individuals (Hobbs 1966a; Hobbs 1966b; Husband 1977), individual foragers are valuable.

The observed behaviour of pollen-collecting bumble bees also indicates that they are sensitive to interspecific variation in pollen protein content. Bee larvae require a sufficient amount of adequate quality protein for proper development and survival (Standifer *et al.* 1960; Standifer 1967). Bumble bee workers selecting plant species based on protein content satisfy this requirement most easily. It is unclear exactly how and when pollen-collecting bees assess protein content during a foraging

trip. However, bees use olfactory (Cameron 1981; Marden 1984; Dobson 1987) and visual (Waser and Price 1983; Galen and Newport 1987; Pellmyr 1988; Lunau 1990; Lunau 1991; Lunau 1992) cues in a variety of different contexts. Pollen-collecting bees may employ such surrogate cues to assess protein content, although the exact mechanism for evaluating protein content remains unclear.

My conclusion that protein content influences choice of pollen sources differs from Schmidt's (1982) results. Schmidt (1982) examined pollen preferences by presenting honeybees with beakers of pollen from almond (*Prunes dulcis*), saguaro (*Cereus gigantea*), creosote (*Larrea tridentata*), pine (*Pinus halepensis*), dandelion (*Taraxacum* sp.), maple (*Acer grandidentatum*) and desert broom (*Baccharis sarothroides*). Feeding experiments were conducted in a greenhouse with 2 honeybee colonies that had been acclimated on sugar solution and a mixed pollen diet. During a trial, 4 beakers, each containing 15 g of a different pollen species, were placed on a table that rotated twice during the trial. Bees were allowed to collect pollen from these beakers and bee behaviour and the amount of pollen collected from each beaker were recorded. Schmidt (1982) found that bees collected the most proteinaceous pollen during one of two trials. My results probably differ from those of Schmidt (1982) for two reasons. First, honeybees encountered pollen species that they typically do not collect (e.g. pine) and so observed behaviour may not accurately reflect pollen preferences. Second, these bees did not experience the foraging costs typically associated with handling a flower, and flying between flowers and inflorescences. Hence, Schmidt's (1982) results may not be representative of pollen collection under natural conditions.

3.4.2 Variation in pollen-collecting behaviour

In contrast to the bees at Stimson Creek, which collected pollen exclusively from *Lupinus sericeus*, many bees at the Hailstone Butte sites (14/17 bees at Hailstone

Butte I; 12/60 bees at Hailstone Butte II) collected pollen from at least one species in addition to their preferred species. For all but two of these bees the minority species was less rewarding in terms of efficiency of protein collection from the site. Pollen collection from these less profitable species could have occurred because of either the necessity to gain information about the foraging environment, or complications due to simultaneous nectar and pollen harvesting.

Bees may have collected pollen from less rewarding plant species to obtain information about the profitability of alternative plant species, as has been demonstrated for nectar-collecting bees (Heinrich 1976b; Heinrich 1979c). If such sampling occurred, then pollen from all plant species should have been encountered in pollen loads from all bees. In contrast, some plant species were never observed in pollen loads. In addition, this explanation should apply to all sites, but bees at Stimson Creek collected only lupine pollen. Hence, sampling by bees provides an unsatisfying explanation for infrequent collection of less rewarding pollen.

The plant species favoured by bees at all sites produce only pollen. In contrast, the minority pollen sources at the Hailstone Butte sites (*Hedysarum*, *Oxytropis*) produce both pollen and nectar so that the bees visiting them may not have collected only pollen. Pollen collection requires energy, so that bees probably have to collect nectar occasionally during a foraging trip to "fuel-up". At the study sites, bees cannot obtain nectar from the highest ranked plant species because in all cases these plant species do not produce nectar. Consequently, pollen-collecting bees would have to visit species with inferior pollen to obtain energy and, in doing so, their pollen loads become "contaminated" with pollen from less valuable species. This interaction between two resources clearly complicates pollen collection.

The bees at Hailstone Butte I probably illustrate another aspect of preferential foraging - the role of learning. Even though *Pedicularis groenlandica* and *Dodecatheon conjugens* were equally rewarding, individual bees concentrated their

pollen collection on one species or the other, rather than visiting these species equally. Pollen collection often requires relatively complicated harvesting techniques (examples relevant to this study: *D. conjugens*, Macior 1964, Harder and Barclay, in press; *P. groenlandica*, Macior 1973; *L. sericeus*, Wainwright 1978, Harder 1990a), including high frequency vibrations. As a result, bees must learn how to acquire pollen from a particular plant species (Lavery 1980). The benefits of experience may limit individual foragers to collecting pollen from only a single profitable species. In fact, foraging efficiency declines when foragers switch between species (Lavery 1985; Lewis 1986; Papaj and Prokopy 1989). Consequently, bees may incur learning costs if they collect pollen from different plant species that seem equally profitable.

