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Dependence of hummingbird movement within inflorescences

on the spatial arrangement of flowers

by

W. Eric Gross

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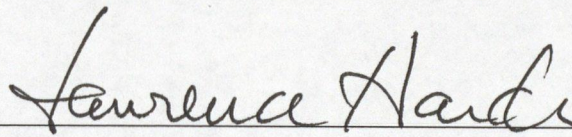
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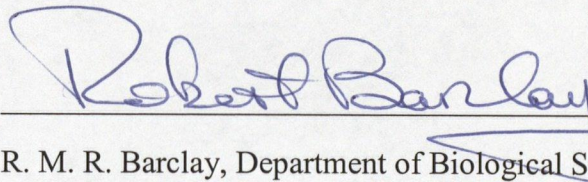
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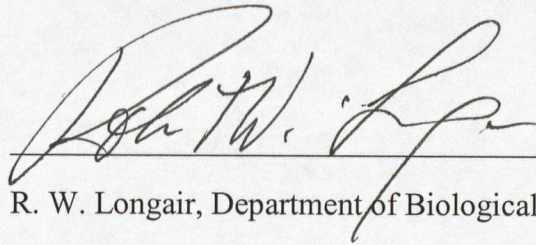
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Dependence of hummingbird movement within inflorescences on the spatial arrangement of flowers" submitted by W. Eric Gross in partial fulfillment of the requirements for the degree of Master of Science.

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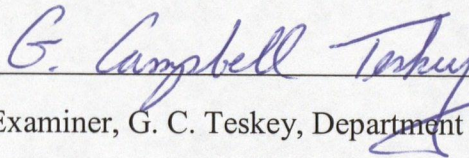Supervisor, L. D. Harder, Department of Biological Sciences

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ABSTRACT

When foraging on flowers that are aggregated into inflorescences, pollinators encounter a three-dimensional problem. Given the potential for inflorescence architecture to manipulate pollinator behaviour, I considered how plant architecture shapes pollinator foraging by observing the responses of free-flying rufous hummingbirds (*Selasphorus rufus*) to artificial panicles, racemes and umbels. Hummingbirds followed several basic rules of movement when foraging within a variety of inflorescences. They treated inflorescences as edges, minimized flight distances and departed inflorescences after revisiting a flower when many flowers had been visited. However, when given a choice, birds did not preferentially visit umbels, the highest rewarding inflorescence. Architecture modified hummingbird behaviour in terms of the proportion of flowers visited, the consistency of foraging routes, and the direction of movement within and between inflorescences. Birds responded differently than bumble bees to similar architectures. The interaction between architecture and pollinator behaviour can have important consequences for plant mating and evolution.

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1 INTRODUCTION

The movement patterns of foraging animals have many important ecological and evolutionary consequences for the foragers themselves and the organisms that serve as their food sources. Most obviously, movement patterns influence an animal's foraging returns as it searches the environment for food (e.g., Baum and Grant 2001). In addition, the pattern of foraging movements can influence an animal's exposure to predation (e.g., Huntingford 1993). As animals feed, they reduce local food abundance, so that foragers can affect the dispersion of their prey. The foraging movements of pollinators also affect the mating patterns of the plants they visit (Thomson and Thomson 1989, Cresswell et al. 2002), with consequences for reproductive isolation (Schemske and Bradshaw 1999, Campbell et al. 2002).

Pollinators experience an atypical situation while foraging. Plants use flowers to advertise the location of discrete energy rewards (nectar) that usually replenish over time. Easily recognized food locations reduce pollinator search time, so that the cost of foraging primarily involves patch choice and handling time. In general, the quality and quantity of rewards in a patch remain somewhat obscure to the pollinator, although in some cases, pollinators may recognize that a reward is not currently available. For example, bumble bees can detect scent marks left during recent visits by conspecifics and leave the inflorescence (Williams 1998, Goulson 1999). As well, hummingbirds avoid flowers whose corollas have been punctured by orioles and nectar robbed (Gass and Montgomerie 1981). Nonetheless, the easily identifiable location of flowers and patches (inflorescences or groups of them) makes pollinator foraging unusual.

Optimal foraging theory has revealed many insights on pollinator behaviour. According to this theory, innate and/or learned behaviour allows individuals to act in manners that enhance their foraging benefits relative to costs (Gass and Roberts 1992). Often, the foraging behaviour of nectar-feeding pollinators maximizes their rate of net energy gain (reviewed by Harder et al. 2001). For example, when exploiting patches of

resources, pollinators must determine how much effort to expend in a patch. The marginal-value theorem predicts that an animal foraging on patchy resources maximizes its long-term rate of energy intake by departing a patch when its marginal rate of energy gain for the patch equals the average rate of gain in the entire habitat (Charnov 1976). This theorem assumes that foragers have complete knowledge of the quality of each patch.

In many cases, pollinators possess limited information about rewards and do not know patch quality perfectly (Valone 1991). Instead, they must estimate patch quality based on two types of information (Gass and Sutherland 1985, Stephens and Krebs 1986, Valone 1991, 1992, Sutherland and Gass 1995). First, foragers can use both their general experience with the environment and past experience in specific patches to develop expectations about foraging returns. Second, foragers acquire information while feeding in a patch (i.e. time spent exploiting a patch, quantity of rewards harvested, or time since last visit). Prior and sample information can be combined to form a Bayesian estimate of patch quality (McNamara and Houston 1980, Valone 1992). Green (1984) demonstrated that Bayesian assessment enhances energy intake rates.

With or without Bayesian assessment, foragers that move non-randomly through patches should achieve higher reward rates than those that do not (Goulson 1999). Random foraging represents nonsystematic movement, but most examples of this refer to independence from external stimuli rather than true random foraging (Pyke 1978a). Systematic movement exposes two central questions: what path should a forager follow and when should it leave a patch? One simple movement rule involves area-restricted search, whereby foragers that encounter a highly rewarding food source move shorter distances and turn more to stay in the patch (Gill and Wolf 1977, Pyke 1978b, Keasar et al. 1996). Conversely, after receiving a small, or no reward, foragers engaged in area-restricted search move a larger distance and turn less (Heinrich 1979, Waddington 1983, Dukas and Real 1993). Pollinators also forage systematically by repeatedly following

established routes ("traplining", e.g. bumble bees, Williams and Thomson 1998; butterflies, Gilbert 1975; hummingbirds, Gill 1988). Baum and Grant (2001) observed hummingbirds using a directional search strategy, whereby the birds followed rows and columns of flowers in an artificial array (see also Valone 1992). Many pollinators incorporate directionality in their foraging, which reduces the probability of revisiting recently visited plants or flowers and thereby increases the efficiency of the search (Pyke and Cartar 1992, Cartar and Real 1997).

An efficient forager's behaviour should reduce the probability that it fails to meet its energetic requirements. An animal should forage in a risk-averse manner when it expects its energy intake to exceed its physiological requirement, whereas an animal should be risk-prone when its energy intake is less than required (Caraco et al. 1990). Stephens and Krebs (1986) referred to this as the energy-budget rule. The above movement patterns and the marginal-value theorem apply rules that increase a pollinator's rate of energy gain. The pollinator stays in a rewarding patch longer, until the patch is no longer more rewarding than the expected return from moving to the next patch. While in a patch, such a forager follows a path that reduces revisits, thereby avoiding low-return visits.

1.1 Pollinator behaviour on inflorescences

When foraging on flowers that are aggregated into inflorescences, pollinators encounter a three-dimensional patch problem. To reduce costs of foraging and stay above some energy threshold, pollinators should still minimize movement distances and use a search pattern that minimizes revisits. How do pollinators respond to inflorescence architecture? Bumble bees have been the focus of most research on this topic. Bees behave very predictably on vertical inflorescences, such as spikes or racemes, generally arriving at the bottom, moving upwards, visiting many of the flowers, and departing from upper flowers (Pyke 1979, Corbet et al. 1981, Best and Bierzychudek 1982, Jordan

2000). Even when nectar patterns were changed to make the topmost flowers more rewarding, bees maintain upward movement, although they start visiting on middle flowers, rather than near the bottom (Waddington and Heinrich 1979). Jordan (2000) contrasted bee behaviour on racemes and more complex branched panicles (both with 12 flowers). When visiting both inflorescence types, bees maintained upward movement. However, they followed less consistent paths on panicles. Bees also modify their departure rules on contrasting inflorescence architectures when nectar volumes differ between flowers. On racemes, bees depart after visiting a single flower with less nectar than a threshold volume (Hodges 1985). However, bees leave more complex panicles only after visiting several empty flowers (Kadmon and Shmida 1992). In general, inflorescence architecture influences bee foraging, but, at most, modifies the stereotypical pattern of movement.

How general are bee movement patterns on inflorescences compared to those of other pollinators? Do pollinators other than bumble bees solve the problem of changing foraging costs with architecture in the same or different manners? Hummingbirds are the only other group of pollinators to be examined in any detail, but analysis of their spatial behaviour is limited. Hummingbirds have often been used to demonstrate spatial learning and memory (reviewed by Healy and Hurly 2001). Many studies of hummingbird foraging incorporate variation in nectar rewards (Gass and Sutherland 1985, Wolf and Hainsworth 1986, Valone 1992, Sutherland and Gass 1995, Waser and McRobert 1998, Biernaskie et al. 2002), which can confound the understanding of basic foraging patterns. Often the focus of these studies is not the behaviour of birds within an inflorescence, but rather their decisions between patches, their use of memory, or risk-aversion. Although all levels of foraging are interdependent, few studies have examined hummingbird behaviour within inflorescences.

Only Pyke (1978c, 1981a), Hainsworth et al. (1983), Devlin and Stephenson (1985) and Wolf and Hainsworth (1986) have examined hummingbird foraging within

inflorescences in any detail. These studies used natural and/or artificial inflorescences that were either racemose or unrepresentative of natural inflorescences. As a result, these studies did not differentiate between inflorescence types that birds might encounter while foraging in natural situations.

On racemes, hummingbirds behave much less predictably than bees. Hummingbirds show little tendency to start visits to racemes at low flowers, rather than other positions. In addition, they exhibit no consistent directionality within racemes and depart from either top or bottom flowers (Wolf and Hainsworth 1986). Pyke (1981a) could detect no obvious movement rule for hummingbirds visiting natural (racemose), spiral, and linear inflorescences. However, he did find that birds tended to move from a flower to a near neighbour, but only showed a weak tendency for directionality. Interestingly, when presented with a top-down nectar gradient in *Lobelia cardinalis* racemes, ruby-throated hummingbirds foraged somewhat more consistently, being twice as likely to start in the middle third of the inflorescence, than at either end, and to then move upwards (Devlin and Stephenson 1985). As well, birds that initially moved downwards from the middle of *L. cardinalis* inflorescences almost always reversed their direction. However, these responses were not universal, as some birds arrived at the top or bottom of the inflorescence and subsequently moved down or up, respectively.

Despite the less consistent movement patterns of hummingbirds, inflorescence structure can influence their foraging (Hainsworth et al. 1983). For example, in their study with artificial inflorescences, Hainsworth et al. found that birds visited fewer flowers on more 'complex' three-dimensional designs compared to relatively 'simple' linear designs somewhat like a raceme. Birds also revisited fewer flowers on complex arrangements, which resulted in a more consistent average rate of energy intake across flower visits. Unfortunately, the vertical, linear designs considered by Hainsworth et al. were two-dimensional and even the three-dimensional designs that they studied were

hemispheres, which arranged flowers unnaturally. Therefore, the relevance of Hainsworth et al.'s results to natural situations is unclear.

Departure rules can also influence foraging within an inflorescence. Pyke (1978c) concluded that hummingbirds use an optimal decision rule when leaving inflorescences. This rule was based on the size of the inflorescence, the number of flowers visited and the amount of nectar in the last flower probed. Wolf and Hainsworth (1986) found that the primary cue for early departure from an *Ipomopsis aggregata* inflorescence was the probing of empty flowers. They also felt that sophisticated departure decisions were impractical for inflorescences that provided little information on reward quality. Hainsworth et al. (1983) found that departures were not influenced by architecture, but demonstrated that the probability of a hummingbird departing an inflorescence was roughly constant after the first few flowers were visited. To explain why hummingbirds visit a small fraction of available flowers on the compact inflorescence of *Calliandra* sp., even when it would be more profitable to visit more flowers, Gass and Montgomerie (1981) speculated that birds may employ a simple rule; leave after visiting *n* consecutive empty flowers because revisits occur frequently on this species. They also found that hummingbirds feeding on other species were more likely to tolerate unrewarding revisits if the volume of reward was expected to be high (also see Valone 1992).

Hummingbirds seem to use general, rather than specific, memory of their foraging experience within inflorescences. Birds use spatial information more than visual cues while foraging (Brown and Gass 1993, Hurly and Healy 2002). While they can remember the locations of individual flowers arrayed in a field and patches of inflorescences, it seems unlikely that hummingbirds can remember the location of each flower in a territory encompassing hundreds of flowers (reviewed in Healy and Hurly 2001). Similarily at a finer spatial scale, Waser and McRobert (1998) claimed that they knew of no evidence that birds can learn the location of individual flowers on inflorescences, which contain many tightly packed flowers. Healy and Hurly (2001)

summarized the available evidence of hummingbird movement and concluded that birds do not use rules like those of bumble bees when foraging within an inflorescence (but consider Devlin and Stephenson 1985). Thus, memory of pattern may account for more aspects of hummingbird performance than simple movement rules or memory of individual flower locations (Sutherland and Gass 1995).

Hummingbird movement between inflorescences has also been examined. Hummingbirds preferentially visit larger inflorescences with many flowers (Pyke 1981b, Wolf and Hainsworth 1990). They also fly short distances between successive inflorescences (Pyke 1981b, Gass and Montgomerie 1981), unless the previous inflorescence was of poorer quality (Wolf and Hainsworth 1990). Pyke (1981b) found that birds moved to inflorescences of the greatest apparent size more frequently than to the inflorescence that was largest, closest, or estimated to have the highest rate of energy gain. Unlike bumble bees, hummingbirds show little general directionality, but instead move to an inflorescence in the direction they face as they leave the preceding inflorescence (Pyke 1981b).

When moving between inflorescences, hummingbirds employ either an area-restricted (Wolf and Hainsworth 1990) or directional search (Baum and Grant 2001), depending on the spatial arrangement of inflorescences. Baum and Grant (2001) simulated and tested birds' search strategies in patches of uniform, clumped and randomly distributed rewards. In uniform patches, hummingbirds moved among inflorescences in a manner that was less efficient than purely directional movement, but more efficient than area-restricted search. On clumped and random resource distributions hummingbirds foraged as efficiently as an area-restricted search pattern and more efficiently than any of the other simulated search patterns. Thus, birds use different foraging strategies in different patch types and incorporate prior and sample information as they forage (see Valone 1991, 1992).

1.2 Hummingbird behaviour and inflorescence design

If contrasting inflorescence architectures represent different foraging environments, and if pollinators modify their foraging to increase net rate of energy gain, then inflorescence design could influence pollen movement and plant mating success (Hainsworth et al. 1983). Pollinator behaviour within and between inflorescences determines how pollen moves among flowers and thus affects the reproductive success of plants (Wyatt 1982, Jordan 2000). Inflorescence designs that pollinators prefer because of patch quality, size, or energetics, can increase a plant's mating opportunities (Iwasa et al. 1995, Harder et al. 2001). For example, Tadey and Aizen (2001) reoriented pendant inflorescences of a hummingbird-pollinated mistletoe to an upright position and found that pollination success declined. Thus, a change in architecture may impact the amount of pollen removed or delivered.

Inflorescence architecture may also affect the number of flowers visited on an inflorescence (Jordan 2000), which determines the incidence of between-flower self-pollination (geitonogamy), which can reduce the pollen available for export to other plants (pollen discounting: reviewed in Harder and Barrett 1996). Repeated movement patterns by pollinators within inflorescences allow plants to modify the temporal segregation of flower sex roles within an inflorescence to decrease geitonogamy (Harder et al. 2000). For instance, many bee-pollinated racemes are protandrous (flowers are male first) and flower sequentially upwards. When the inflorescence is in full bloom, older, lower flowers are female and younger, upper flowers are male. Because bumble bees move upwards on racemes and leave from the top, the chance of self-pollen moving to a female-phase flower is reduced. Outcrossing is also promoted because bees typically fly to lower, female-phase flowers of the next inflorescence. In contrast to the stereotypic behaviour of bumble bees, the inconsistent movement patterns that have been reported for hummingbirds on racemes may change the incidence of self-pollination within inflorescences.

Although bees and hummingbirds differ in their movements on racemes, whether birds forage differently on other natural architectures, or whether their movement patterns on other architectures differ from those of other pollinators is unknown. Thus, a comparison of bumble bee foraging with hummingbird foraging on a range of architectures would provide insight into the consequences for the evolution of inflorescence architecture of a transition from one type of pollinator to another. For example, Miller (1985) suggested that plant architecture forced hummingbirds to hover, rather than perch, while foraging, so that plants, rather than the energetics of the pollinator, drive behaviour. However, birds should still respond in an optimal way within the constraints imposed by inflorescence architecture. Therefore, Miller suggested that questions concerning the foraging patterns of hummingbirds should be approached from the point of view of the plants, rather than exclusively from that of the hummingbird (also see Healy and Hurly 2001).

1.3 Objectives

Given the potential for inflorescence architecture to manipulate pollinator behaviour, an integrated approach is warranted that considers how plant architecture shapes pollinator foraging, whether pollinators forage efficiently on alternate architectures, and the consequences of the interaction between architecture and pollinator behaviour on plant mating and evolution. In this thesis, I adopt this perspective to assess experimentally the influence of inflorescence architecture on foraging by free-living rufous hummingbirds (*Selasphorus rufus*). I specifically address the following questions:

1) does inflorescence architecture (raceme, panicle, umbel) alter the number of flowers that hummingbirds visit per inflorescence, their movement patterns, and their flight times?

2) do hummingbirds follow recognizable rules when moving within and between inflorescences?

3) does behaviour differ between sexes, given that females weigh more and males have higher wing loading, which could affect maneuverability and energetics (Calder 1993, Chai and Dudley 1999)?

4) when given a choice between alternate inflorescence architectures, does the behaviour of hummingbirds maximize their rate of net energy gain?

5) to what extent does hummingbird behaviour on architectures differ from that observed for bumble bees on similar architectures?

6) how might differences in foraging between architectures and pollinator groups affect plant mating and evolution?

2 METHODS

2.1 Artificial Inflorescences

I studied the behaviour of hummingbirds as they foraged on 12-flowered inflorescences with three different architectures: racemes, umbels and panicles (Fig. 2.1). These architectures, which are common in nature, present distinctly different three-dimensional distributions of flowers to a forager. The design of each inflorescence type closely followed that used in Jordan's (2000) study of bumble bee foraging in both flower number and arrangement. In particular, racemes were arranged with four whorls of three flowers on a vertical axis. Each whorl was rotated 60° from the previous whorl. Panicles had four branches arranged on a central vertical axis. Each branch had 4, 3, 3, and 2 flowers, respectively, starting from the bottommost branch. Umbels presented flowers in a plane, with an outer ring of eight flowers and an inner ring of four flowers. I designed the vertical inflorescences with twice the distance between flowers compared to Jordan's (2000) inflorescences to facilitate videotaping of a larger, faster species. In addition, the umbels I used differed from Jordan's (2000) arrangement by the symmetrical arrangement of flowers.

The experimental inflorescences were constructed by arranging 12 artificial flowers on a doweling frame. I used surgical needle tips (length of well = 16 mm, orifice diameter = 4 mm) as flowers, following Pyke (1981a), and painted them red on the outside, so that they resembled flowers commonly visited by hummingbirds in size, shape and colour. At the start of training and experimental trials, each flower was filled with 4 μL of 20% (mass/mass) sucrose solution with an Eppendorf repeatable micropipette (I used 5 μL for the Bamfield female and the first male studied at Kananaskis). These nectar characteristics are typical of hummingbird-pollinated plant species (Baker 1975, Pyke and Waser 1981, Heyneman 1983). After a trial, I removed all flowers and replaced them with clean ones. Flowers were washed with soapy water, rinsed, and dried in a drying oven before being used again.

Figure 2.1. The three inflorescence types presented to rufous hummingbirds; a) raceme, b) umbel, and c) panicle. Numbered flowers are the flower positions referred to for each architecture.
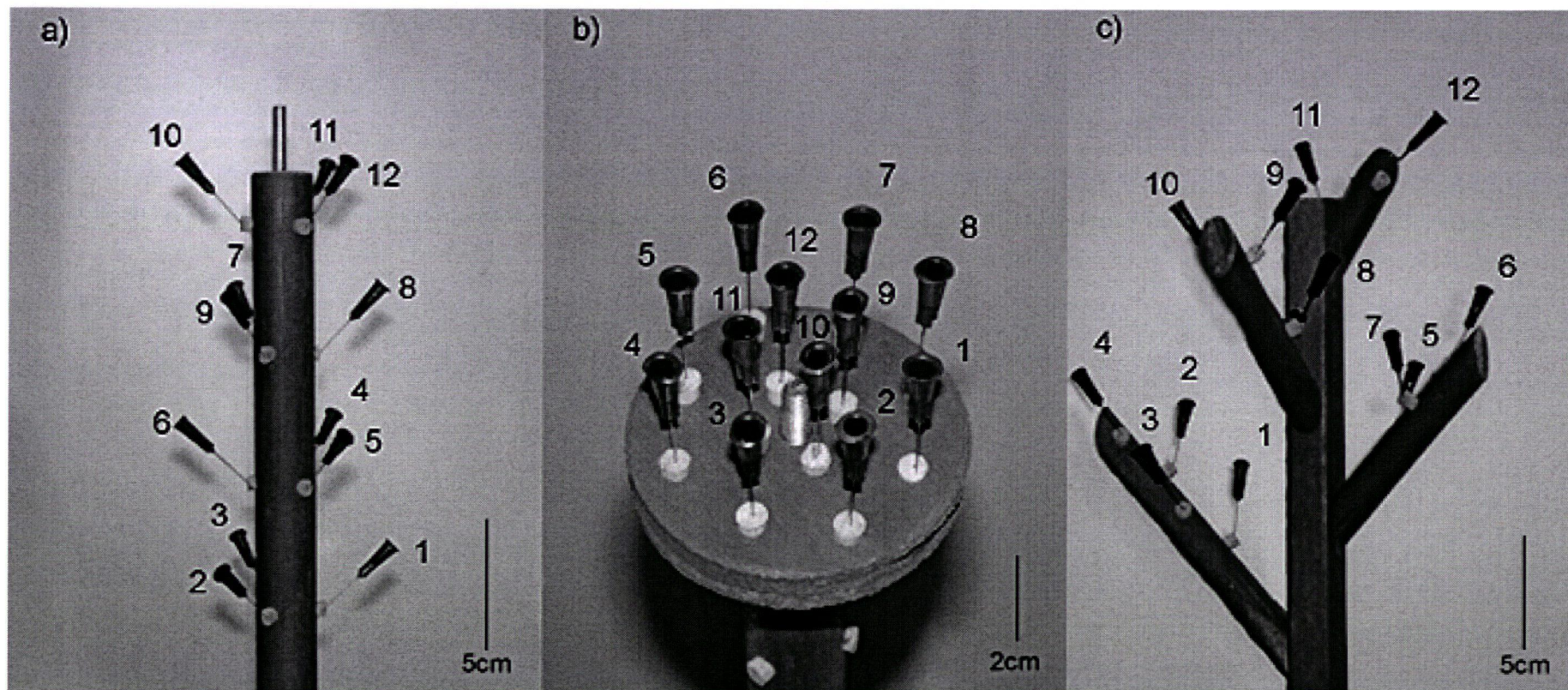
During experimental trials, I presented a hummingbird with five identical inflorescences arranged in a row, with 50 cm between adjacent inflorescences. Each inflorescence was placed on top of an aluminum pipe embedded in the ground, so that the bottom of the inflorescence was approximately 1 m above the ground. For racemes and panicles, the supporting pipes were vertical, whereas they were tilted approximately 40° from the vertical for umbels, so that I could distinguish which flowers birds visited. In arrays of panicles, I arranged the inflorescences so that the longest arm pointed in opposite directions on adjacent inflorescences. During the first trial, the longest arm of the leftmost inflorescence pointed 45° from the axis of the array, the next inflorescence pointed 135°, the next inflorescence pointed 45°, etc. Between trials, I rotated each inflorescence 180°, so that a bird was never presented with the longest arm in the same position during successive bouts. At the end of each foraging bout, I moved the array between 2 and 5 m to preclude birds from using their memory of visited flowers in a static array.

Assessment of the patterns of movement by hummingbirds within inflorescences required knowledge of inter-flower distances. To calculate these distances, I first measured the coordinates of each flower in two (umbels) or three dimensions (racemes and panicles) and then used geometric mathematics to calculate the Euclidean distances between flowers. In some cases, I modified the calculated distances to reflect the path that birds followed between particular flowers. While foraging on panicles, birds moved between flowers on opposite sides of a branch by flying around the branch tip, rather than by crossing the branch. Therefore, I calculated the distance between flowers on either side of a tip of a branch (i.e. flower 6 and 7) as the length of a circular arc that included these flowers. When visiting racemes, birds could not fly through the central axis, but instead treated the inflorescence as a cylinder. For racemes, I therefore calculated distances between flowers on the surface of the cylinder defined by the positions of the mouths of the 12 flowers.

2.2 Subjects, Initial Training and Experimental Trials

I conducted hummingbird foraging experiments near the Bamfield Marine Station, B.C. (48°50'N, 125°08'W), from mid-May to early June (1 female), and at the Kananaskis Field Station, Alberta (51° 02'N, 115° 03'W), during June and July, 1999 (4 females and 7 males). In total, I studied 12 experimentally naïve rufous hummingbirds (*Selasphorus rufus*) which had established territories locally.

To induce birds to establish individual feeding territories, I set up commercial hummingbird feeders containing 15% sucrose solution around the field stations. Once a male bird had established a territory incorporating a feeder, I marked his breast feathers with coloured, indelible ink to recognize the test subject. Females that visited feeders repeatedly were not marked because they were distinguished using their unique patches of throat feathers (Jones 1993).

To mark male birds, I used a technique developed by T.A. Hurley (personal communication 1999). I wired a 21-gauge needle tip beneath the perch of a feeder with the needle point bent upwards so that it pointed towards the breast of a perching bird. I placed 0.05 mL of xylene-free ink in the needle reservoir and attached the 10-m tube of a photographer's pneumatic shutter release to the mouth of the reservoir. When a bird perched at the feeder, I squeezed the release bulb, spraying ink onto the bird's breast.

I trained birds to feed on inflorescences, rather than the feeder, in a series of steps. Once a bird visited a feeder regularly, I placed five inflorescences with nectar-filled flowers nearby and lowered the feeder to the height of the inflorescences. After the bird had visited inflorescences during several foraging bouts, I removed the feeder so the bird could forage from only the artificial inflorescences. Flowers were replenished with sucrose solution between foraging bouts. After the bird had approximately half a day to become accustomed to the artificial inflorescences and flowers, I allowed it 10 additional trials to learn to forage on the array before experimental trials began. I also allowed each bird 10 learning trials when I changed the inflorescences in an array to a novel type, so

that it was accustomed to that design before I collected observations. I implemented these learning trials because my questions deal with foraging choices for experienced pollinators, rather than the effects of inflorescence architecture on learning.

After a bird had been trained on a specific inflorescence type, I recorded its behaviour during at least five experimental trials. A trial comprised a continuous foraging bout during which the bird visited flowers on at least two inflorescences. I videotaped birds from approximately 5 m with a Sony DCR-TRV900 digital video camera mounted on a tripod. Because the camera shuts off after being idle for 5 min, I occasionally missed the first probe of a trial while turning the camera on again. In addition, while zooming the camera in on a bird at a particular inflorescence or tracking the bird as it foraged, I occasionally missed the first flower visited on an inflorescence.

This sequence of training and experimental trials was repeated for an individual bird with each of the three inflorescence types. The order of presentation of inflorescence types was randomized for each bird. Because three birds stopped returning to the experimental area before they had completed all trials, their observations are incomplete. In particular, one male and one female (sm and sf) were filmed only on racemes and another male (k7) was filmed on racemes and umbels.

To quantify bird behaviour, I viewed the videotape of each experimental trial frame by frame (1/30 s). Each flower on an inflorescence type was numbered so that I could record the bird's foraging path (Fig. 2.1). I numbered panicles and racemes from the bottommost flowers upward and umbels from the outer ring of flowers to the inner ring. The start and finish times of each flower probe were also recorded with flower number to allow me to calculate probe and flight durations. I defined the start of a probe as the first frame in which the bird's bill was within a flower's tube. The time that birds hovered (stationary flight, no vector) was subtracted from a flight time if the period of hovering $\geq 5/30$ s. I used this criterion because hovering substantially increased the flight time between flowers and birds often changed their trajectory after hovering.

When most birds (five males at Kananaskis and one female at Bamfield) had completed foraging trials on pure arrays for all three inflorescence types, I presented them with a 4 X 4 array containing all three inflorescence types. I videotaped each bird for six trials on the choice array. Within this mixed array, a randomly selected inflorescence type was placed in position 1 and each subsequent inflorescence was then placed in a repeating sequence (e.g. panicle, raceme, umbel, panicle, etc.). As a result, no inflorescence was directly adjacent to a like architecture (Fig. 2.2a). Adjacent inflorescences were separated by 50 cm, with umbels placed on top of flowerless racemes rather than on angled conduit so that all inflorescences were the same distance apart. As a result, flowers on umbels were located higher in the array than the average height of flowers on panicles or racemes (Fig. 2.2b).

2.3 Data Analysis

2.3.1 General statistical analysis

Most statistical analyses considered either general linear models (Neter et al. 1996, mixed procedure of SAS, release 8.2, SAS Institute Inc., 1999) or generalized linear models (McCullagh and Nelder 1989, genmod procedure of SAS, release 8.2, SAS Institute Inc., 1999) that reflected the factorial design of the experiment. Because I measured individuals repeatedly, I used either restricted maximum likelihood (general linear models: Jennrich and Schluchter, 1986) or generalized estimating equations (generalized linear models: Liang and Zeger, 1986) to characterize the covariance between responses for the same individual. In almost all cases, a model of compound symmetry was more appropriate than one of independent responses ($P<0.05$). Denominator degrees of freedom for F-tests of the general linear models were calculated by Satterthwaite's approximation (Littell et al. 1996), which resulted in fractional denominator degrees of freedom.

Variables were transformed as necessary to assure that the data conformed to the

Figure 2.2. Design of arrays used to assess preferences by rufous hummingbirds for three types of artificial inflorescences. Panel a presents a top-down view of one possible arrangement of panicles (P), racemes (R), and umbels (U). Panel b depicts the relative heights of flowers for all three inflorescence types.

a)

U	P	R	U
P	R	U	P
R	U	P	R
U	P	R	U

b)

Raceme	Panicle	Umbel
		all flowers
	11 12	
10 11 12	9 10	
	8	
7 8 9	6 7	
	2 4 5	
4 5 6	1 3	
1 2 3		

Inflorescence type

requirements of the statistical analysis. Analyses of generalized linear models involved logit transformation for proportions (binomial distribution) and ln-transformation for count data (Poisson distribution). For ease of interpretation, I present results from these analysis using back-transformed means and estimates of reliability. This procedure results in asymmetrical standard errors and confidence intervals.

The independent variables differed among analyses, depending on the hypothesis being tested. All analyses considered a bird's sex as a categorical factor, except analyses of the preference experiment, which involved only one female bird. In addition, analyses comparing birds' responses to different inflorescence types considered type and its interaction with sex as categorical factors. Some analyses also assessed the effects of continuous covariates. Such analyses first considered all covariates and their interactions. If terms did not explain a significant proportion of the variation in the dependent variable by themselves and they were not involved in a more complicated, significant interaction (α=0.05), they were excluded from a model by stepwise, backward elimination. However, the interaction between sex and inflorescence type was always retained in a model to reflect the experimental design. I analyzed significant differences between main effects with Tukey's multiple comparisons (Kirk 1995). To interpret significant interactions, I used a posteriori Dunn-Šidák contrasts (Kirk 1995).

I will not discuss two types of significant effects, as they reflect sampling intensity, rather than biological differences. These cases involve the effect of a bird's sex for analyses involving counts (e.g., number of flowers visited) and the effect of array for analyses comparing pure and mixed arrays, when these effects are not involved in a significant interaction with another effect.

My analyses of the frequencies of birds' arrivals to and departures from inflorescences considered groups of flowers (whorls for racemes, branches for panicles, and rings for umbels). These analyses compared frequencies both between groups and with respect to expectations based on the proportions of flowers within each group (1/4

for each whorl on racemes; 1/3, 1/4, 1/4, 1/6, for the bottom through top branches on panicles; and 3/4 and 1/3 for the inner and outer rings on umbels). When presenting the comparisons to these expectations, I provide 95% confidence intervals, which should include the expectation if the observed mean does not differ significantly.

When I considered flight and probe duration in my analyses, I removed trials where birds visited flowers containing 5 μL of nectar. The volume of nectar affected visit duration and I used probe duration as a covariate in flight duration analyses. When I assessed the flight duration of hummingbirds between inflorescences, I considered only flights between adjacent inflorescences because other distances comprised only 3% of flights in pure arrays.

2.3.2 Analysis of preference experiment

I used two approaches to assess whether hummingbirds visited particular inflorescence types preferentially when confronted by a mixed array of racemes, panicles and umbels. The first approach used maximum likelihood analysis (Burnham and Anderson 2002) to contrast five alternate hypotheses for the observed proportions of visits to each inflorescence type. For a given hypothesis, the expected probability that a bird would visit an inflorescence of type i during visit v equals

$$p_{vi} = \frac{w_i n_{vi}}{w_u n_{vu} + w_r n_{vr} + w_p n_{vp}},$$

where: w_i is the bird's hypothetical relative preference for type i, and n_i is the number of unvisited inflorescences of type i immediately adjacent to the bird's current position in the array ($i = p$ for panicles, $i = r$ for racemes, and $i = u$ for umbels). The hypotheses differed in the relative preference of birds for the three inflorescence types, w_i (Table 2.1). For example, the hypothesis of random movement is represent by $w_i = 1$ for all inflorescence types. Given the birds' observed choices ($o_{vi} = 0$ if type i was not visited, $o_{vi} = 1$ if type i was visited), the likelihood of a particular hypothesis is

Table 2.1. Relative preference of hummingbirds for umbels, racemes and panicles in mixed arrays specified for five alternate hypotheses. Free parameters were estimated by maximum likelihood.

Model	Inflorescence type			Number of parameters estimated
	Umbel	Raceme	Panicle	
A = Random movement	1	1	1	0
B	1	1	free	1
C	free	1	1	1
D	1	free	1	1
E	1	free	free	2

$$LL\left(w_u, w_r, w_p \mid o\right) = \sum_{v=1}^{V} \ln\left[p_{vu}o_{vu} + p_{vr}o_{vr} + p_{vp}o_{vp}\right].$$

For each hypothesis, I used numerical techniques, which varied any free parameters to find the maximum log-likelihood. The results for alternate models were compared to that for random movement using Akaike's information criterion (Burnham and Anderson 2002). I also used replicated goodness-of-fit tests (Sokal and Rohlf 1995) to examine the homogeneity of inflorescence choice among trials for a bird, among trials for all birds, and among birds.

The second approach explicitly considered whether hummingbirds moved among inflorescences in mixed arrays in a manner that maximized their rate of net energy intake (RNEI). This rate is given by

$$\text{RNEI} = \frac{ne\rho SV - M_s\left(c_i T_i + c_b T_b\right)}{\left(T_i + T_b\right)} \tag{2.1}$$

where: n is the number of flowers visited on an inflorescence; e is the energy content of 1 mg of sucrose (16.5 J); ρ is the density of nectar (1.945 mg/μl); S is the nectar concentration (20%); V is the volume of nectar (4 or 5 μl); M_s is the average bird's mass depending on its sex (males, 3.34 g; females, 3.58 g: Calder 1993); c_i and c_b are the mass-specific rates of energy expended while flying within (hovering: 0.25 J g^{-1} s^{-1}: Wolf et al. 1975) and between inflorescences (forward flight: 0.21 J g^{-1} s^{-1}: Wolf et al. 1975); and T_i and T_b are the within and between inflorescence flight durations, respectively. Within-inflorescence flight duration is the sum of flights between flowers and the probe durations on flowers. My analysis of foraging energetics contrasted a bird's realized rate of net energy intake with the rate that it could have achieved had it moved to the most rewarding inflorescence among the neighboring inflorescences in a mixed array. When calculating a bird's realized rate of net energy intake, I used values specific to each visit: the number of flowers visited, the total time on the inflorescence and the duration of the flight to the inflorescence. If the duration of the approach flight was missing, I used the

average flight time between inflorescences calculated for that bird based on flights between adjacent inflorescences. For each hummingbird, I also estimated its average (expected) rate of net energy intake for each inflorescence type. This calculation was based on eq. 2.1 with the bird's average within- and between-inflorescence flight durations and the average number of flowers visited.

When calculating both average and realized rates of net energy intake, I calculated the energetic cost of visiting an inflorescence as though birds hovered constantly. On umbels, birds hovered throughout their visit, whether probing a flower or moving between flowers. However, on panicles and racemes, flight costs may have been less, because birds used forward flight, rather than hovering to move between some flowers. To investigate the extent to which such variation in flight costs affected foraging energetics, I reduced the cost of foraging within an inflorescence for panicles and racemes by dividing the duration of within-inflorescence flight into probe (hovering) and forward flight duration. I calculated the average probe duration for each bird on an architecture using pure arrays and then subtracted the total averaged times spent probing flowers from the inflorescence visit duration. This modification had minimal effect on rate of net energy intake, so I did not investigate it further.

I examined situations in which birds flew to an inflorescence with a lower average RNEI than they could have achieved by visiting an inflorescence type from three perspectives. First, I considered whether such "incorrect" decisions represented a reaction to poor energetic return on the preceding inflorescence. In each case, I categorized the bird's rate of net energy intake on the preceding inflorescence as either falling below the average return on that inflorescence type, or equaling or exceeding the average. I then used a chi-square test to assess whether these contrasting outcomes occurred with equal frequency. The second test compared whether birds' realized rates of net energy intake on the chosen inflorescence exceeded their average rate for that inflorescence type, again using a chi-square test for equal proportions. The third test

assessed whether birds' realized rates of net energy intake on the chosen inflorescence exceeded their average (expected) rate for the best option among the available neighbouring unvisited inflorescences.

3 RESULTS

3.1 Movements within and between racemes

3.1.1 Arrivals and departures

When hummingbirds foraged on racemes, the position of their arrivals to an inflorescence generally differed from that of their departures. Birds arrived at the four whorls within racemes with equal frequency ($F_{3, 40} = 0.63$, $P>0.5$; Fig. 3.1a). Because each whorl presented three flowers, this equal distribution of arrivals did not deviate from the pattern expected based on the number of flowers per whorl (Fig. 3.1a). Overall, the arrival patterns of female and male hummingbirds did not differ significantly (sex x whorl interaction, $F_{3, 40} = 0.07$, $P>0.75$).

In contrast to the above, birds departed from whorls unequally ($F_{3, 15.7} = 46.27$, $P<0.001$), leaving from the bottom or top whorls three to four times more frequently than from either of the middle two whorls (Fig. 3.1b). Departures from whorls at each position differed from expectation based on the distribution of flowers among whorls, except for departures from the bottom whorl (Fig. 3.1b). Specifically, birds departed racemes more often than expected from the top whorl and less than expected from the middle two whorls. In addition to this general pattern, female and male hummingbirds departed racemes somewhat differently (sex x whorl interaction, $F_{3, 15.7} = 3.43$, $P<0.05$), with females departing from the middle two whorls in different proportions, whereas males departed from these whorls with equal frequency.

Because hummingbirds often departed from the top whorl, they typically moved to the equivalent or a lower whorl on the next raceme ($F_{2, 30} = 7.54$, $P<0.005$; Fig. 3.2). However, they were less likely to fly upwards to higher whorls than laterally when departing from the bottom whorl. Overall, birds moved either laterally or down twice as often as upward.

Figure 3.1. The distribution of arrivals and departures by rufous hummingbirds among the four whorls of flowers on artificial racemes. Panel a depicts the average (± 95% CI) proportions of arrivals to each whorl, whereas panel b illustrates the mean (± 95% CI) proportion of departures from each whorl. The dotted lines represent the proportions of arrivals and departures expected at each whorl based on the equal distribution of flowers among whorls.

a)

b)
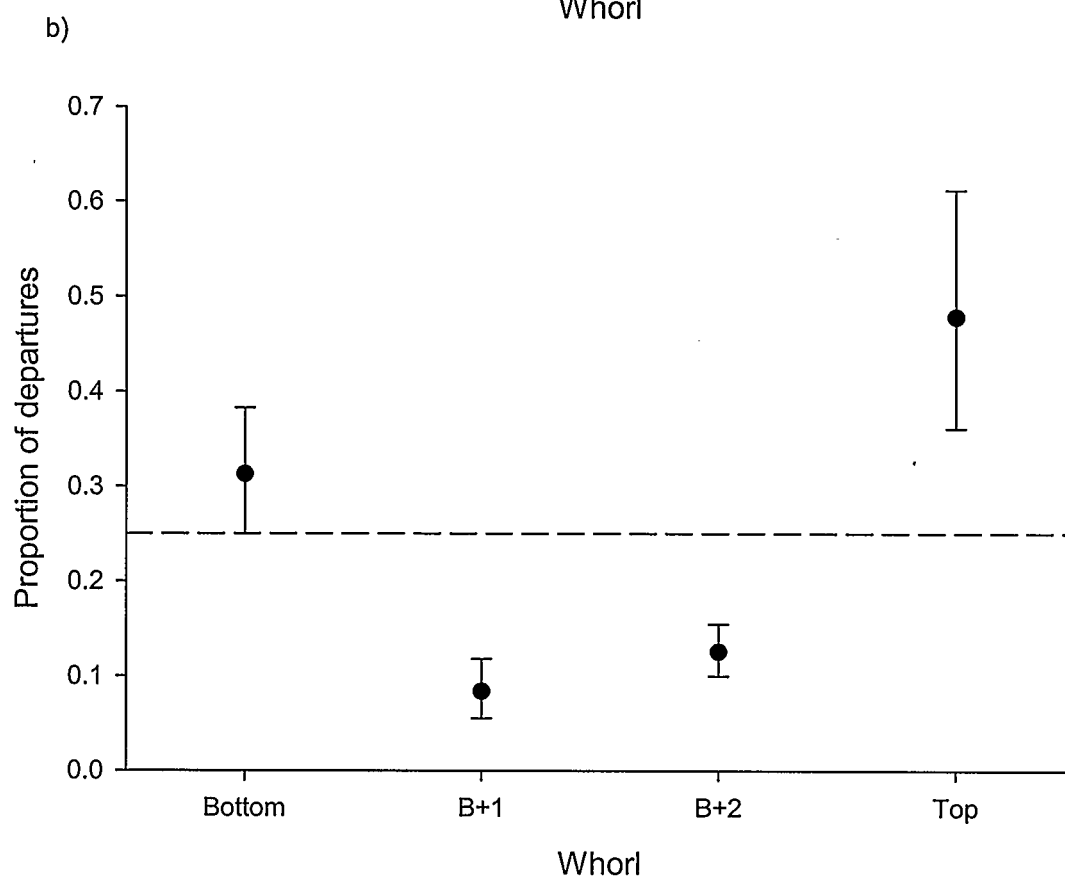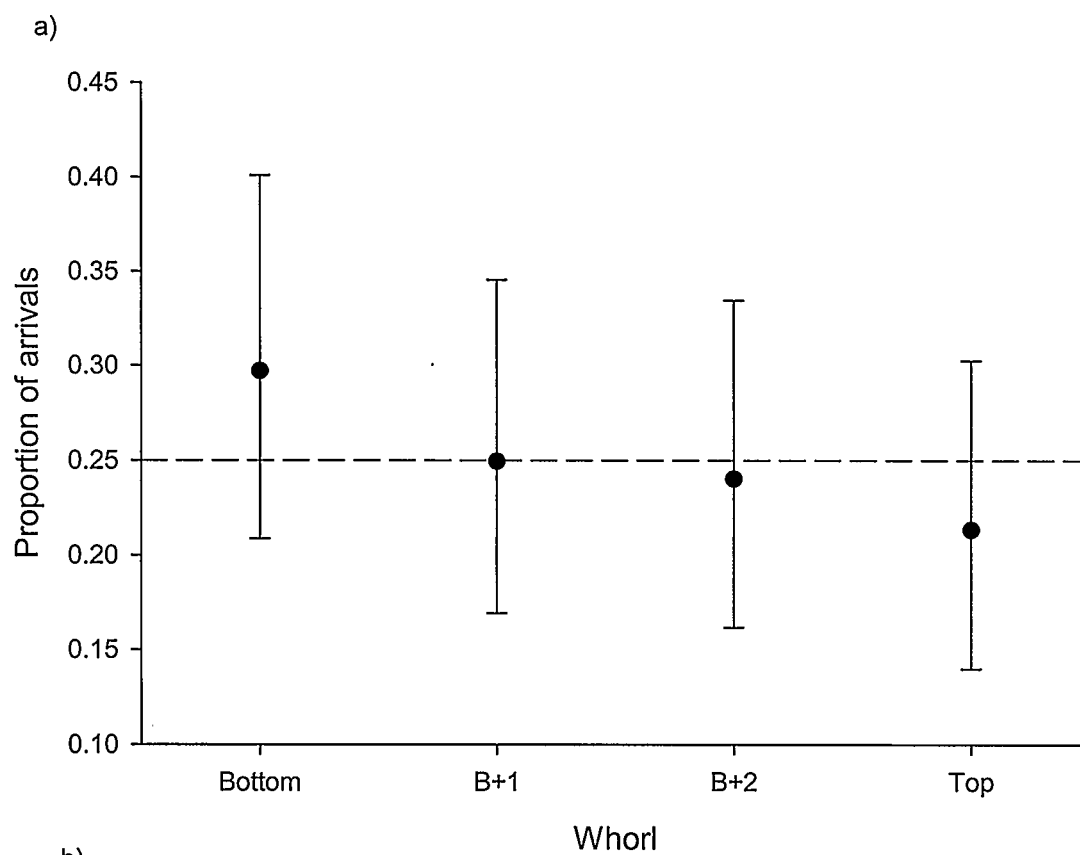
Figure 3.2. The average (± SE) proportions of movements by rufous hummingbirds to a lower, equivalent or higher whorl on the next raceme visited.
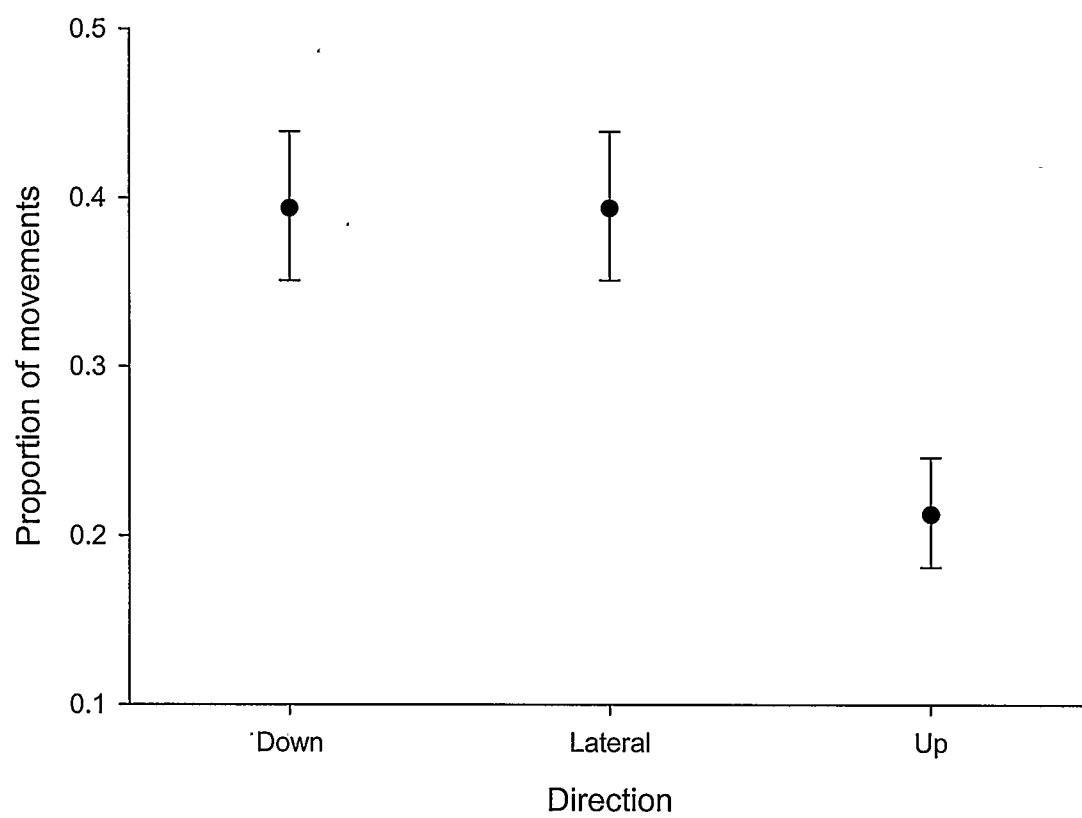
3.1.2 Within raceme movements