3.4.3 Pollen-collection behaviour

Whether choosing between species (this chapter) or selecting flowers of a single species (Chapter 2), pollen-collecting bumble bees behave as though they maximize the ratio of benefits to foraging costs. This consistency in behaviour has two implications. First, it indicates that pollen-collecting bees encounter similar ecological constraints within and between plant species. Although foraging behaviour may be context specific in terms of benefits accrued, the general metabolic costs associated with foraging are similar for different situations. Second, this observation along with other studies (Schmid-Hempel 1986; Schmid-Hempel and Wolf 1988; Wolf and Schmid-Hempel 1989; Cartar 1992b) suggests that individual foragers are sensitive to physiological senescence and behave in a manner that prolongs life expectancy. In general, maximization of pollen collection efficiency should return the most pollen to the hive during an individual's lifetime regardless of whether the bee species involved is solitary or social.

4 Conclusions

Foraging bumble bees must decide which plant species to collect pollen from and how to behave to maximize returns from the chosen plant species. Pollen-collecting bumble bees are sensitive to foraging costs when foraging from both a single plant species, as well as from different plant species. Behaving efficiently when collecting pollen probably allows foragers to maximize both their lifespan, and consequently, their net contribution to the colony during their life. In addition, when collecting pollen from different plant species bumble bees visit plant species with the most abundant, proteinaceous pollen. Collecting protein-rich pollen should improve larval survival and development, and promote reproductive success.

Polylectic foragers, such as bumble bees, typically are sensitive to variation in resource availability and so presumably are labile in their preferences. Many studies have demonstrated that individuals use numerous characteristics to guide foraging behaviour, including visual and chemical cues. However, unless plant species advertise reliably, foragers that are sensitive to resource variation are unlikely to continue foraging from that particular species. Pollen characteristics potentially provide information about the quality of available pollen and so may maintain pollinator constancy to a particular plant species.

Foraging behaviour of eusocial species may differ from solitary species because the ecological consequences associated with sociality are different than those associated with solitary life (Michener 1974). For example, solitary individuals and individuals from a eusocial colony live for approximately two-four weeks. For a solitary individual, contributions to the next generation cease at the end of this period, whereas individual genetic contributions in a social colony, even of deceased workers do not cease until the hive stops producing reproductives. Also, net individual contribution differs for solitary and eusocial species because the number of young per foraging effort can be accurately accounted for among solitary species, whereas this is

not the case for individuals from eusocial species. As a result, eusocial individuals, unlike solitary individuals, cannot accurately assess how their contributions to the nest influence reproductive success. Additionally, individuals from eusocial species recognize colony members, and in some instances communicate with them.

Interactions between individuals from eusocial species may result in selection for individuals with increased learning and memory, and so eusocial individuals may be more sensitive to their foraging environment than solitary individuals. Differences between eusocial species and solitary species in terms of contribution to the reproductive success per individual and learning may make individuals from eusocial species, specifically bumble bees more sensitive to foraging costs. However, specific comparisons between eusocial and solitary species in foraging behaviour, especially foraging currency, remain to be addressed.

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Appendix 2.1. Estimates of optimal starting position when the proportion of pollen removed from a flower decreases exponentially as the bee moves up the inflorescence.

To simplify presentation of the optimal starting positions on lupine inflorescences (eq. 6a and 6b) I treated the proportion of pollen removed from individual lupine flowers (k) as a constant. However, for *L. sericeus* this proportion actually increases down the inflorescence according to

$$k = s(1-e^{-vn}) \quad (7)$$

(see Fig. 2.6), where s and v are parameters that describe how the proportion of pollen removed changes specifically for *L. sericeus*. Optimal starting positions that reflect this relation can be obtained by substituting equation 7 into equation 2, differentiating the corresponding versions of equations 4 and 5 with respect to optimal starting position (n^*), and solving for optimal starting position. The following equalities result,

$$\begin{aligned} \text{RATE} \quad & [(t_f+t_h)(bn^*+vn^*) + (t_i-t_f)(v+b) + t_f + t_h]e^{-bn^*} + [(t_f+t_h)(-bn^*-1) + b(t_f-t_i)]e^{-bn^*} \\ & + t_h + t_f = -[(t_f+t_h)(-vn^*-1) - v(t_i+t_f)]e^{vn^*} \end{aligned} \quad (8a)$$

$$\begin{aligned} \text{EFFICIENCY} \quad & [(t_f c_f + t_h c_h)(bn^*+vn^*) + (t_i c_f - t_f c_f)(v+b) + t_f c_f + t_h c_h]e^{-bn^*} + [(t_f c_f + t_h c_h)(-bn^*-1) \\ & + b(t_f c_f - t_i c_f)]e^{-bn^*} + t_h c_h + t_f c_f = -[(t_f c_f + t_h c_h)(-vn^*-1) - v(t_i c_f + t_f c_f)]e^{vn^*} \end{aligned} \quad (8b)$$

Although these equalities are more complicated than 6a and 6b, numerical solutions indicate that they yield qualitatively similar relations between optimal starting position and the parameters (Fig. 2.2 and Fig. 2.3).