Movements by hummingbirds among flowers within racemes (Fig. 3.3) reflected both their tendency to limit movement distance and the flower spacing within and between whorls. During 96% of flights within racemes, hummingbirds moved between adjacent flowers (Fig. 3.4). Because of the design of these racemes, flowers on adjacent whorls were closer to each other (66 mm) than were neighbouring flowers on the same whorl (86.2 mm). In response, birds frequently moved between adjacent whorls (Fig. 3.3), often in a zigzag pattern. On the two internal whorls, in particular, <5% of a bird's movements kept it on the same whorl. In contrast, on the top or bottom whorl, the chance of lateral movement increased to about 15%. As a result, birds flew either up or down between flowers far more frequently than laterally ($F_{2, 16.8}$ = 119.37, $P<0.001$; Fig. 3.5a), with no difference between the sexes (sex x direction interaction, $F_{2, 16.8}$ = 2.39, $P>0.1$). Because of this tendency for both upward and downward movement, whether a bird had arrived at the top or bottom whorl of a raceme did not influence the whorl from which it departed ($F_{1, 49.8}$ = 0.30, $P>0.75$). In fact, if a bird arrived at the bottom or top whorl, it departed from that whorl 36 or 34% of the time, respectively.

The mean durations of flights between nearest flowers within a whorl and between adjacent whorls depended on both a bird's sex and its direction (and distance) of movement (sex x direction interaction, $F_{2, 20}$ = 5.82, $P<0.025$; Fig. 3.5b). Both males and females flew downwards between whorls faster than upwards, even though the distance was identical. Males flew between whorls more quickly than laterally between flowers on the same whorl, whereas for females the durations of lateral and upward flights were equal. Females and males did not differ in mean flight duration within a direction.

Figure 3.3. The proportions of flights by rufous hummingbirds from individual flowers to other flowers within artificial racemes. Numbered circles represent flowers (see Fig. 2.1). Flowers represented by solid circles and transitions depicted by solid arrows represent the side of the raceme closest to the observer, whereas dashed circles and transitions are at the back of the raceme. Only transition probabilities >0.1 are presented and transitions among back flowers are omitted for clarity. Brackets at the right identify whorls on the raceme.

33
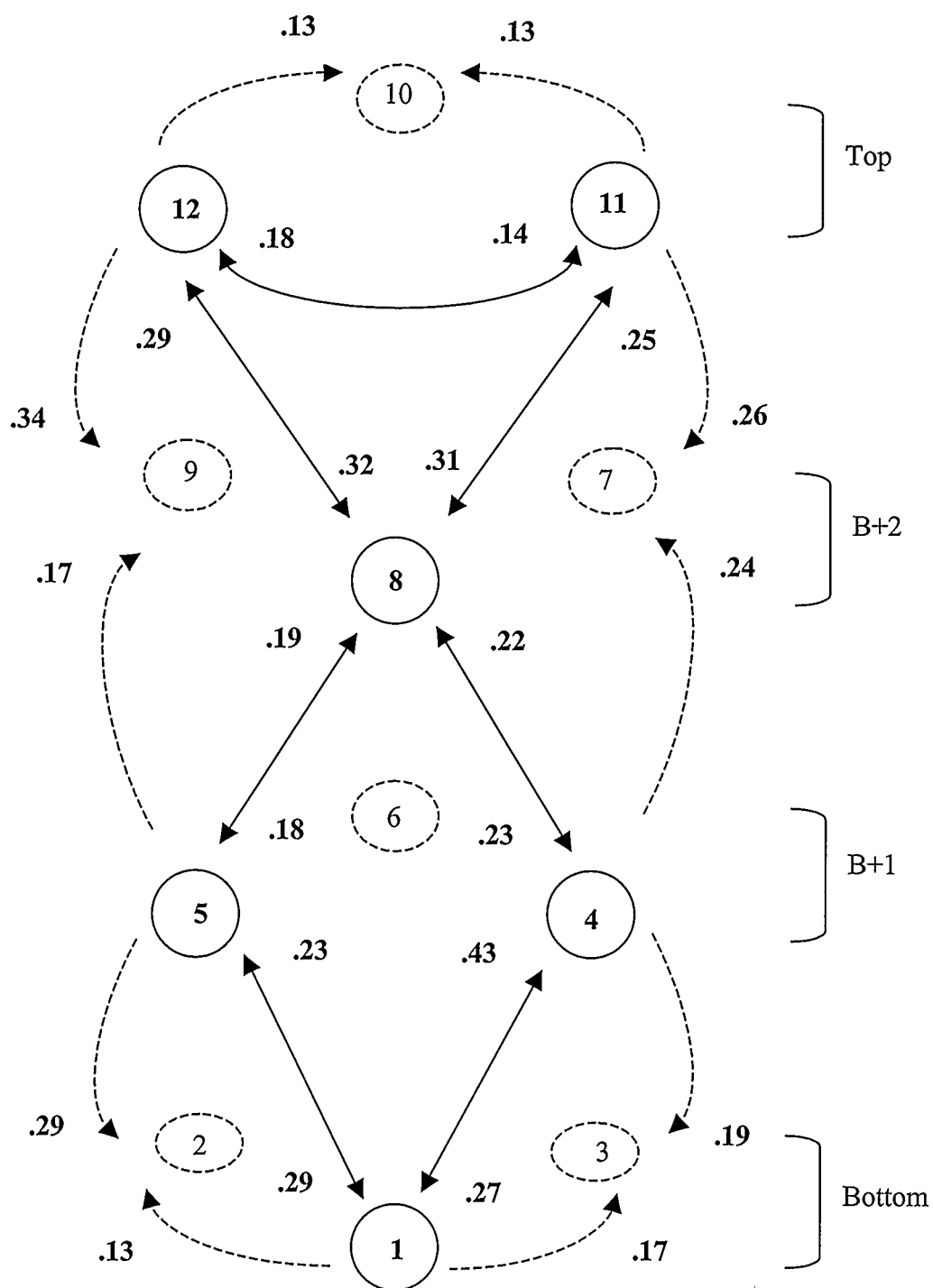
Figure 3.4. The mean (± SE) percentage of flights between flowers for each possible distance within racemes.
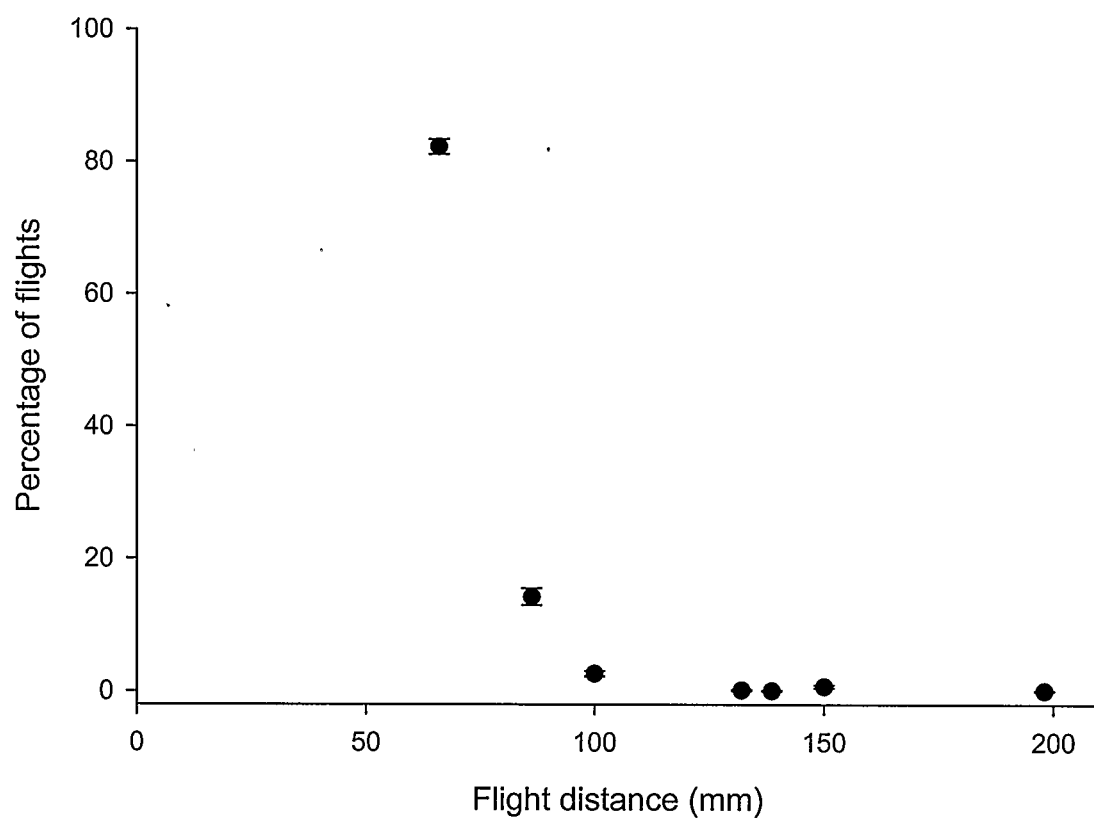
Figure 3.5. Mean (± SE) characteristics of movements within artificial racemes by rufous hummingbirds, including a) the proportions of movements up, down, and laterally by all birds, and b) the duration of movements by females (●) and males (△). Letters in panel b indicate the outcomes of Dunn-Šidák multiple comparisons among whorls for each sex, with capital letters for females and lower-case letters for males (based on ln-transformed data).

a)

b)
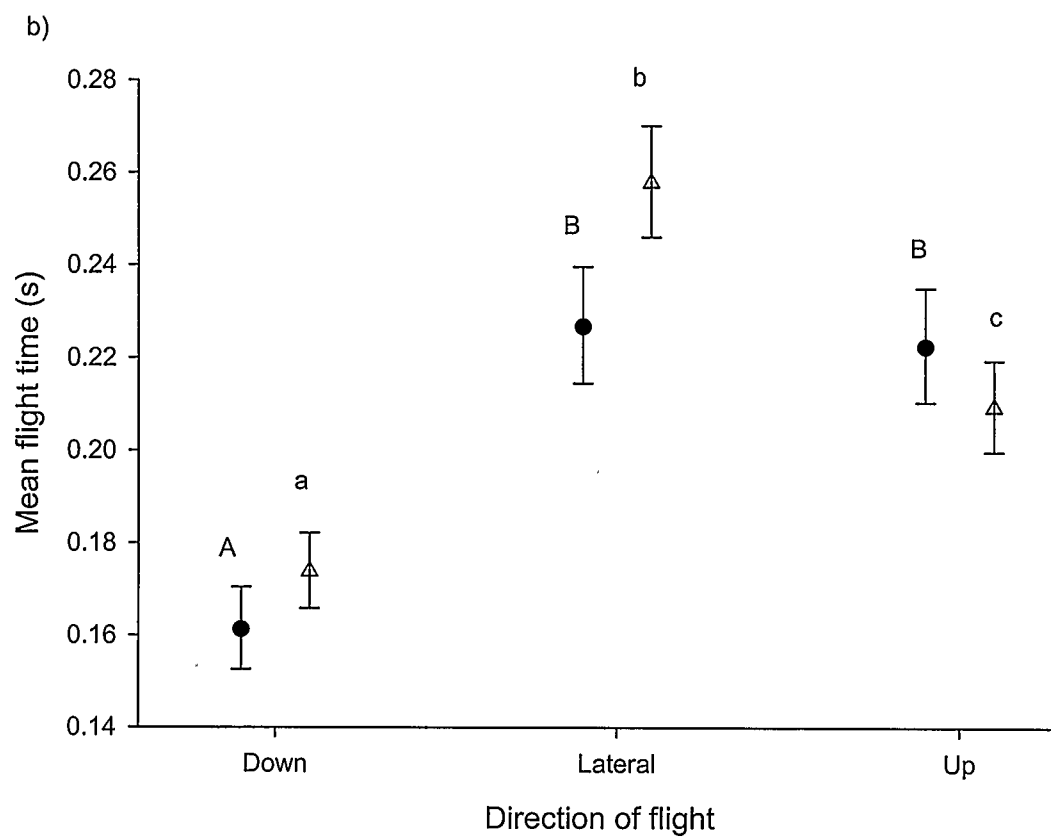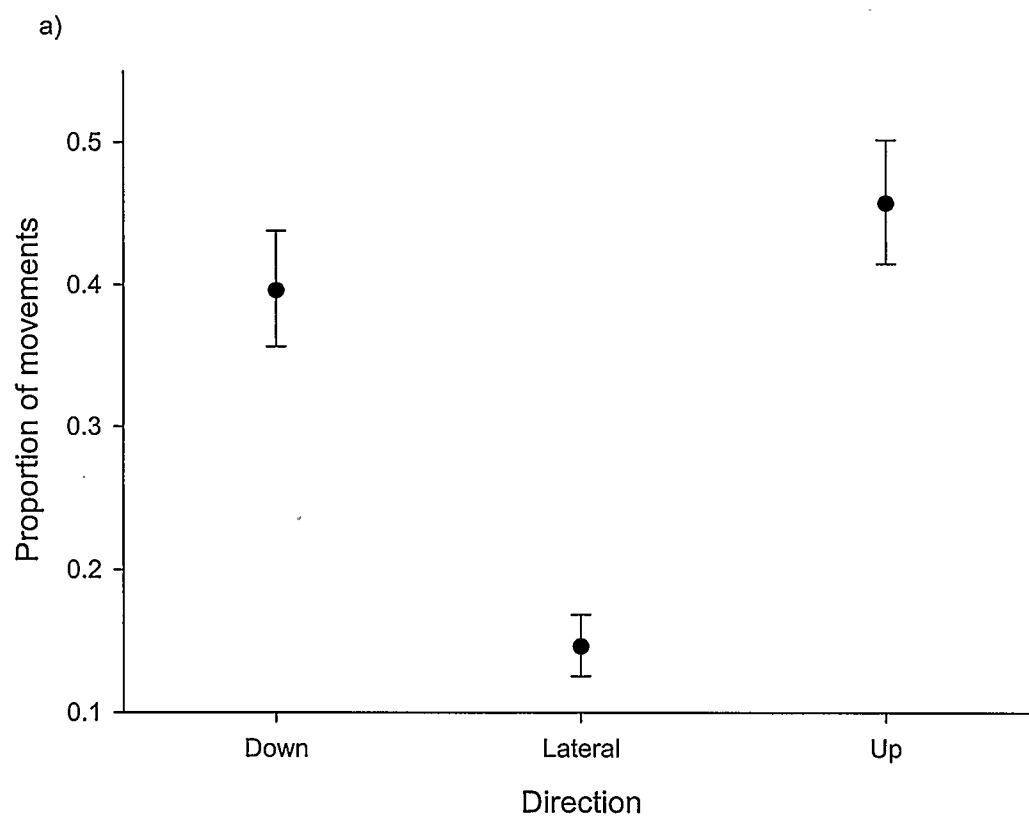
3.2 Movements within and between panicles

3.2.1 Arrivals and departures

Unlike their relatively unstructured movement patterns while traveling between racemes, hummingbirds arrived and departed somewhat more systematically while feeding on artificial panicles. About 50% of arrivals at panicles involved the four flowers at the tips of the bottom two branches, with the remaining arrivals being distributed equally among the remaining eight flowers ($F_{11, 54.9} = 2.29$, $P<0.025$; Fig. 3.6a). As a result, birds arrived at the lower two branches, especially branch B+1, significantly more often than at the upper two branches ($F_{1, 27} = 9.57$, $P<0.005$; Fig. 3.6b). The greater frequency of arrivals at lower branches may partly reflect their greater numbers of flowers. However, birds arrived at branch B+1 slightly more often than expected based on flower density, whereas they arrived at branch B+2 somewhat less often than expected (Fig. 3.6b).

In contrast to their arrival position, hummingbirds tended to leave panicles from the top (flower position, $F_{11, 58.9} = 7.89$, $P<0.001$; branch position, $F_{3, 19.2} = 4.11$, $P<0.025$: Fig. 3.7). The uppermost flower (flower 12) served as the departure point for almost 20% of birds' transitions between panicles (Fig. 3.7a), which was almost twice the frequency of departures from any other flower ($F_{1, 57.4} = 65.18$, $P<0.001$). Overall, birds left from the top branch more often than expected based on flower density, whereas they left from the bottom branch much less often than expected (Fig. 3.7b). The most obvious exception from the tendency to leave panicles from upper flowers involved flower 8, the basal flower on branch B+2 (Fig. 3.7a). Birds departing from other basal flowers (flowers 1, 3 and 5) left with the same frequency as distal flowers ($F_{1, 60.5} = 6.48$, $P>0.05$).

Not surprisingly given the preceding results, hummingbirds tended to descend to a branch on the next inflorescence lower than the branch from which they had departed while moving between panicles ($F_{2, 20} = 57.42$, $P<0.001$; Fig. 3.8). Overall, downward

Figure 3.6. The distribution of arrivals to artificial panicles by rufous hummingbirds. Panel a depicts the average (± SE) proportion of arrivals by birds at each flower position. Flower positions connected by a line are located on a common branch on the panicle, with flowers ordered from basal to distal within a branch. Open squares represent the outer flowers on the two lower branches. Panel b illustrates the mean (± 95% CI) proportion of arrivals to each branch. The dotted lines represent the proportion of arrivals expected at each branch based on the number of flowers available at a branch.

a)

b)
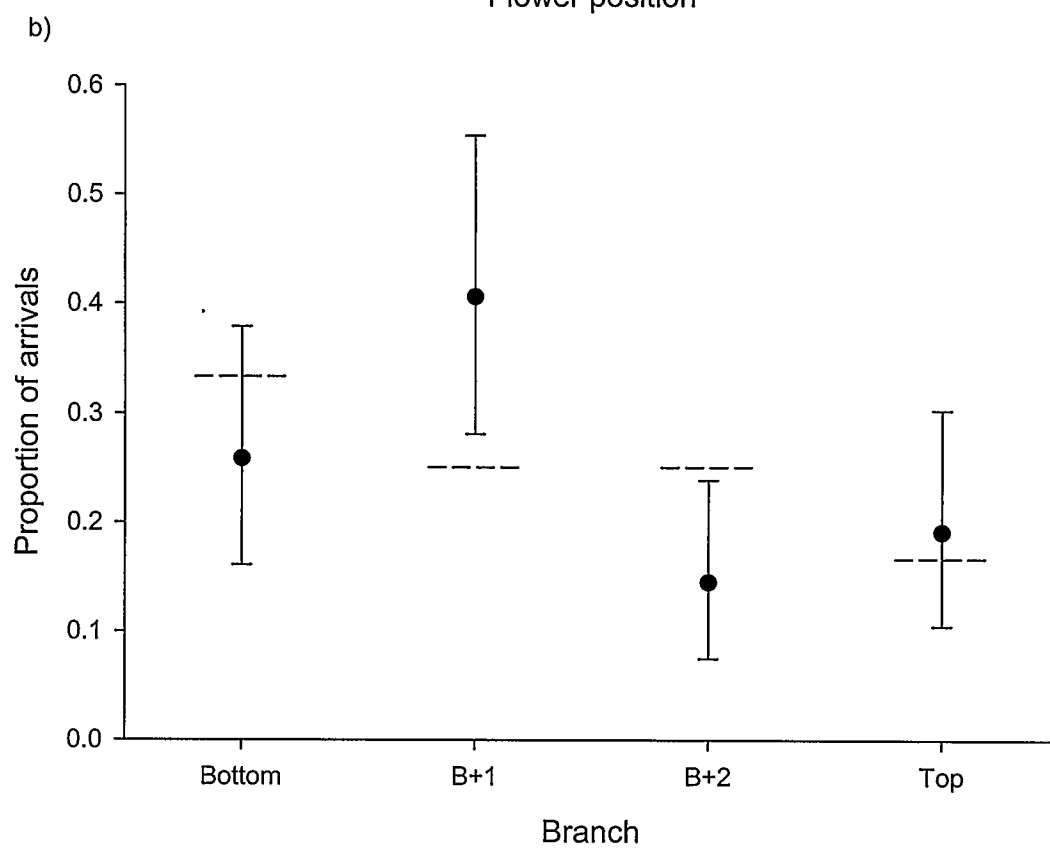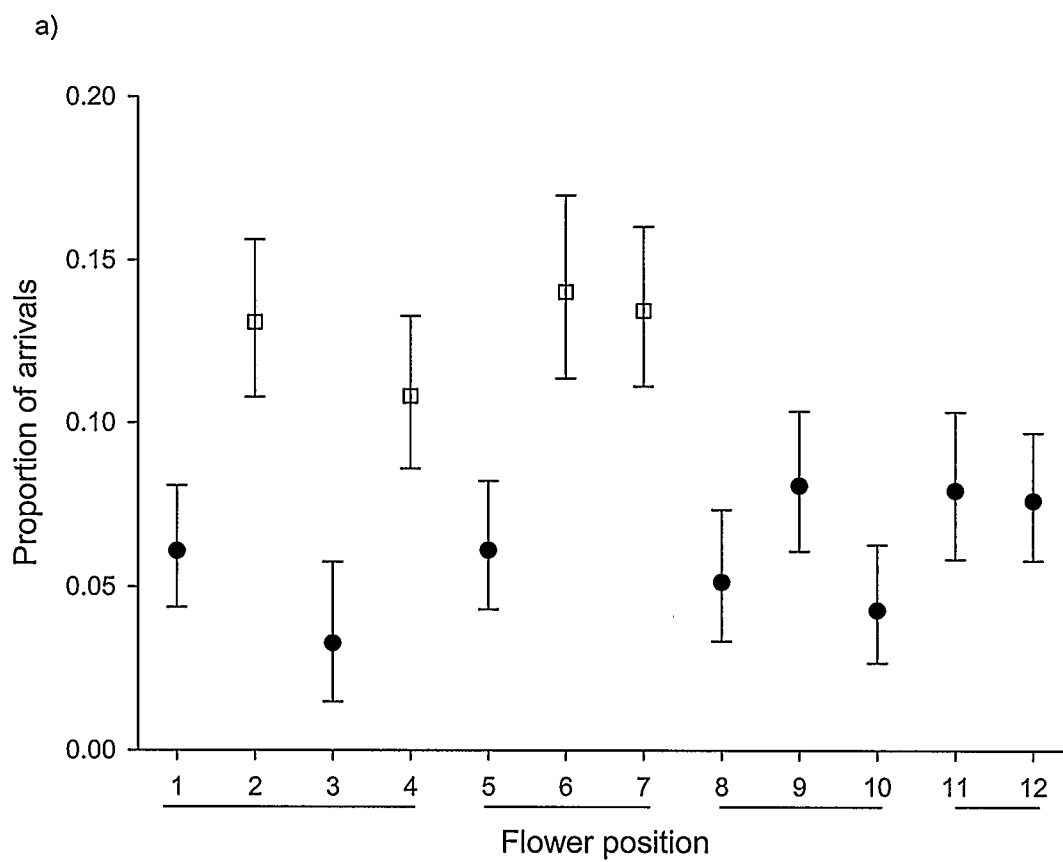
Figure 3.7. The distribution of departures from artificial panicles by rufous

hummingbirds. Panel a depicts the average (± SE) proportion of departures by birds at

each flower position. Flower positions connected by a line are located on a common

branch on the panicle, with flowers ordered from basal to distal within a branch. Open

squares represent the basal flowers on branches. Panel b illustrates the mean (± 95% CI)

proportion of departures from each branch. The dotted lines represent the expected

proportion of departures from each branch based on the number of flowers available at a

branch.

a)

b)
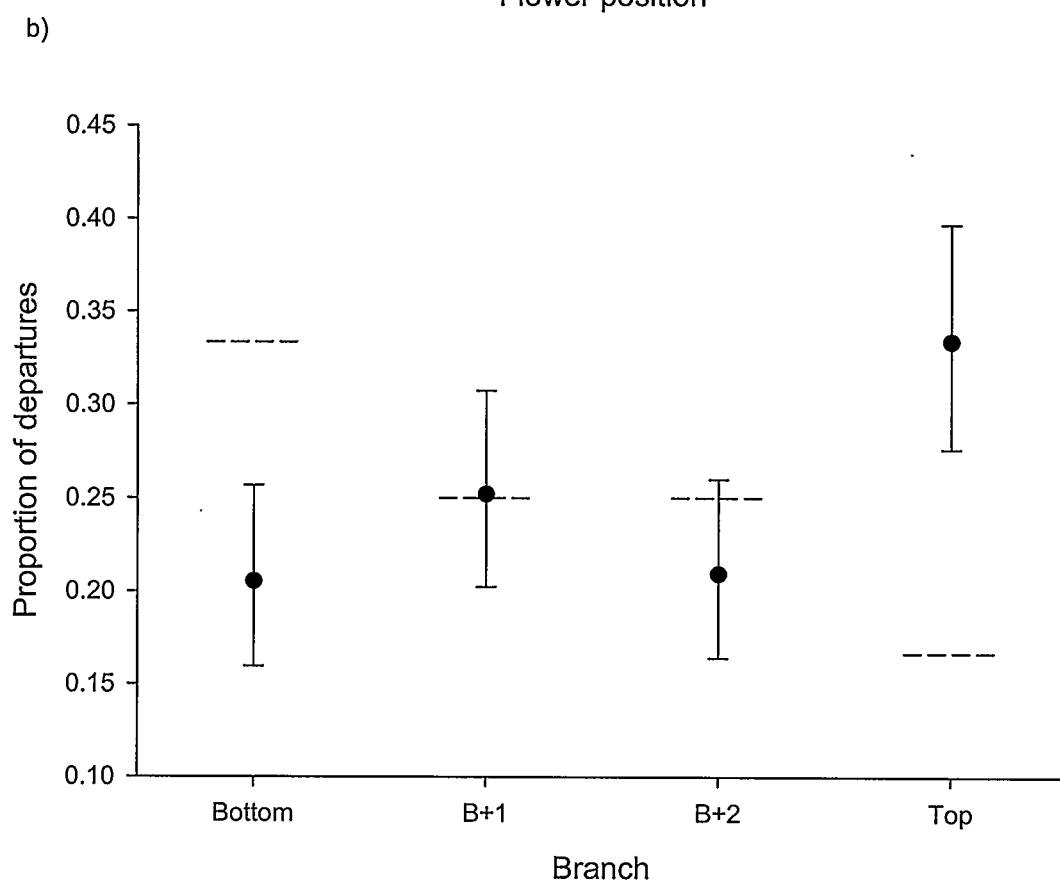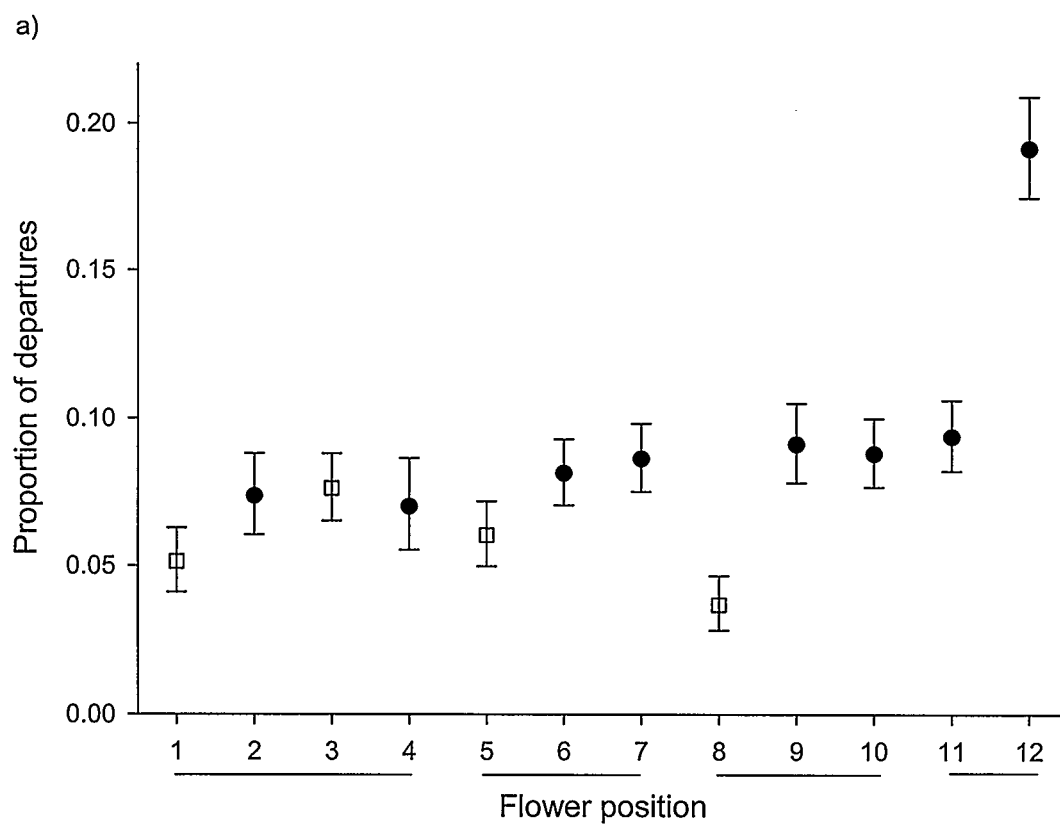
Figure 3.8. The mean (± SE) proportions of movements to a lower, equivalent or higher branch on the next panicle visited by female (●) and male (△) rufous hummingbirds.
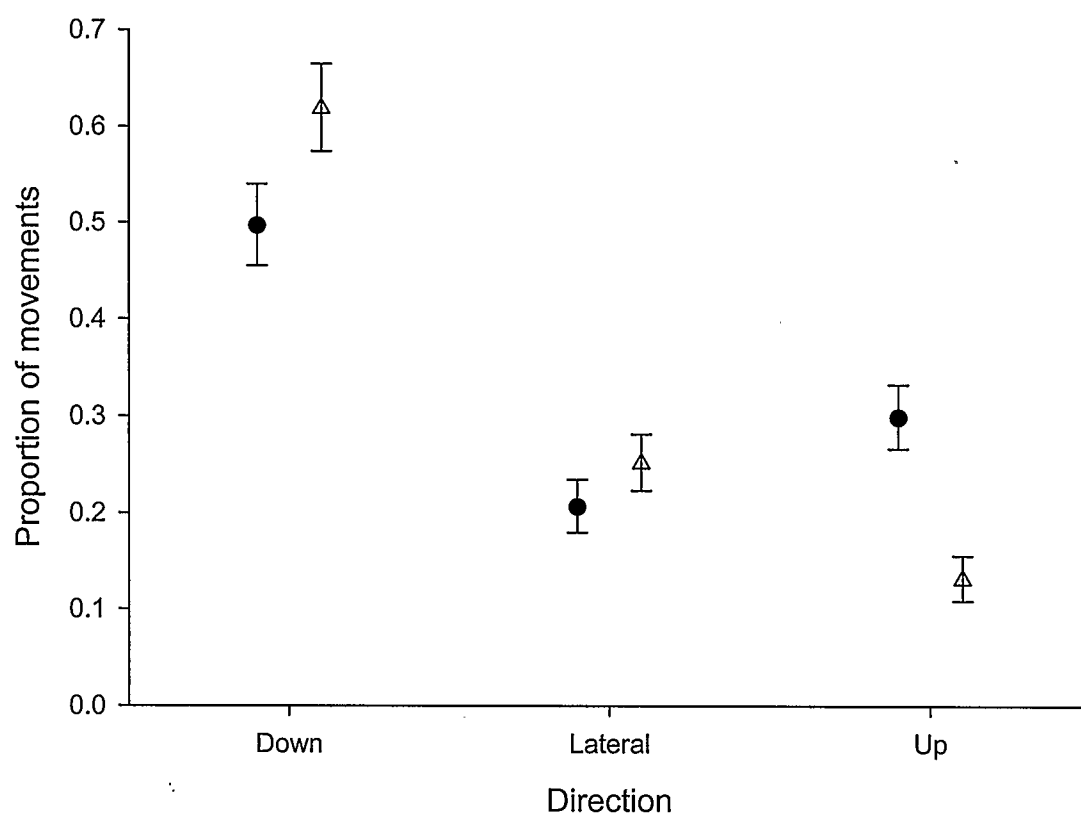
transitions occurred twice as frequently as movements to the same or a higher branch on the next panicle. Female and male birds differed somewhat in their movement between panicles (sex × direction interaction, $F_{2, 20} = 10.03$, $P<0.001$), as females moved up or laterally with equivalent frequency, whereas males moved upwards less frequently than laterally.

3.2.2 Within panicle movements

Hummingbirds exhibited considerable consistency in their movement patterns within panicles (Fig. 3.9). Birds tended to move systematically to the closest adjacent flower, especially within the lower and upper pairs of branches. As birds foraged along a branch, they never crossed over the branch to access the nearest flower on the other side (Fig. 3.9). Instead, they flew around the tip of the branch. Thus, hummingbirds visited panicles as a series of edges.

While foraging on panicles, birds adopted three recurring routes (Fig. 3.10a): route a took birds along the side of the lower two branches that presented a total of four flowers; route b involved the two flowers on the opposite side of the bottom branch and the nearest flowers on the upper two branches; and route c involved the opposite side of branch B+1 and the nearest flowers on the upper two branches. In total, almost 70% of all movements within panicles involved these three routes, with transitions between routes occurring much less frequently ($F_{6, 41.1} = 260.35$, $P<0.001$; Fig. 3.10b). As a result of birds following these three routes, nearly 40% of all flights involved adjacent flowers on the same branch (4 possible combinations of flowers; mean labeled a in Fig. 3.11). An additional 15% of flights took birds around the tip of a branch (4 possible combinations, e.g. from flower 2 to 4: Fig. 3.11, point b) as they moved from one route to another. Thus, birds typically moved laterally within panicles (along the branch or around the tip), rather than up or down between branches ($F_{2, 14} = 86.33$, $P<0.001$; Fig. 3.12). However, both routes b and c include transitions between the lower and upper pairs of branches,

Figure 3.9. Proportions of flights by rufous hummingbirds between flowers within artificial panicles. The upper diagram represents transitions among flowers on the upper two branches, viewed from above, and the lower diagram depicts the lower two branches. Flowers are represented by numbered circles (see Fig. 2.1). Transitions between flowers depicted by dashed lines indicate movements to a flower on the lower or higher pair of branches. Only transition probabilities >0.15 are presented for clarity.

Branches: B+2 & Top

Branches: Bottom
& B+1
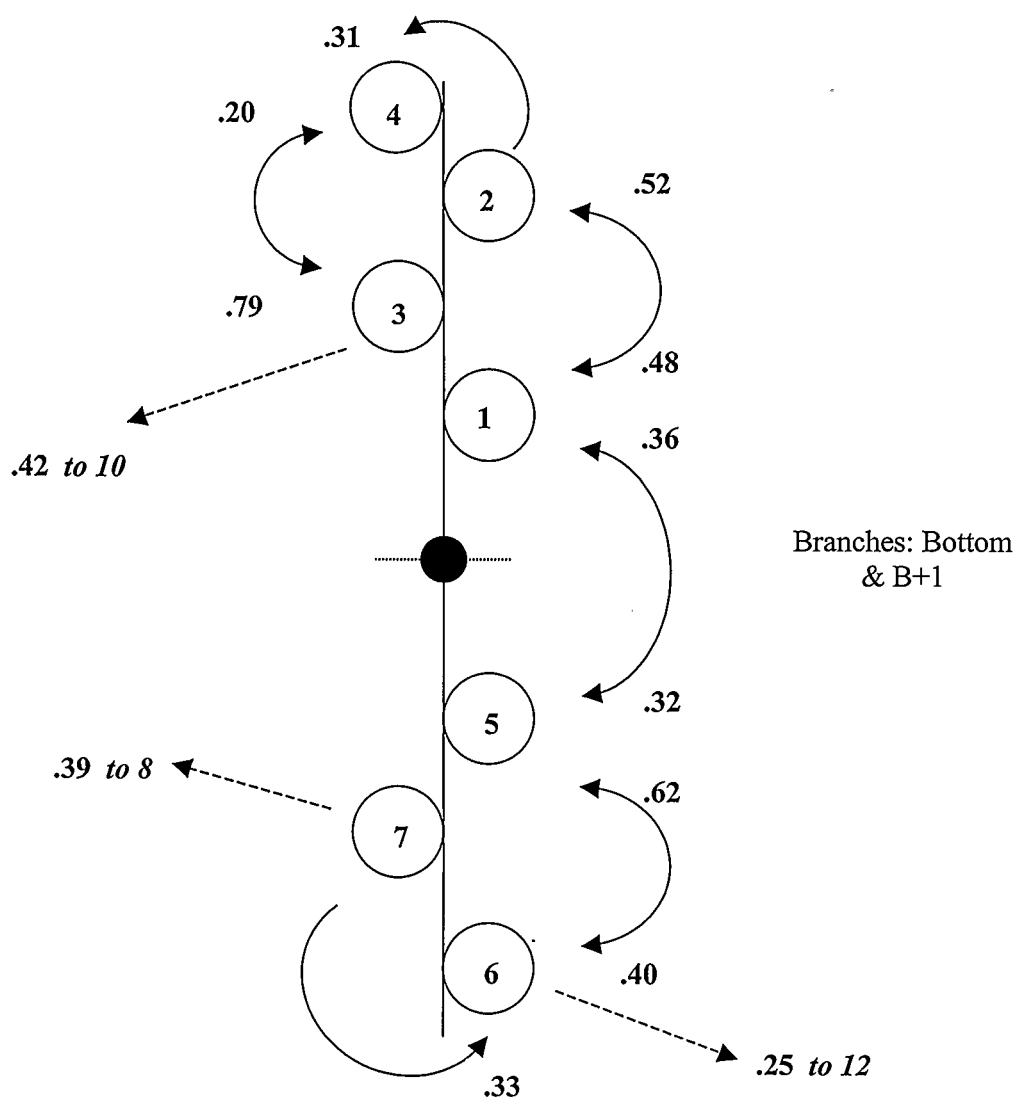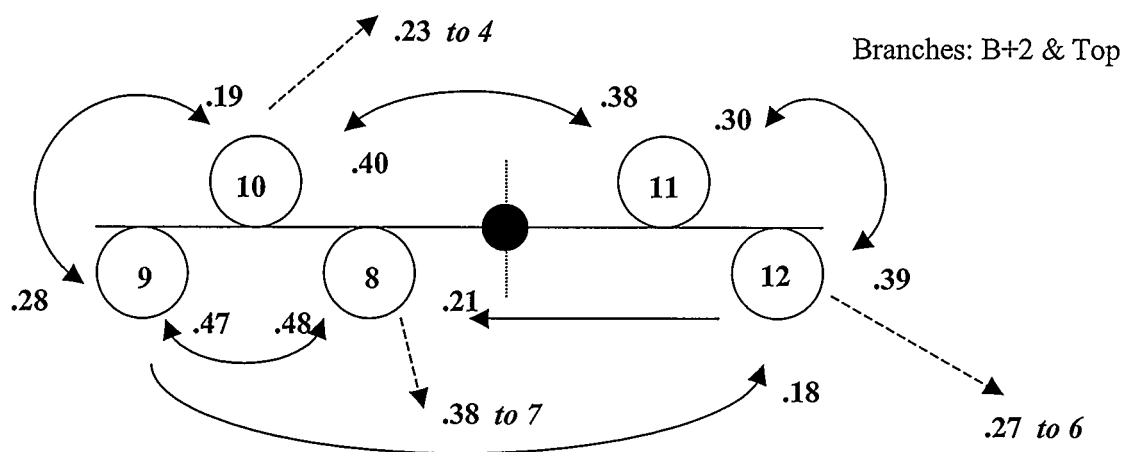
Figure 3.10. Recurring routes used by rufous hummingbirds while foraging on artificial panicles. Panel a illustrates the three routes (a – dashed line, b – dash-dotted line, and c – dotted line) along the four panicle branches, as viewed from above. Numbered circles represent flowers (see Fig 2.1). Panel b depicts the average (± SE) proportion of movements between or within routes.