Appendix 2.2. Summary of conditions for the seven samples of pollen-collection behaviour by bumble bees. Foraging parameters (mean $\pm$ SE) include handling time (t_h), flight between whorls (t_f) and flight between inflorescences (t_i), log(initial pollen production) (a) and slope of the relation between log(pollen standing crop) and flower position within an inflorescence (b). The number of bees observed for a particular flight time are indicated parenthetically below each time. The number included parenthetically below a indicates the number of sampled inflorescences.

Location	Date	Lupine species	Bee species	t_h (s)	t_f (s)	t_i (s)	a	b
Burnell Lake, B.C. (49°13'N; 119°36'W)	05/29-31/92	<i>L.wyethii</i> S.Wats	<i>B.bifarius</i> Cresson	0.6 $\pm$ 0.04 (8)	0.7 $\pm$ 0.07 (8)	2.0 $\pm$ 0.38 (9)	10.28 $\pm$ 0.10 (40)	0.44 $\pm$ 0.03
			<i>B.flavifrons</i> Cresson	0.6 $\pm$ 0.02 (3)	0.8 $\pm$ 0.04 (3)	2.0 $\pm$ 0.32 (4)		
Chain Lakes, Alta. (50°16'N; 114°11'W)	07/11-14/91	<i>L.sericeus</i> Pursh	<i>B.bifarius</i>	0.7 $\pm$ 0.02 (20)	1.1 $\pm$ 0.05 (20)	2.2 $\pm$ 0.36 (10)	9.96 $\pm$ 0.07 (40)	0.44 $\pm$ 0.02
			<i>B.occidentalis</i> Greene	0.6 $\pm$ 0.02 (11)	1.1 $\pm$ 0.05 (11)	1.6 $\pm$ 0.25 (8)		
			<i>B.rufocinctus</i> Cresson	0.6 $\pm$ 0.03 (4)	0.9 $\pm$ 0.08 (4)	1.7 $\pm$ 0.65 (4)		
Creston, B.C. (49°09'N; 116°23'W)	06/06-15/91	<i>L.burkeii</i> S.Wats	<i>B.bifarius</i>	0.9 $\pm$ 0.03 (10)	1.1 $\pm$ 0.04 (10)	2.8 $\pm$ 0.72 (10)	9.77 $\pm$ 0.10 (30)	0.24 $\pm$ 0.05

....continued 

Location	Date	Lupine species	Bee species	t_h (s)	t_f (s)	t_i (s)	a	b
Porcupine Hills, Alta. (50°00'N; 114°06'W)	07/29- 08/04/91	<i>L. wyethii</i>	<i>B. bifarius</i>	0.8±0.03 (11)	0.8±0.03 (11)	1.6±0.64 (12)	9.86±0.08 (60)	0.57±0.02
			<i>B. mixtus</i> Nylander	0.7±0.05 (5)	0.9±0.06 (5)	1.5±0.13 (5)		
			<i>B. occidentalis</i>	0.8±0.03 (8)	0.9±0.05 (8)	1.3±0.26 (9)		
			<i>B. rufocinctus</i>	0.8±0.05 (6)	0.9±0.07 (6)	1.9±0.38 (4)		
Stimson Creek, Alta. (50°17'N; 114°19'W) first visit	06/27- 07/01/91	<i>L. sericeus</i>	<i>B. bifarius</i>	0.7±0.02 (18)	1.0±0.03 (18)	1.9±0.27 (30)	10.06±0.09 (40)	0.43±0.03
			<i>B. occidentalis</i>	0.7±0.05 (10)	1.0±0.04 (10)	1.6±0.24 (12)		
Stimson Creek, Alta. second visit - day 1	07/15/91	<i>L. sericeus</i>	<i>B. bifarius</i>	0.8±0.02 (11)	1.0±0.03 (11)	1.3±0.21 (6)	9.93±0.10 (20)	0.54±0.04
Stimson Creek, Alta. second visit - day 3	07/17/91	<i>L. sericeus</i>	<i>B. bifarius</i>	0.8±0.03 (19)	1.0±0.05 (19)	1.3±0.21 (18)	10.03±0.12 (20)	0.74±0.05
Waterton Lakes, Alta. (49°06'N; 113°52'W)	06/15-24/91	<i>L. lepidus</i> Doug.	<i>B. bifarius</i>	0.5±0.03 (8)	1.0±0.07 (8)	2.5±0.57 (18)	9.93±0.10 (100)	0.36±0.03
			<i>B. occidentalis</i>	0.6±0.02 (8)	1.0±0.04 (8)	2.3±0.41 (12)		