a)
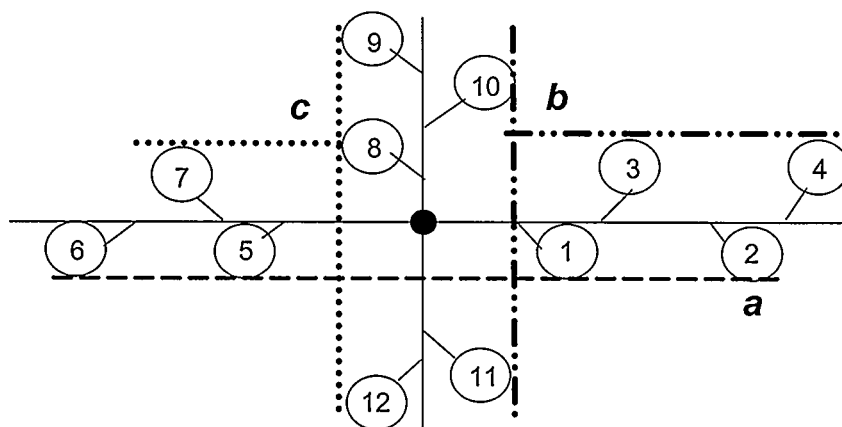
b)
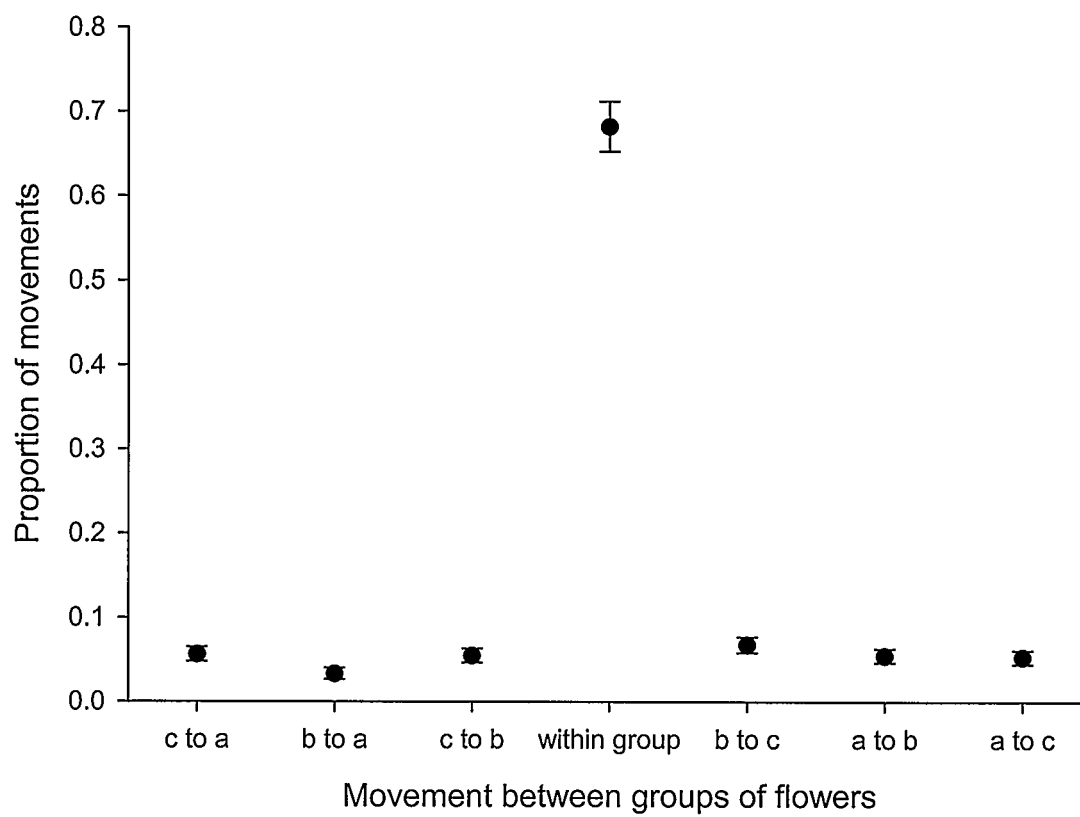
Figure 3.11. The relation of the mean (± SE) percentage of flights by rufous hummingbirds to the distances between flowers within artificial panicles. Birds never moved across a branch to access a flower on the other side, so these transitions have been excluded. Except for a and b, all points represent the distance between single pairs of flowers.
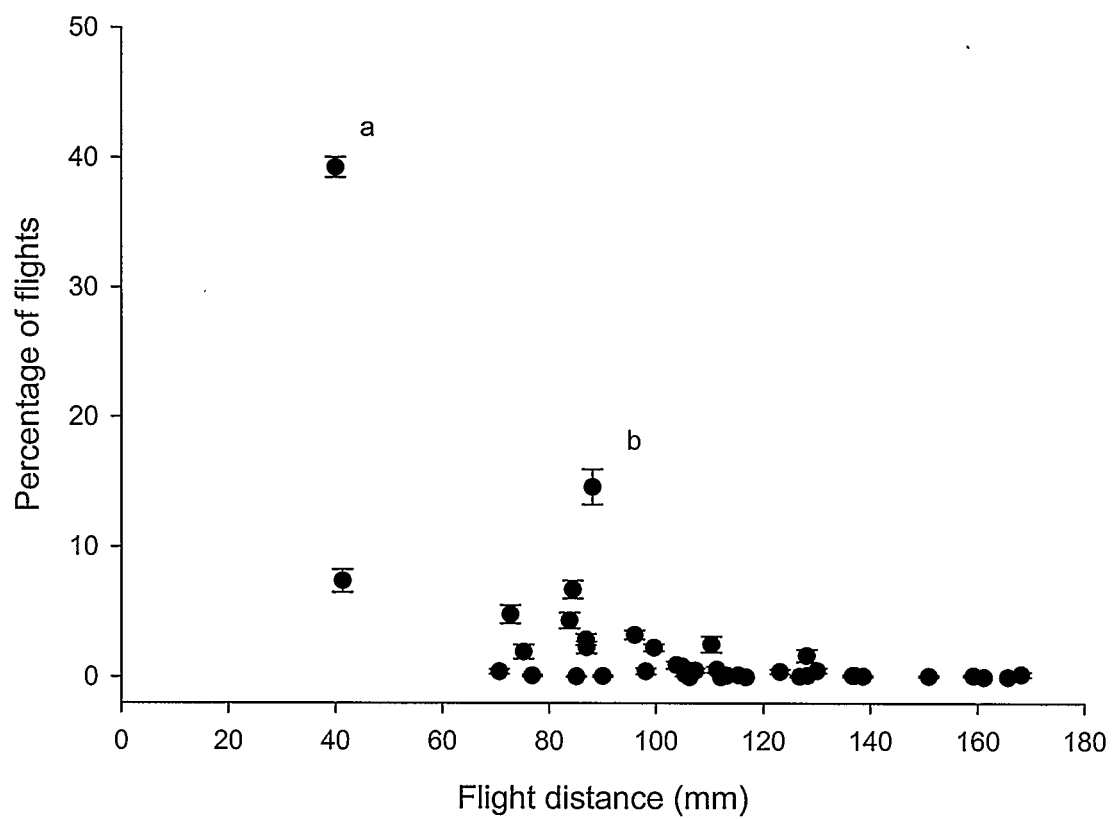
Figure 3.12. The average (± SE) proportions of up, down, and lateral movements within artificial panicles by rufous hummingbirds.
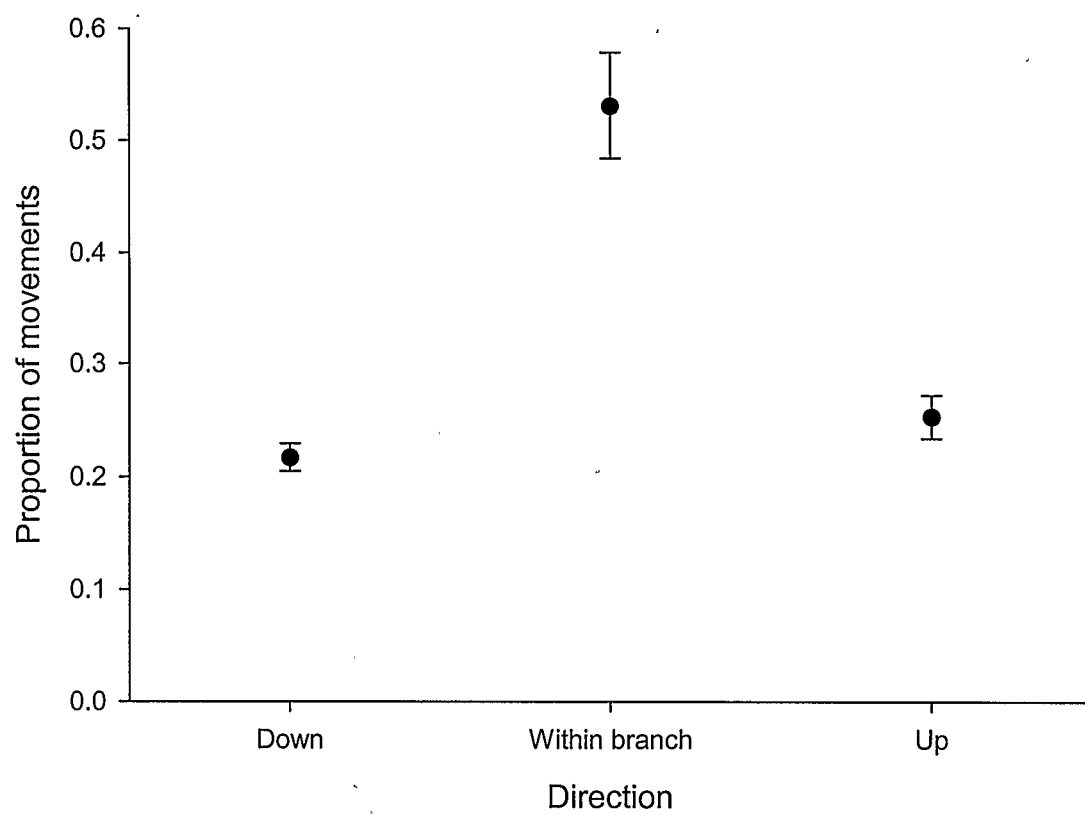
and movements up and down at these locations occurred with equal frequency (Fig. 3.12). Hummingbirds exhibited some preferential directionality while moving between specific pairs of flowers on panicles (Fig. 3.9). Birds generally flew in one direction around the tips of the lower branches (from flower 2 to 4 and from flower 7 to 6), but seldom in the opposite direction. In contrast, on the upper branches birds flew around the tips in both directions. Directionality was also apparent in the movements between the bottom branch and flower 10 on branch B+2, as birds typically flew from flower 3 to 10 when moving up, but from flower 10 to 4 when moving down. Interestingly, hummingbirds tended to fly from flower 9 to 12, but not from flower 12 to 9. Instead, birds flew from flower 12 to 8. As well, flower 8 frequently appeared to be in the middle of the visitation sequence of flowers 7, 8, and 9 or the reverse. Thus, birds combined routes and transitions between routes in different sequences, depending on the first flower visited on a particular panicle and the distances of the closest unvisited flowers.

3.3 Movements within umbels

3.3.1 Arrivals and departures

While foraging on umbels, hummingbirds almost always arrived and departed from the outer ring of eight flowers, rather than the inner whorl of four flowers (arrivals, $F_{1, 1.98} = 3157.59$, $P<0.001$; departures, $F_{1, 8} = 102.39$, $P<0.001$: Fig. 3.13). Birds started and finished foraging on the outer ring more frequently than expected from the proportion of available flowers (Fig. 3.13).

3.3.2 Within umbel movements

The foraging patterns of hummingbirds within umbels (Fig. 3.14) strongly reflected the spatial arrangement of flowers, as 98% of transitions involved neighbouring flowers (Fig. 3.15a). Overall, 40% of flights took birds between adjacent flowers on the outer ring of eight flowers and another 20% were within the inner ring. On average, birds flew within a ring of flowers more often than between the two rings ($F_{2, 16} = 122.74$,

Figure 3.13. The mean (± 95% CI) proportions of a) arrivals to and b) departures from the two rings of flowers on artificial umbels by rufous hummingbirds. The dotted lines represent the expected proportions of arrivals to and departures from each ring based on the number of flowers available on a ring.

a)

b)
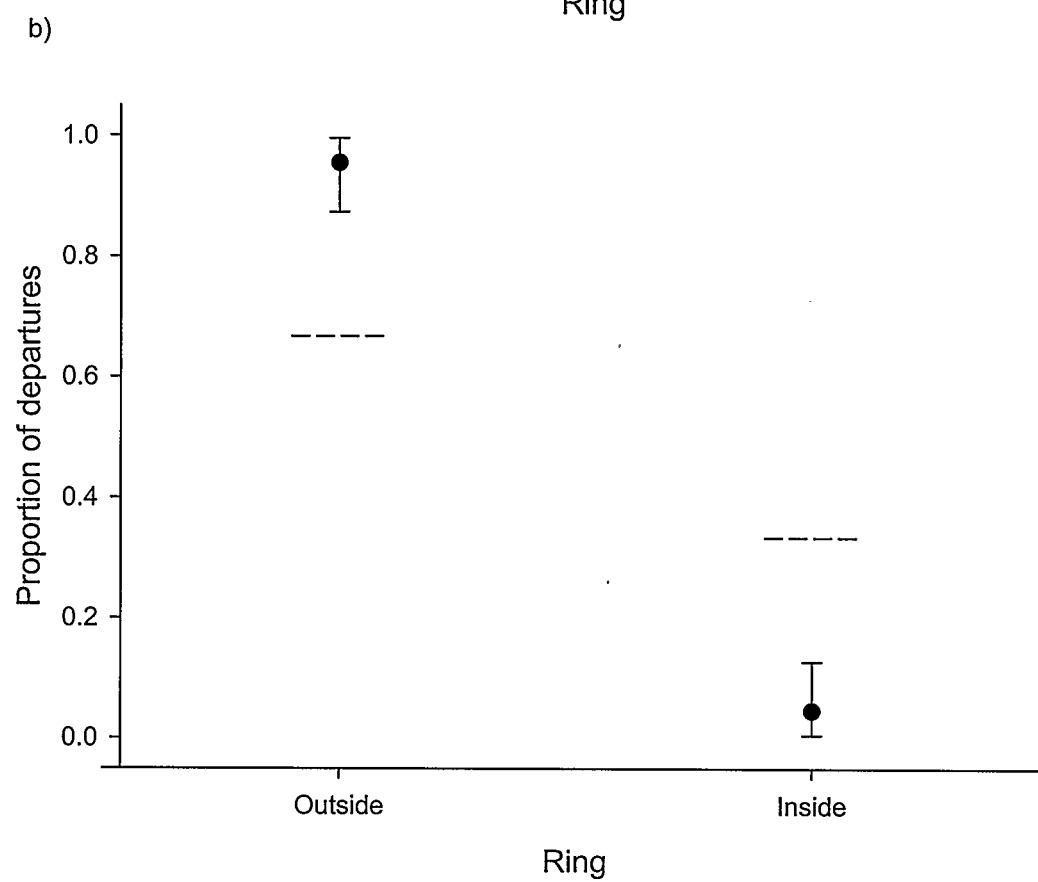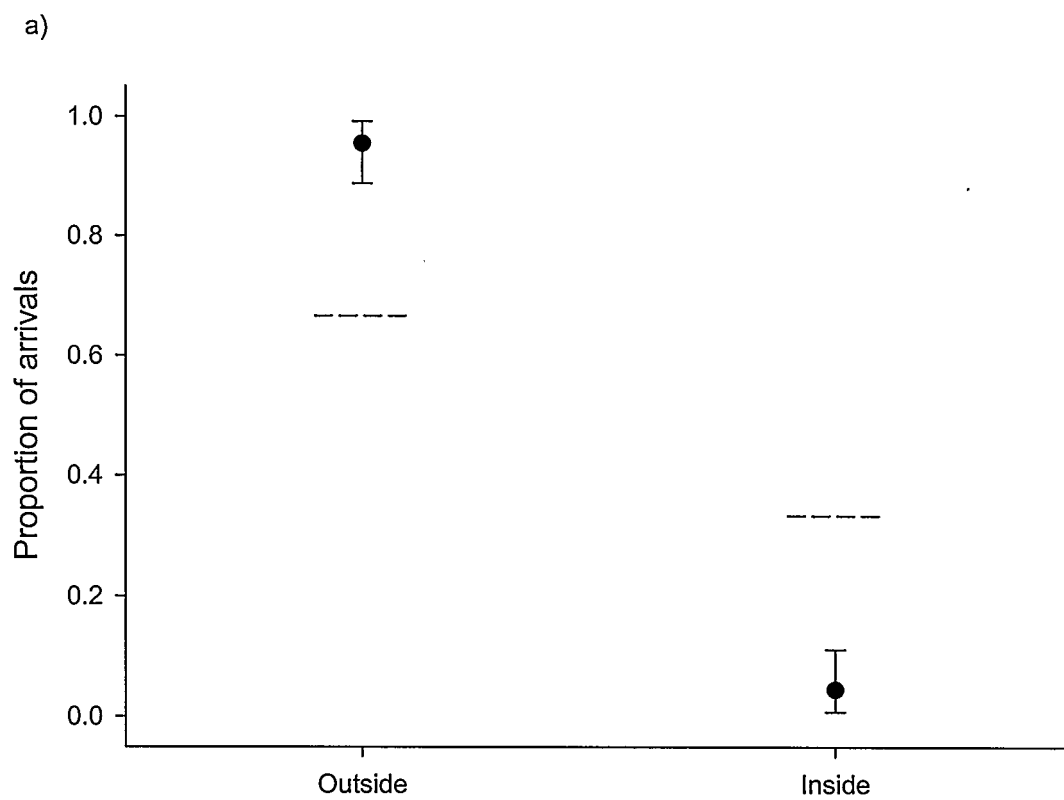
Figure 3.14. The proportions of flights by hummingbirds between individual flowers within umbels. Flowers are represented by numbered circles (see Fig. 2.1). Only transition probabilities >0.1 are presented for clarity.
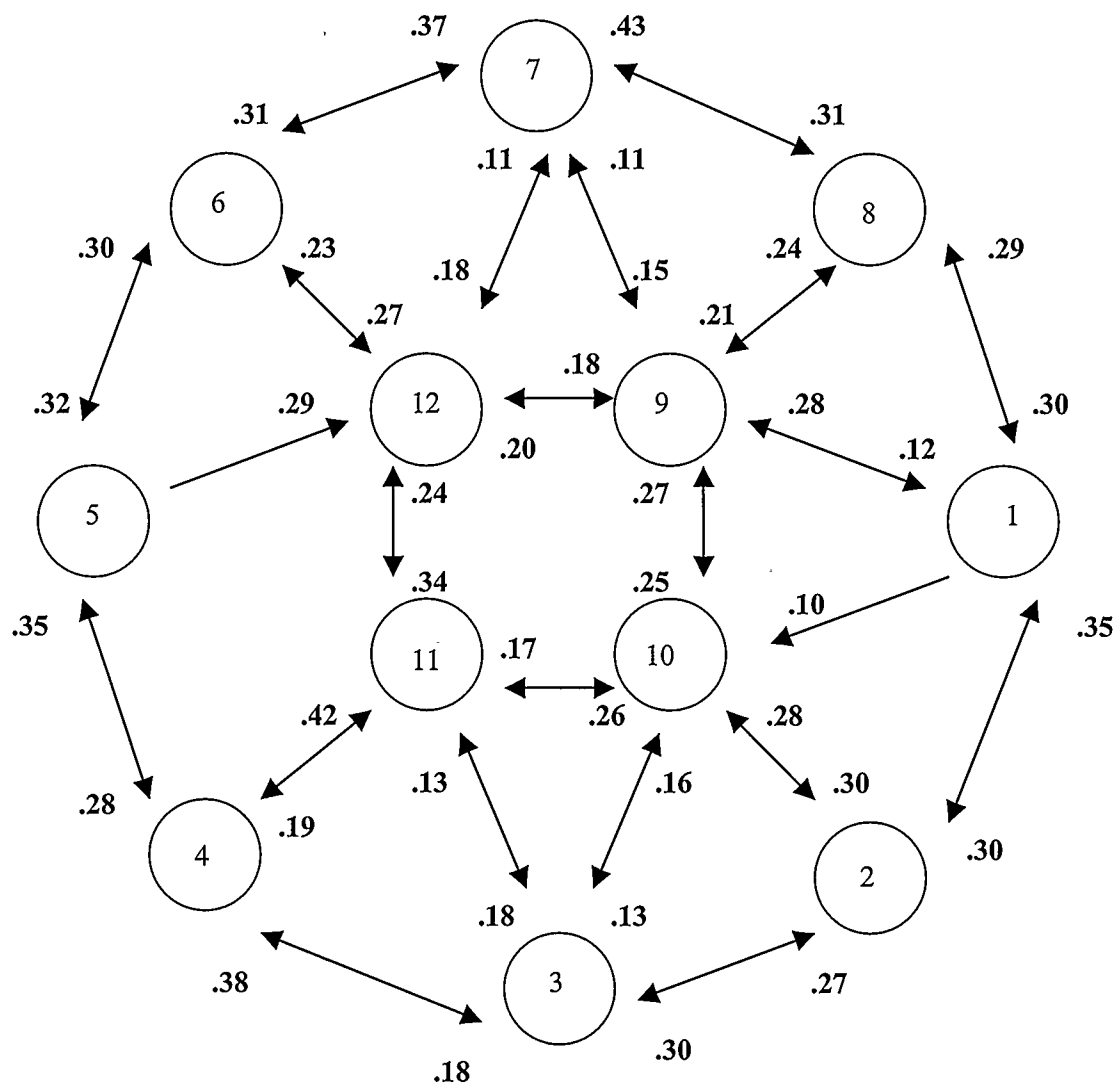
Figure 3.15. The distribution of flights by rufous hummingbirds within umbels. Panel a depicts the mean (± SE) percentage of flights between flowers in relation to the distance flown. Panel b presents the average (± SE) proportion of hummingbird movements (to the inner ring of flowers, to the outer ring, or within a ring) within umbels.

a)

b)
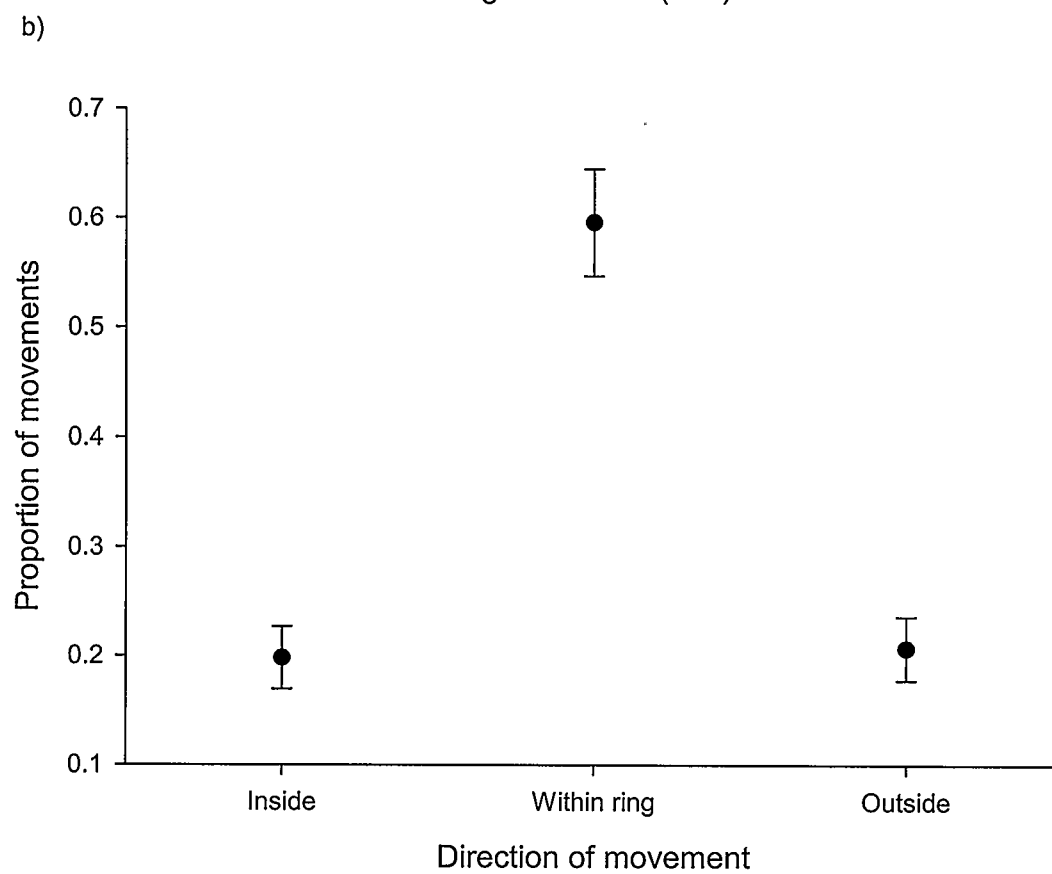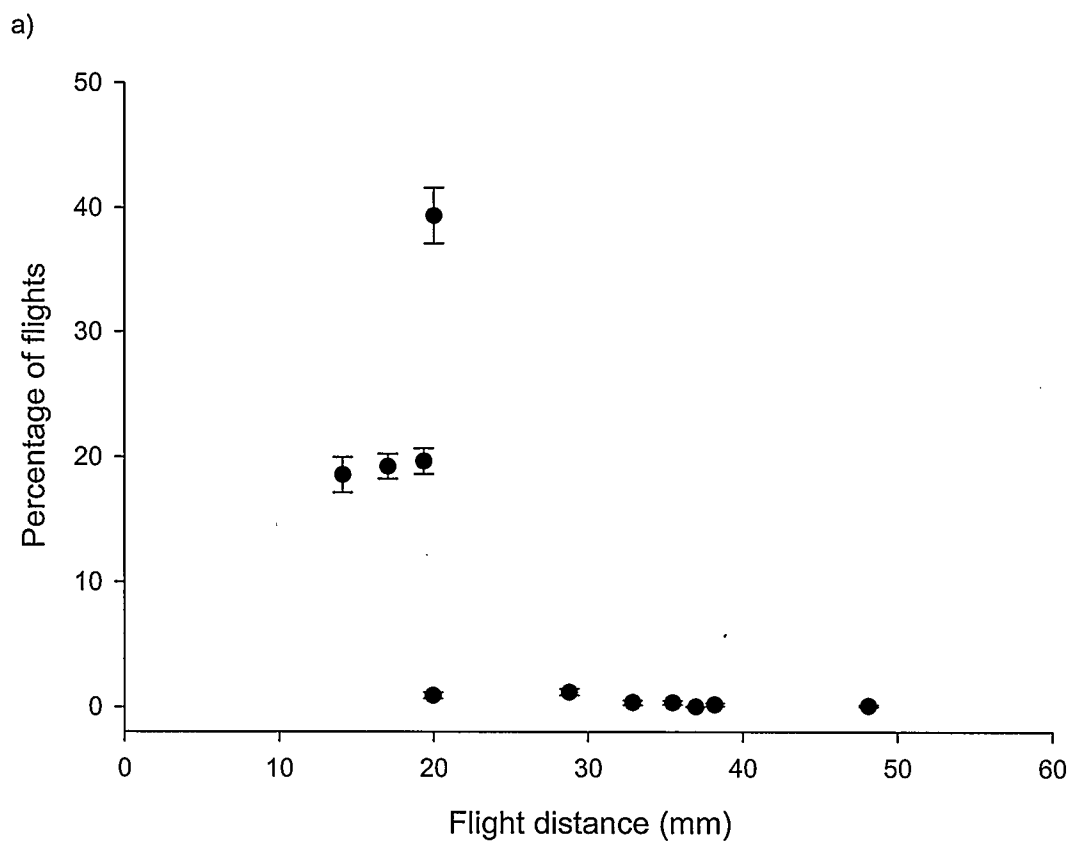
$P<0.001$; Fig. 3.15b). Flights between the outer and inner rings accounted for another 39% of total flights by birds (Fig. 3.15a), with birds moving equally from the outer to the inner whorl and vice versa.

During a typical visit to an umbel, a bird repeatedly visited short sequences of flowers in one ring before switching to the other ring (Fig. 3.14). Specifically, from a flower on the outer ring a bird moved to an adjacent, unvisited outer flower approximately 60% of the time (total of 30% in either direction) and to the closest interior flower another 30% of the time. Depending on which outer flower a bird had just probed, it confronted one or two nearest flowers on the inner ring (e.g. flower 10 is the closest inner flower from flower 2, whereas flowers 10 and 11 are equally close to flower 3). After visiting an inner flower, hummingbirds moved to an adjacent inner flower approximately 50% of the time. While moving between an inner and outer flower, birds typically moved to the nearest of the three options (e.g. from flower 9 to 8, rather than 7 or 1).

Transitions between inner and outer rings involving flowers 1 or 5 did not reflect the symmetrical placement of flowers. As hummingbirds moved to the inside ring from flower 5, they flew mostly to flower 12, rather than 11, which was equally distant. Similarly, flights from flower 1 to flower 9 were almost three times as frequent as flights to flower 10. Birds rarely flew from flower 12 or 11 to flower 5, or from flower 10 to 1.

3.4 Comparisons of hummingbird foraging between architectures
3.4.1 Flight and probe durations

The time taken to ingest the nectar in individual flowers varied among birds and circumstances, even when the analysis considered only flowers with 4 μl of nectar (Fig. 3.16). Probe duration varied differently among inflorescence types for females and males (sex x type interaction, $F_{2,4588} = 56.51$, $P<0.001$). Females visited flowers on

Figure 3.16. The duration of visits by rufous hummingbirds to artificial flowers. Panel a illustrates the relation of the time taken by birds to probe flowers to the duration of the preceding flight between flowers. The fitted line is based on a repeated-measures analysis. Note natural logarithmic scales on both axes. Panel b depicts the mean ($\pm$ SE) durations of visits to flowers on artificial panicles, racemes and umbels by female ($\bullet$) and male ($\triangle$) rufous hummingbirds.

a)

b)
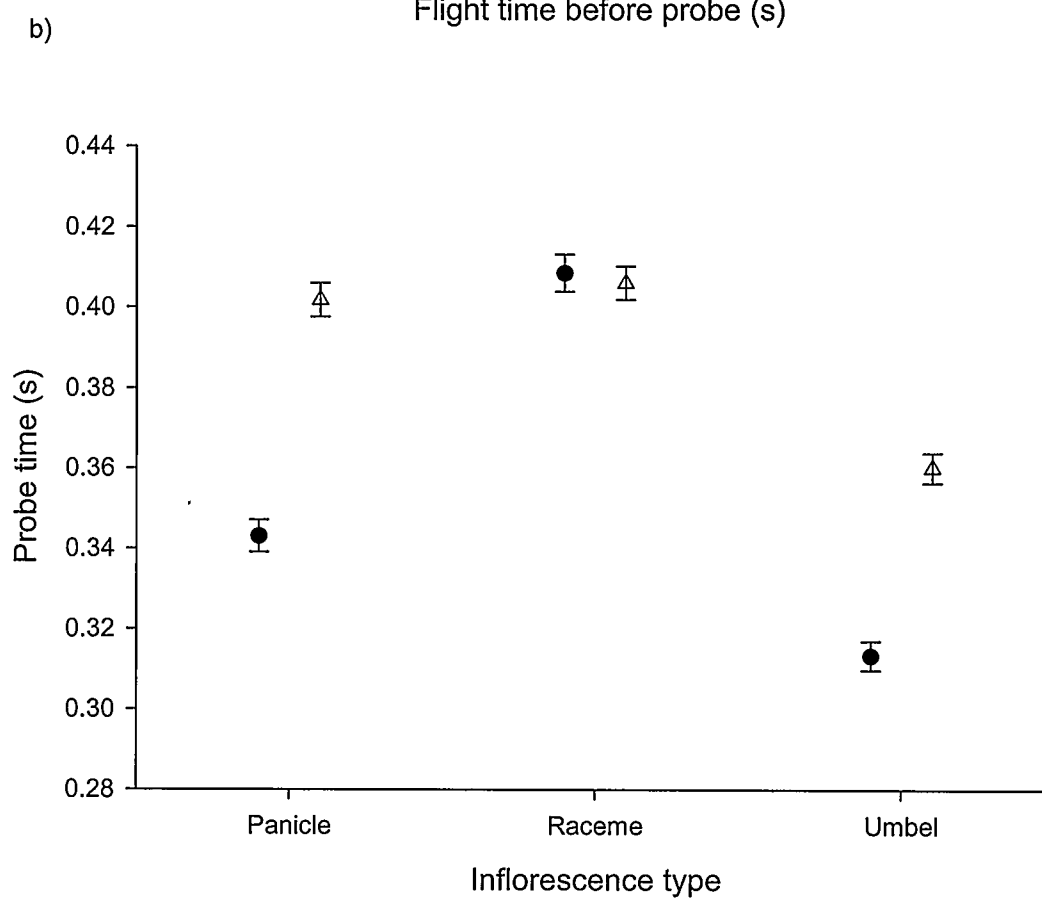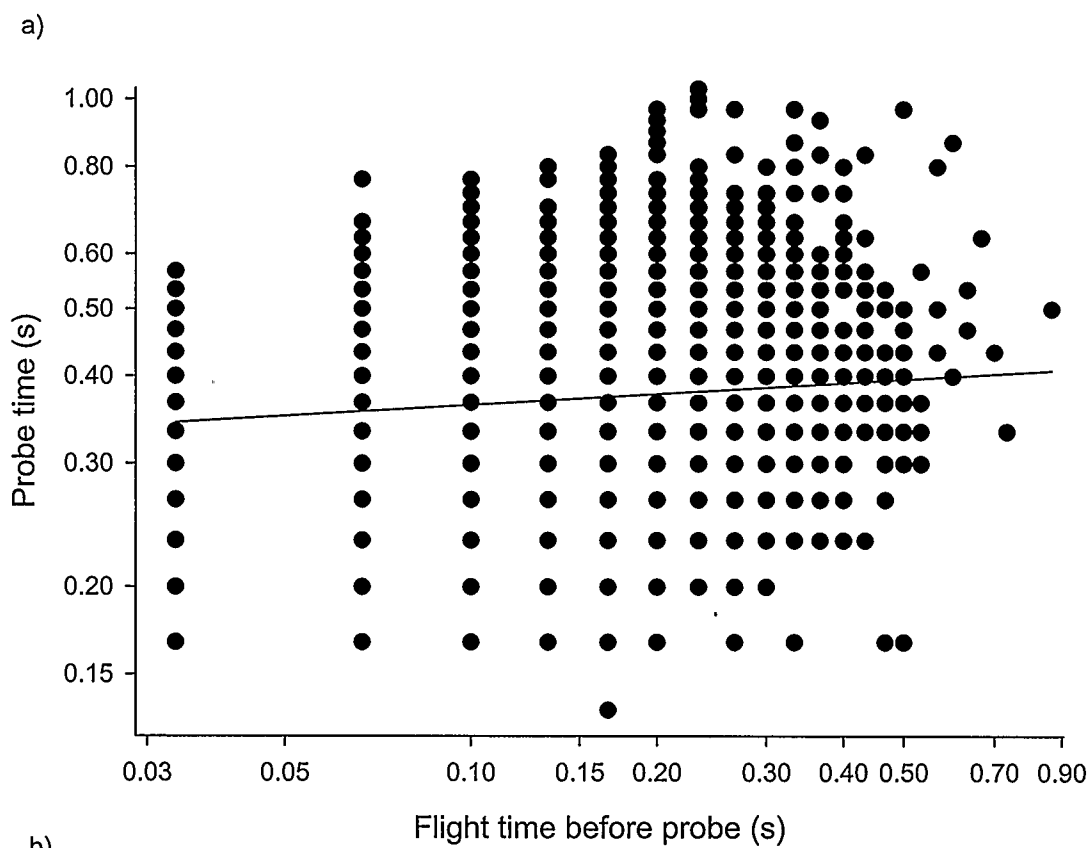
umbels faster than those on panicles, which they in turn visited faster than flowers on racemes. Males also visited flowers on umbels faster than on the other inflorescence types, but their ingestion rates did not differ between panicles and racemes. Birds probed flowers longer after longer approaching flights ($b \pm$ SE = 0.053 $\pm$ 0.009, t_{4586} = 6.00, $P<0.001$, based on ln-transformed data; Fig. 3.16a).

The average duration of flights between flowers within inflorescences varied with the distance that a hummingbird flew and the architecture on which it foraged (Table 3.1). Mean flight time increased with increasing distance for all three architectures (Fig. 3.17), although this relation differed among inflorescence types (distance x type interaction, Table 3.1a). In particular, flight duration varied in direct proportion to distance (i.e., $b=1$) for racemes and umbels, whereas for panicles flight duration increased in a decelerating manner with distance ($b<1$, Table 3.1b). The partial regression coefficient for panicles differed significantly from that for umbels (t_{235} =3.85, $P< 0.001$), but not from racemes (t_{236} =1.31, $P>0.1$). Because flight time between flowers generally increased with distance, birds flew faster between the closely spaced flowers on umbels than between the more widely separated flowers on other inflorescence types.

Variation in the duration of flights between adjacent inflorescences (97% of all transitions) depended on interacting effects of inflorescence type and the sex of the bird ($F_{2, 781}$ = 9.86, $P<0.001$). Inflorescence architecture had no effect on flight times for male hummingbirds (Fig. 3.18). In contrast, females flew significantly faster between racemes than between either panicles or umbels.

3.4.2 Flower visits and revisits

Over all inflorescence types, female hummingbirds visited 60% more flowers during a foraging bout than did males (G_1 = 7.41, $P<0.01$: females = 40.3 flowers, LSE = 2.4, USE = 2.5; males = 25.1 flowers, LSE = 1.4, USE = 1.4). This pattern did not vary

Table 3.1. Analysis of the durations of flight between flowers within artificial panicles, racemes and umbels by female and male rufous hummingbirds. The analysis also included flight distance, with flight times averaged for each bird at a given distance. Analysis is based on ln-transformed averages of flights for a given distance for each bird.

a) Overall analysis

Source of variation	Test statistic
Sex	$F_{1, 9.84} = 2.43$
Inflorescence type	$F_{2, 236} = 4.97**$
Sex x Inflorescence type	$F_{2, 238} = 0.92$
Distance	$F_{1, 236} = 239.08***$
Distance x Inflorescence type	$F_{2, 236} = 7.54***$

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

b) Partial regression coefficients and hypothesis tests

Inflorescence type	$b \pm SE$	$H_0: b = 0$	$H_0: b = 1$
Panicle	0.723 ± 0.061	$t_{233} = 11.84***$	$t_{233} = 4.54***$
Raceme	0.919 ± 0.136	$t_{237} = 6.74***$	$t_{237} = 0.60$
Umbel	1.198 ± 0.107	$t_{235} = 11.18***$	$t_{235} = 1.85$

$*** P<0.001$

Figure 3.17. The influence of the distance between flowers on the mean (± SE) durations of flights by individual rufous hummingbirds while foraging on artifical panicles (▲, solid regression line), racemes (□, dashed regression line) and umbels (●, dash-dotted regression line). Fitted lines are based on the repeated measures analysis presented in Table 3.1. Note natural logarithmic scales on both axes.
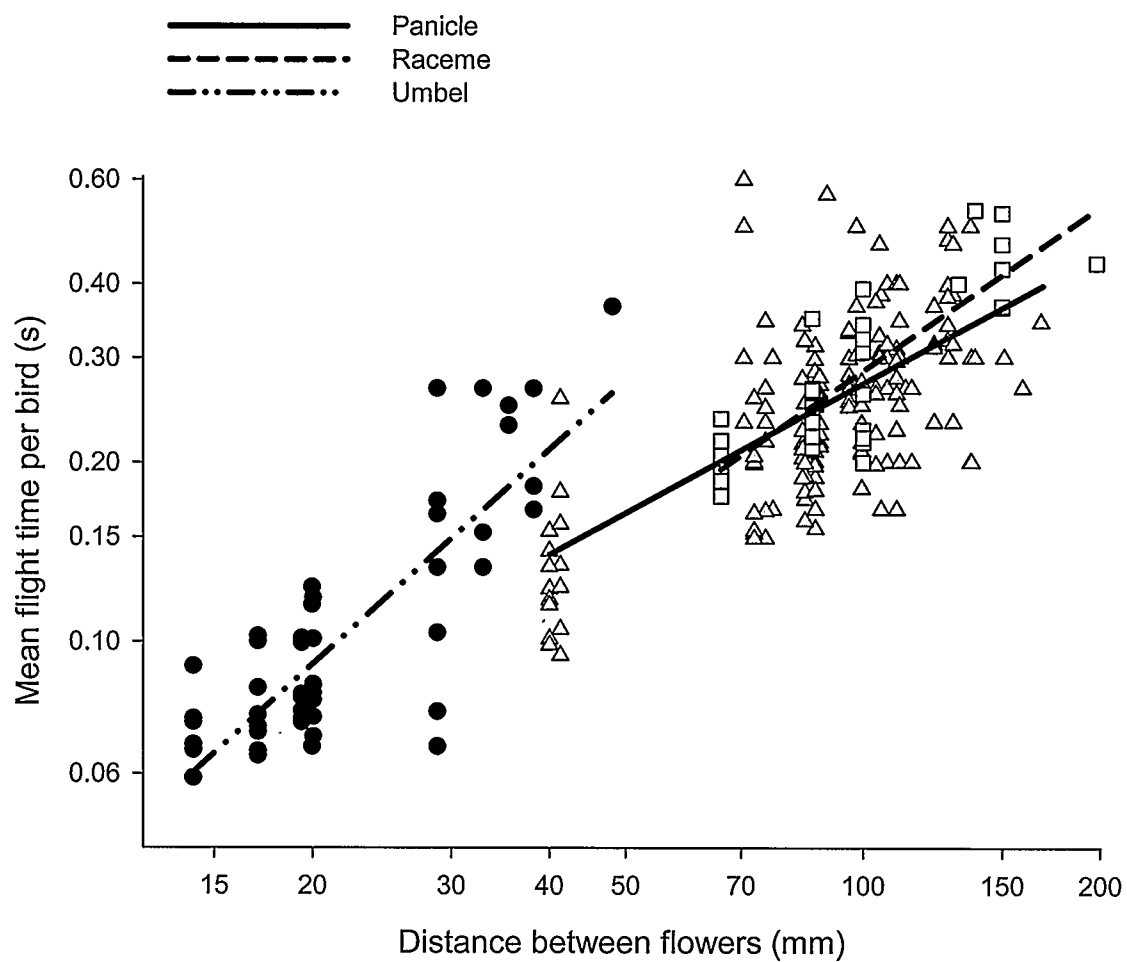
Figure 3.18. Mean (± SE) durations of flights between adjacent inflorescences by female (●) and male (△) rufous hummingbirds with respect to inflorescence architecture.
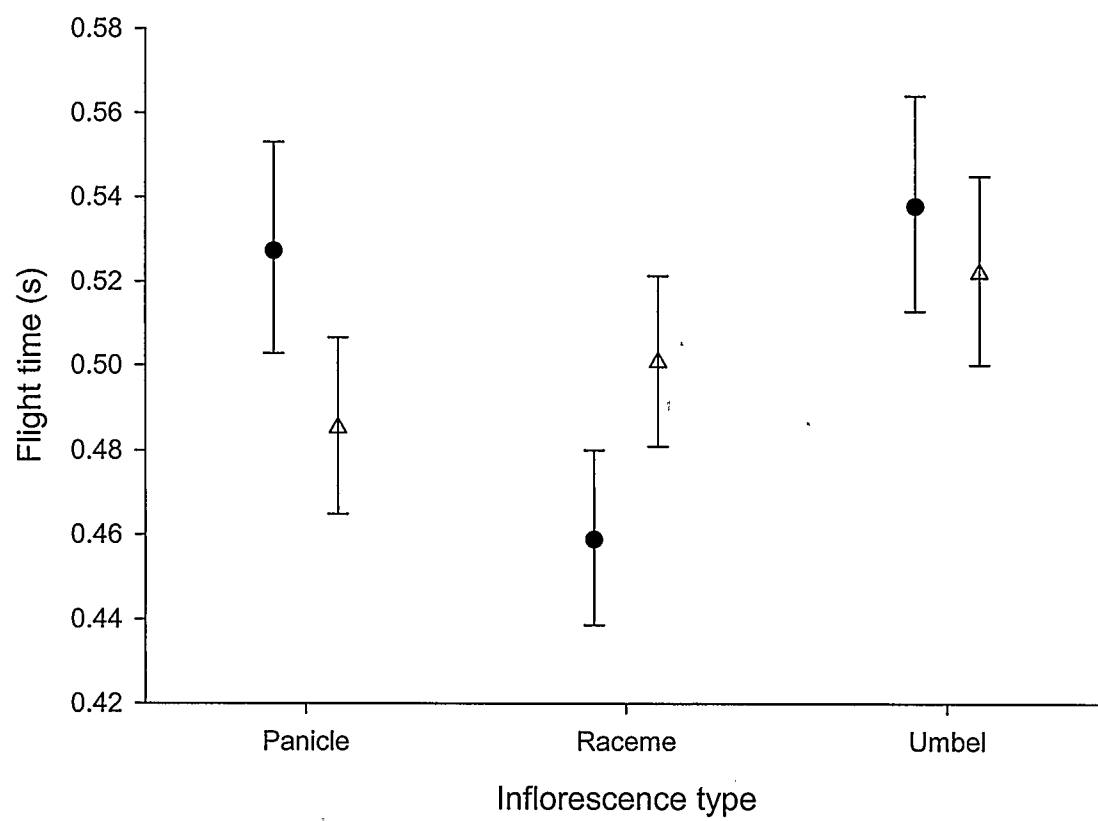
significantly among inflorescence architectures (sex x type interaction, $G_2 = 3.26$, $P > 0.1$).

The mean number of virgin flowers visited by a hummingbird depended on the bird's sex and inflorescence type. Birds visited fewer flowers on panicles and racemes than on umbels ($G_2 = 7.62$, $P < 0.025$; Fig. 3.19a). On average, female birds visited two more flowers per inflorescence than did males (females = 8.5, LSE = 0.49, USE = 0.46; males = 6.7, LSE = 0.25, USE = 0.25: $G_1 = 5.56$, $P < 0.025$). Contrasts in number of flowers visited between architecture types and the sexes did not differ qualitatively if the analysis considered only unvisited flowers, or also included revisited flowers (results not shown).

The mean number of flowers that male and female hummingbirds visited on an inflorescence changed with the position of the inflorescence during the bird's foraging bout (sex x sequence interaction, $G_2 = 6.28$, $P < 0.05$; Fig. 3.19b). On average, birds probed the most flowers on the first inflorescence visited during a bout, regardless of sex. However, the sexes behaved differently on subsequent inflorescences. Both sexes visited significantly fewer flowers on the second inflorescence, with females visiting two fewer flowers and males probing three fewer. On the last inflorescence of their bout, females probed one more flower than they had on the second inflorescence, whereas males visited an equivalent number as on the second inflorescence. This within-bout pattern in the number of flowers visited per inflorescence did not differ significantly among inflorescence types ($G_4 = 2.04$, $P > 0.5$).

Less than 1% of flower visits involved a bird revisiting a flower that it had visited previously during that foraging bout. Neither inflorescence architecture ($G_2 = 4.71$, $P > 0.05$) nor the sex of a bird ($G_1 = 0.52$, $P > 0.1$) influenced the number of revisits. Hummingbirds were more likely to revisit a flower as the number of virgin flowers visited on an inflorescence increased ($b \pm$ SE $= 0.464 \pm 0.029$, $G_1 = 258.59$, $P < 0.001$; Fig. 3.20). They also were less likely to remain at an inflorescence after revisiting a

Figure 3.19. Mean (± SE) number of flowers visited by rufous hummingbirds on artificial panicles, racemes and umbels. Panel a indicates the average number of flowers visited with respect to inflorescence architecture, whereas panel b illustrates the number of flowers visited by female (●) and male (△) birds according to an inflorescence's position in a foraging bout.

a)

b)
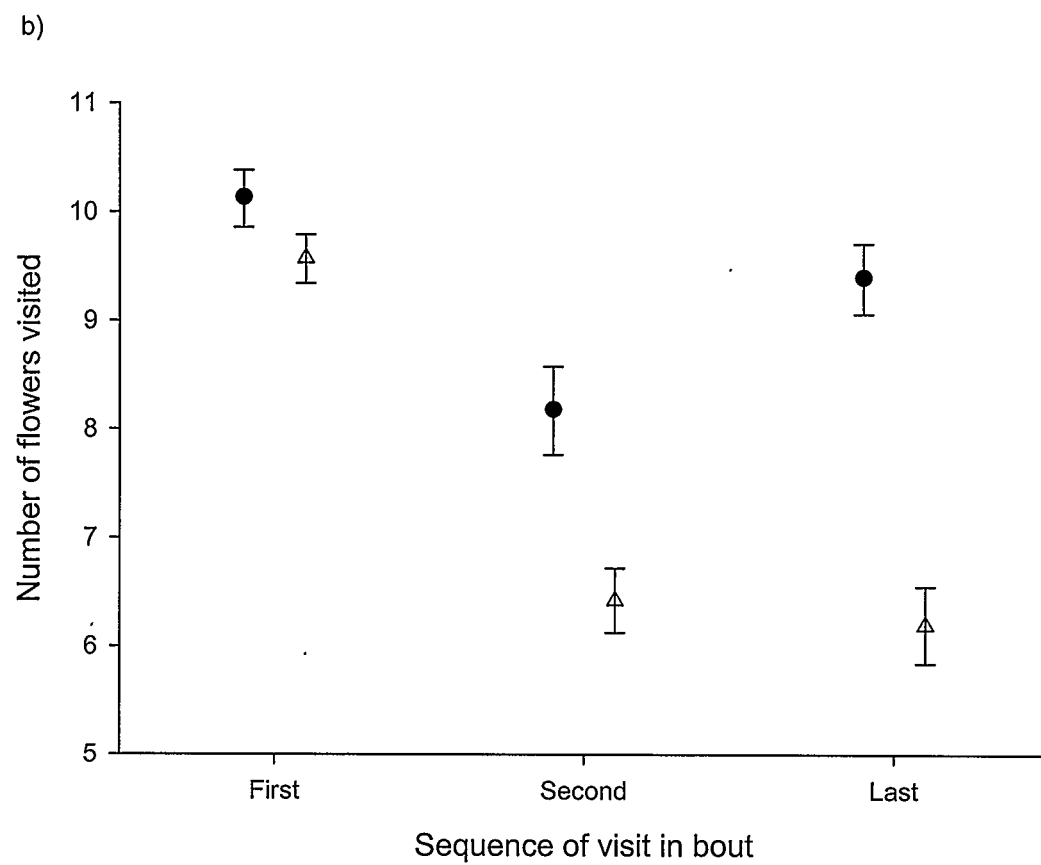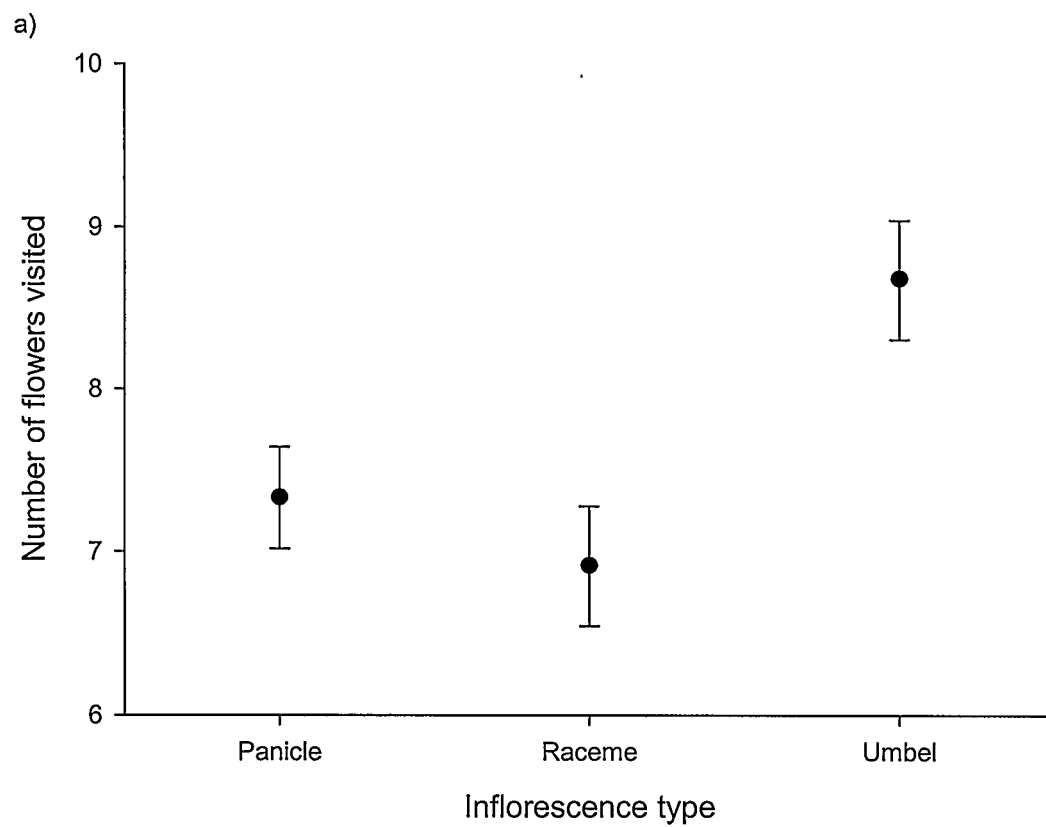
Figure 3.20. The number of revisits to flowers on an inflorescence with respect to the number of virgin flowers already visited by a hummingbird. Values indicate the numbers of observations at a given point.

The y-axis is labeled "Number of revisits to flowers" with values 0, 2, 4, 6, 8, 10. The x-axis is labeled "Number of virgin flowers visited on an inflorescence" with values 0, 2, 4, 6, 8, 10, 12.

Data points:

Revisits	Values by virgin flowers visited
10	1 (at 10)
7	1 (at 10)
6	1 (at 11), 4 (at 12)
5	1 (at 11), 2 (at 12)
4	1 (at 11), 6 (at 12)
3	2 (at 9), 3 (at 10), 7 (at 11), 10 (at 12)
2	1 (at 6), 1 (at 7), 3 (at 8), 5 (at 9), 6 (at 10), 20 (at 11), 12 (at 12)
1	1 (at 3), 2 (at 4), 6 (at 5), 11 (at 6), 7 (at 7), 16 (at 8), 30 (at 9), 27 (at 10), 31 (at 11), 26 (at 12)
0	35 (at 1), 21 (at 2), 40 (at 3), 59 (at 4), 73 (at 5), 78 (at 6), 68 (at 7), 71 (at 8), 61 (at 9), 56 (at 10), 33 (at 11), 30 (at 12)

flower as the number of flowers they had already probed increased ($b \pm$ SE = -0.426 $\pm$ 0.069, $G_1 = 38.61$, $P<0.001$; Fig. 3.21).

3.4.3 Inflorescence visits and revisits

On average, female hummingbirds visited 4.7 (LSE = 0.06, USE = 0.05) of the five available inflorescences during a foraging bout, whereas males visited 3.5 (LSE = 0.23, USE = 0.21) inflorescences ($G_1 = 7.21$, $P<0.01$). The number of inflorescences visited did not differ significantly among inflorescence types ($G_2 = 3.04$, $P>0.1$). In general, birds that visited more flowers per inflorescence visited fewer inflorescences ($b \pm$ SE = -0.205 $\pm$ 0.047, $G_1 = 18.75$, $P<0.001$; Fig. 3.22).

The mean number of inflorescences revisited during a foraging bout varied with interacting effects of a bird's sex and the number of virgin inflorescences already visited ($G_1 = 5.65$, $P<0.025$). Hummingbirds of either sex revisited more inflorescences as the number of virgin inflorescences visited increased (Fig. 3.23). However, the rate at which female birds revisited inflorescences changed more quickly than did that for males (females, $b \pm$ SE = 0.747 $\pm$ 0.059, $G_1 = 162.70$; males, $P<0.001$; $b \pm$ SE = 0.188 $\pm$ 0.089, $G_1 = 4.48$, $P<0.05$).

3.5 Hummingbird behaviour during the preference experiment

3.5.1 Flower and inflorescence visits

Overall, rufous hummingbirds visited an average of 38.7 (LSE = 3.8, USE = 4.2) flowers on 5.28 (LSE = 0.51, USE = 0.54) inflorescences during a single foraging bout in a 16-inflorescence mixed array. As in pure arrays, the average number of flowers that a hummingbird visited per inflorescence depended on the inflorescence type ($F_{2, 136} = 10.21$, $P<0.001$). Birds visited fewer flowers on panicles and racemes than on umbels (Fig. 3.24a).

Figure 3.21. The average (± SE) probability of a hummingbird remaining on an inflorescence after its first revisit to a flower occurs.
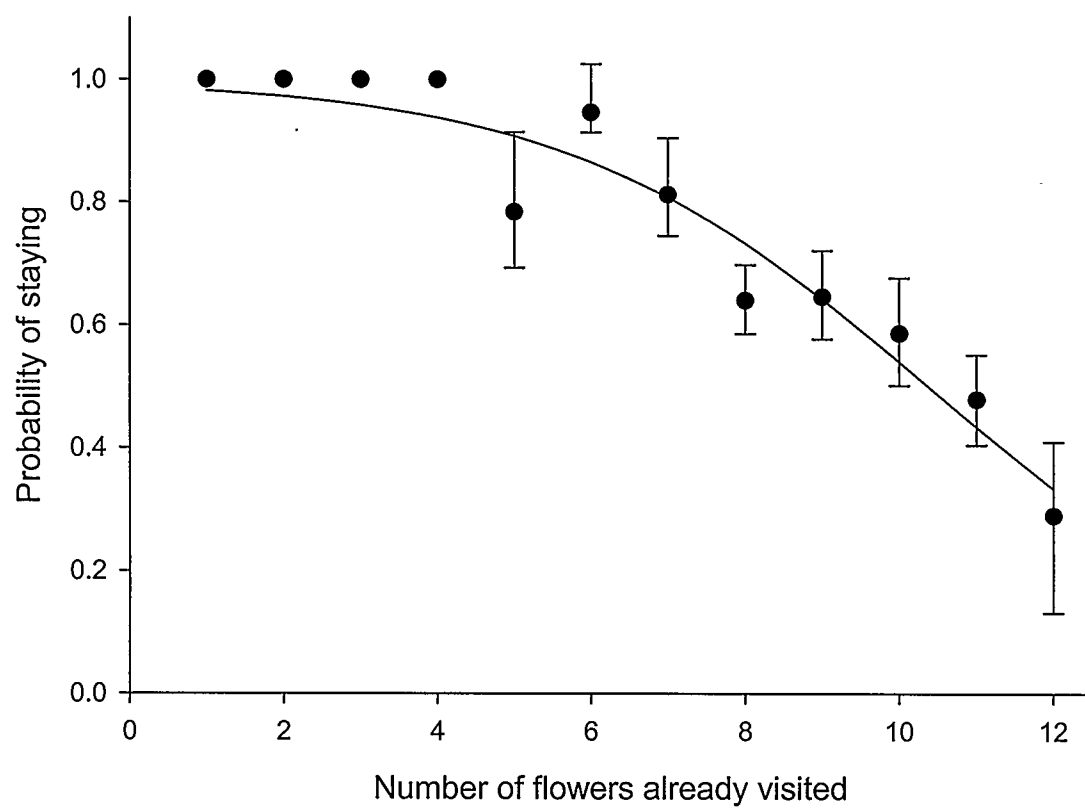
Figure 3.22. The relation of the proportion of inflorescences visited during a foraging bout by hummingbirds to the average number of flowers that the bird probed per inflorescence during that bout.
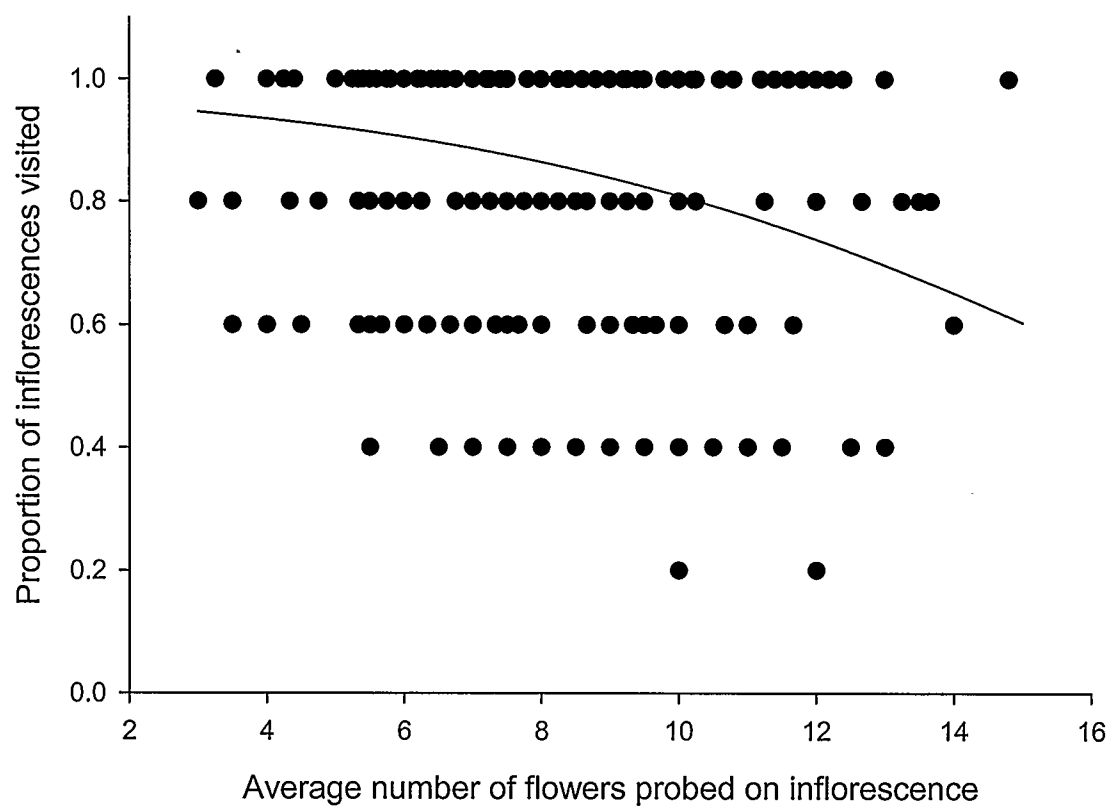
Figure 3.23. Number of revisits to inflorescences by female (bold symbols, solid line) and male (non-bold symbols, dashed line) hummingbirds during a foraging bout with respect to the number of virgin inflorescences visited in a bout. Values indicate the number of observations at a given point.

The y-axis is labeled "Number of revisits to inflorescences" with values 0 through 7. The x-axis is labeled "Number of virgin inflorescences visited" with values 2 through 5.
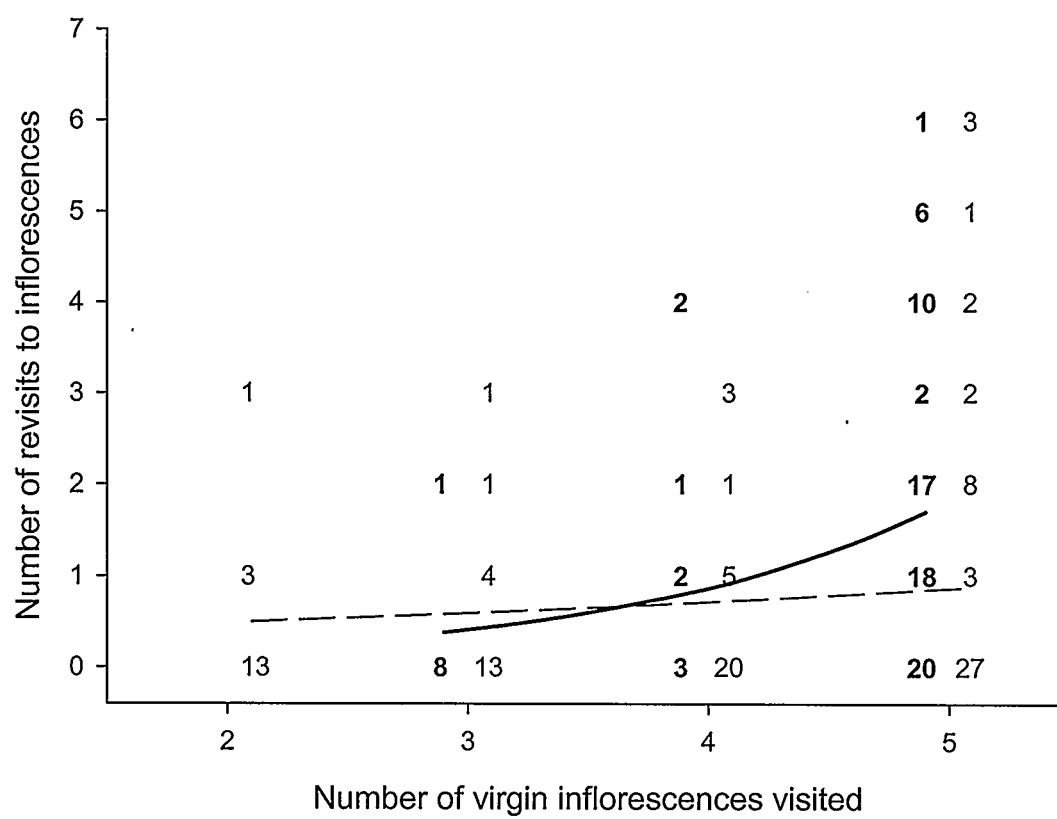
Figure 3.24. Mean (± SE) number of flowers visited by rufous hummingbirds foraging in

an artificial array containing artificial panicles, racemes and umbels. Panel a indicates

the average number of flowers visited with respect to inflorescence architecture, whereas

panel b illustrates the number of flowers visited by birds according to an inflorescence's
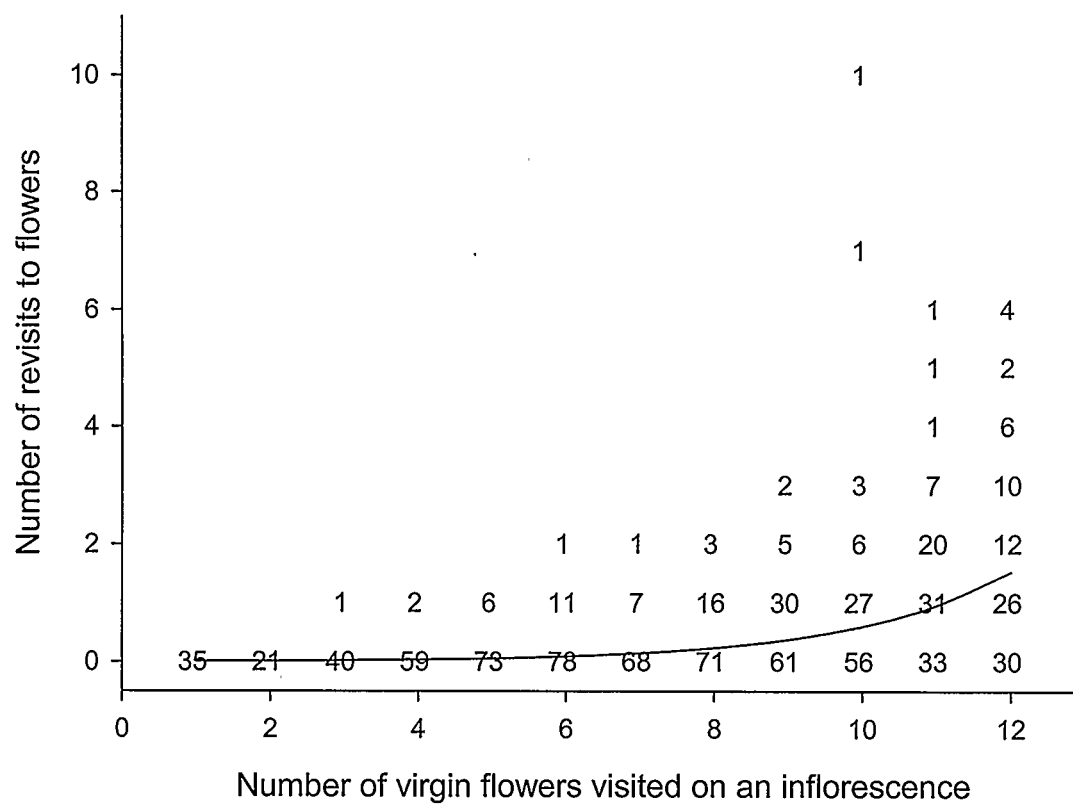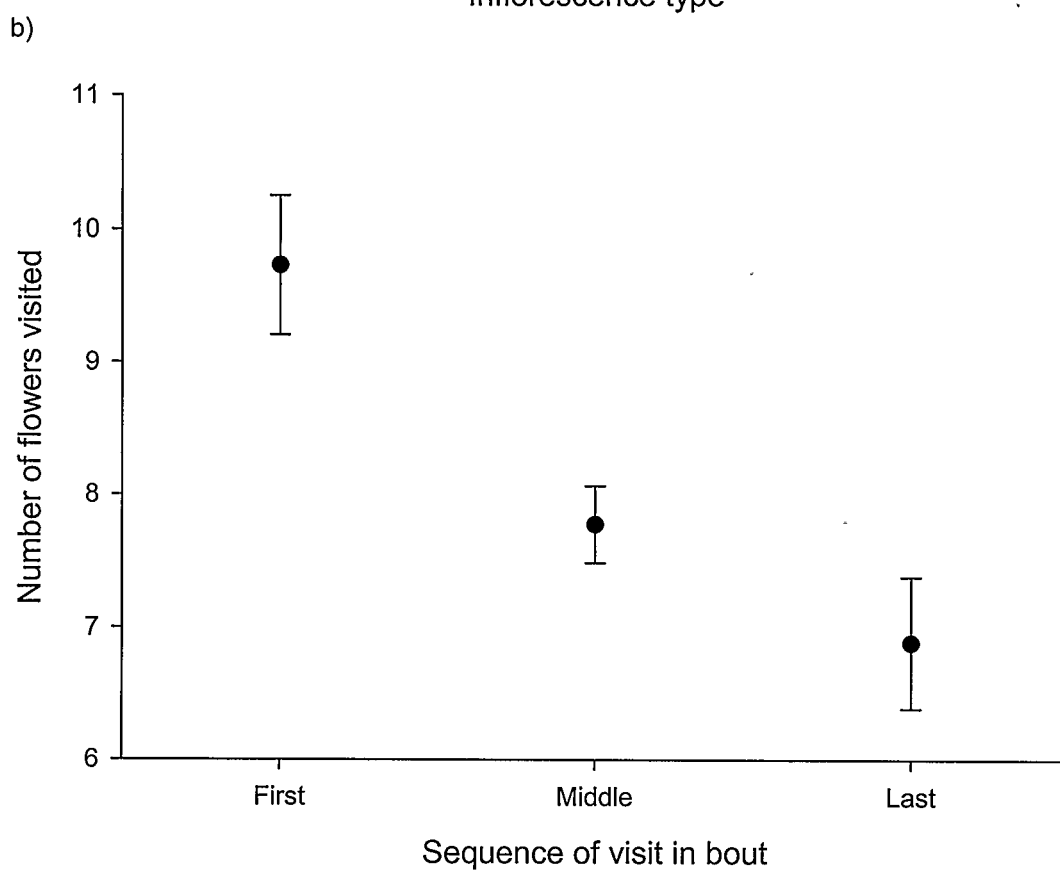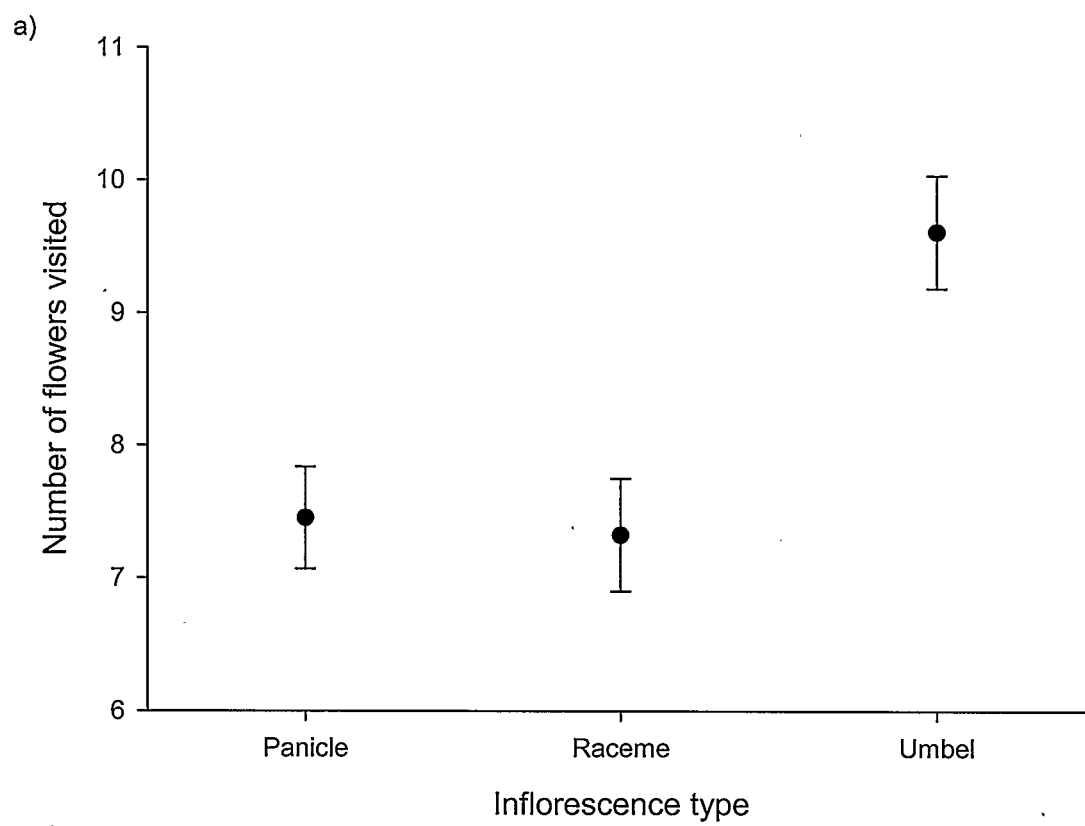
position in a foraging bout.

a)

b)

84

The mean number of flowers that hummingbirds visited on an inflorescence changed with the position of the inflorescence during a foraging bout ($F_{2,136}= 8.21$, $P<0.001$; Fig. 3.24b). As with their bouts on pure arrays, birds probed the most flowers on the first inflorescence visited. On the second inflorescence, birds visited two fewer flowers on average. On the last inflorescence of their bout, hummingbirds visited an equivalent number of flowers to the second inflorescence, much like males on pure arrays (see Fig. 3.19b). The relation of the number of flowers visited on an inflorescence to its position in a bird's foraging bout did not differ significantly between pure and mixed arrays (array x sequence interaction, $G_2 = 4.59$, $P>0.1$), although the power to detect such differences may be limited by the reduced number of birds that experienced both types of arrays.

3.5.2 Movement between inflorescences

Hummingbirds consistently limited the distance that they moved between inflorescences in the 4 x 4 mixed array. Birds moved between adjacent inflorescences during 96% of inflorescence transitions. Significantly more transitions involved the closest inflorescence along an array row or column (50 cm, 73% of flights), rather than along a diagonal (71 cm, 27% of flights: $\chi^2 = 31.67$, $df= 1$, $P<0.001$). Birds visited interior and peripheral inflorescences in proportion to their occurrence in the array ($\chi^2 = 3.57$, $df= 1$, $P>0.05$).

The positions at which hummingbirds arrived and departed racemes and panicles differed somewhat between pure and mixed arrays. For racemes, array type significantly affected the pattern of arrivals (array x whorl position interaction, $F_{3,34}= 6.97$, $P<0.001$; Fig. 3.25a), but not departures ($F_{3,33}= 2.03$, $P>0.1$). In particular, birds arrived at the lower two whorls of racemes less often in mixed arrays than when they foraged solely amongst racemes. In contrast, for panicles array type significantly affected the pattern of departures (array x whorl position interaction, $F_{3,35}= 4.05$, $P<0.025$; Fig. 3.25b), but not

Figure 3.25. The effects of array type on the distributions (mean ± SE) of a) arrivals within racemes and b) departures from panicles by rufous hummingbirds.

a)
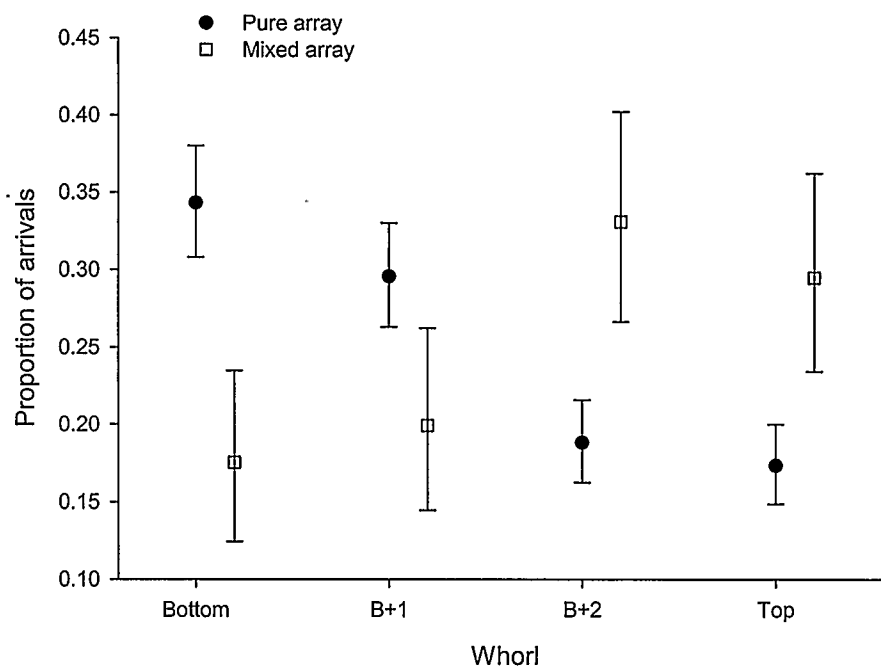
b)
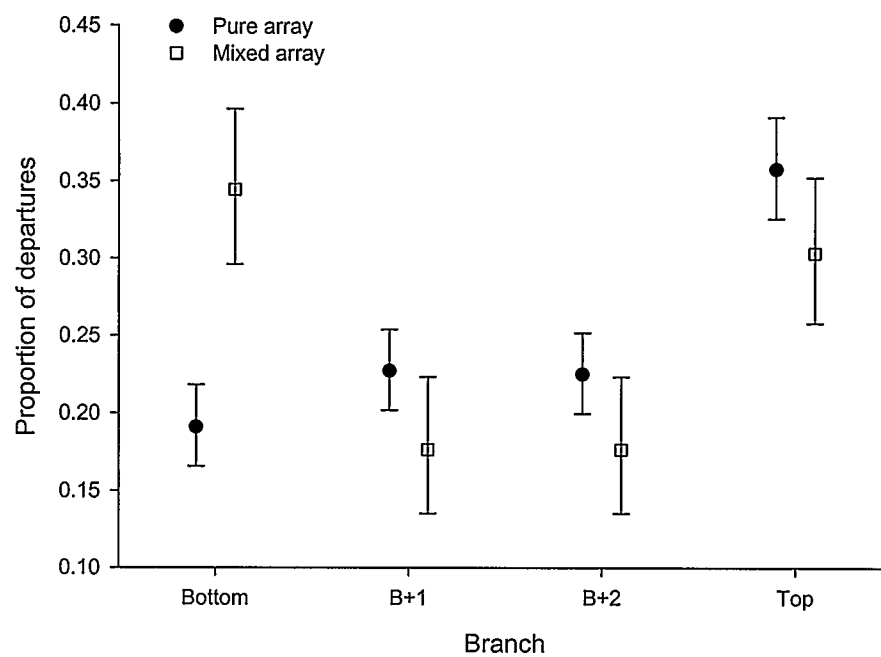
arrivals ($F_{3,35}$ = 2.22, P>0.1). When foraging on pure arrays, hummingbirds left panicles more often from the top branch than from the lower three branches, whereas birds in mixed arrays departed from the bottom and top branches with equal frequency. .

The arrival and departure positions of hummingbirds flying between panicles and racemes in mixed arrays varied with context. On racemes, the lower two whorls were situated lower in the array than all the flowers on panicles (Fig. 2.2b). Thus, when birds departed from the lower two whorls on racemes, they were more likely to arrive at the lower two branches of a panicle than at the upper two branches (χ^2 = 6.23, df = 1, P<0.025). In contrast, when birds left from the upper two whorls on racemes, they arrived equally on the upper and lower branches of the subsequent panicle (χ^2 = 0.33, df = 1, P>0.5). Similarly, birds that departed from the lower two branches on panicles, arrived equally on the upper and lower whorls of a raceme (χ^2 = 1.92, df = 1, P>0.1). However, when birds departed from the upper branches of a panicle they never flew to the lower whorls on a raceme.

In mixed arrays, the flowers on umbels were higher than those on either panicles or racemes (Fig. 2.2b), so that flights to and from umbels might have been expected to involve the upper two branches or whorls of panicles or racemes, respectively. However, when departing from umbels, birds arrived equally at the upper and lower branches or whorls (panicles: χ^2 = 0.6, df = 1, P>0.1; racemes: χ^2 = 0.08, df = 1, P>0.1). As well, when flying to umbels, hummingbirds did not differ in the number of departures from the upper and lower branches or whorls of panicles and racemes, respectively (panicles: χ^2 = 0.39, df = 1, P>0.1; racemes: χ^2 = 3.00, df = 1, P>0.05). The power to detect a difference for racemes may have been limited by the small number of transitions from umbels to racemes (N = 12).

3.5.3 Choice of inflorescences

Different spatial arrangements of flowers on inflorescences changed the rate of net energy intake (RNEI) realized by hummingbirds as they foraged ($F_{2, 124}$ = 48.37, P<0.001; Table 3.2). Birds visited more flowers per inflorescence with no difference in total foraging time while feeding from umbels compared to either panicles or racemes. As a result, birds gained energy about 25% faster while foraging on umbels than they did on either panicles or racemes. This result suggests that hummingbirds feeding in the mixed arrays should have visited umbels preferentially, if they foraged in a manner that maximized their rate of net energy intake.

Despite the differences in the rate of net energy intake among inflorescence types, hummingbirds visited the three types with equal frequency. Birds did not favour a particular architecture when starting a foraging bout in the mixed array (G_2 = 1.34, P>0.5). During a bout, birds also chose inflorescences in proportion to their availability in the array (Table 3.3). Maximum-likelihood analysis of alternate models that assessed inflorescence preference based on the variety of unvisited inflorescences immediately adjacent to a bird's current position revealed that a model of random foraging is most consistent with the observed behaviour (Table 3.4). In particular, the random-movement model was associated with a lower value of Akaike's information criterion than any of the models that allowed preference for one or more inflorescence type.

Given the large difference in average rate of net energy intake between inflorescence types, what was the energetic consequence of birds not visiting the neighbouring inflorescence type with the highest expected rate of energy gain (typically an umbel)? The chance of a bird moving to a low-return inflorescence depended on their intake rate on the preceding inflorescence if they had visited an umbel, but not if they had visited a panicle or raceme (G_2 = 13.01, P<0.005). In particular, preceding 87.0% of the 23 movements from an umbel to a low-return inflorescence a bird had ingested energy at a below-average rate. In contrast, a bird was equally likely to have experienced a below-

Table 3.2. Summary of the foraging characteristics of rufous hummingbirds that affect their rate of net energy intake while foraging on artificial panicles, racemes and umbels. On average (± SE), flights between inflorescences lasted 0.53 ± 0.015 s.

Inflorescence type	Average (± SE) number of flowers visited	Average (± SE) duration of an inflorescence visit (s)	Average (± SE) rate of net energy intake (J s^{-1})
Panicle	7.3 ± 0.38	4.3 ± 0.32	23.3 ± 2.4
Raceme	7.5 ± 0.44	4.4 ± 0.35	23.2 ± 2.4
Umbel	9.2 ± 0.42	4.3 ± 0.34	29.3 ± 2.4

Table 3.3. Replicated goodness-of-fit tests comparing the choice of inflorescence types by rufous hummingbirds to their relative frequencies in mixed arrays.

Bird	Pooled results among birds or trials	Heterogeneity among birds or trials	Total results
All combined	$G_2 = 1.76$	$G_{10} = 2.80$	$G_{12} = 4.56$
BMSF	$G_2 = 0.55$	$G_6 = 3.70$	$G_8 = 4.25$
K1	$G_2 = 0.79$	$G_{10} = 7.59$	$G_{12} = 8.38$
K2	$G_2 = 0$	$G_{10} = 5.09$	$G_{12} = 5.09$
K3	$G_2 = 0.19$	$G_{10} = 6.23$	$G_{12} = 6.42$
K4	$G_2 = 2.30$	$G_{10} = 5.97$	$G_{12} = 8.27$
K5	$G_2 = 0.73$	$G_{10} = 3.91$	$G_{12} = 4.64$

Table 3.4. Maximum-likelihood analysis of the relative frequencies of visits to panicles, racemes and umbels by rufous hummingbirds on mixed arrays. The values listed for each inflorescence type represent the estimated relative preference for that type for a specific model. Values of 1 indicate that the relative preference for that inflorescence type was fixed. Smaller values of Akaike's information criterion (AIC) indicate models that are more consistent with the observed use of the three inflorescence types.

Model	Inflorescence type			Number of parameters estimated	AIC
	Umbel	Raceme	Panicle		
A = Random movement	1	1	1	0	100.4
B	1	1	1.19	1	102.0
C	0.79	1	1	1	101.8
D	1	1.06	1	1	102.4
E	1	1.22	1.32	2	103.7

or above-average RNEI on a panicle (50% below average) or a raceme (38% below average) before moving to a low-return inflorescence. Having moved to a low-return inflorescence, birds were equally likely to realize below or above average rates of net energy intake for that inflorescence type ($\chi^2 = 2.15$, $df = 2$, $P > 0.1$). As a result, birds did not realize a rate of net energy intake equal to or greater than the average rate of the most rewarding inflorescence type in the immediate vicinity ($\chi^2 = 14.78$, $df = 2$, $P < 0.001$). Therefore hummingbirds seem not to have maximized their rate of net energy intake while foraging on mixed arrays of panicles, racemes and umbels.

4 DISCUSSION

Hummingbirds modify their behaviour when confronted by different three-dimensional arrangements of flowers. These behavioural changes involve the primary direction of vertical movement within and between inflorescences, the consistency of foraging routes among flowers (including start and end positions), and the proportion of flowers visited. Despite considerable variation among inflorescence types, the observed behaviour includes recurring responses, which reveal dominant characteristics of hummingbirds' solutions to the problem of foraging in three dimensions. I now discuss these foraging characteristics and their influences, compare them to the behaviour of bumble bees in similar situations, and consider their implications for plant reproduction and the evolution of inflorescence architecture.

4.1 Foraging rules

"With little evidence that birds use movement rules between making flower choices, the spatial distribution pattern of flowers also seems of little consequence" (Healy and Hurly 2001, p.144). My results directly contradict this statement. Hummingbirds appear to follow some basic rules of movement when foraging within a variety of inflorescences. First, hummingbirds seem to treat inflorescences as edges. When arriving at panicles and umbels, birds are more likely to arrive at the outer flowers (Figs. 3.6a and 3.13a, respectively). As well, birds move along edges when foraging within all three architectures. On panicles, hummingbirds followed three general routes around the inflorescence (Figs. 3.9 and 3.10). These routes moved birds along the sides of inflorescence branches wherever possible. Birds never crossed a branch to visit adjacent flowers on the other side. Instead, they moved along a branch and then around the tip to the other side. On racemes, when hummingbirds encountered an edge of the inflorescence (top and bottom whorls), they treated it as such. They rarely moved within

a whorl on the middle two whorls, whereas when they were foraging at the top or bottom whorls, birds increased the frequency of their lateral movements even though a zigzag pattern would have enabled a bird to visit closer flowers (Fig. 3.3). In addition, hummingbirds moved around racemes as they zigzagged, rather than generally up or down through the inflorescence. On umbels, hummingbirds moved within rings of flowers more than between them (Fig. 3.15b). Also, they often rotated their body as they foraged around the outside ring. If hummingbirds generally treat inflorescences as edges, then their movement on spiral artificial inflorescences should follow the spiral much of the time as reported by (Pyke 1981a).

Hummingbirds also minimize flight distance while foraging. In mixed arrays, birds flew to an adjacent inflorescence 96% of the time. Within those flights, nearly three-quarters were to the closest available inflorescence. Wesselingh and Arnold (2000) found that hummingbirds visited nearest neighbours in almost 80% of between-flower movements on their array. Likewise, Baum and Grant (2001) found that birds often followed rows and columns of flowers in a uniform grid of 36 flowers, the shortest movement possible. Waser (1982) and Wolf and Hainsworth (1990) also found that birds move short distances to nearest neighbouring inflorescences. Hummingbirds seem to follow this pattern at other scales, as they also move between the closest clumps of inflorescences (Wolf and Hainsworth 1991).

At a finer scale, hummingbirds also minimize their flight distances within inflorescences, as most of their flights involve the closest flowers (Figs 3.4, 3.11, and 3.15a). For instance, in racemes, 80% of hummingbird flights are to the nearest flower on an adjacent whorl (Figs 3.3 and 3.4). This transition is shorter than between neighbouring flowers on the same whorl. Therefore, adjustment of the spacing of flowers within and between whorls would probably alter the manner in which birds move through racemes.

Minimization of flight distance appears to be modified by the availability of adjacent flowers. On panicles, the shortest flight distance is between flowers 7 and 8. However, birds flew around the tips of the four branches more frequently than this single transition due to the availability of these transitions during a visit sequence (Fig. 3.11). Similarly, on umbels opportunities for transitions between rings of flowers and flights within the inner ring are less frequent than movements between adjacent outer-ring flowers (Fig. 3.15a). Thus, more flights occur between outer ring flowers, despite the greater distance. Interestingly, birds rarely flew diagonally between inner-ring flowers, as this distance is greater than moving to an adjacent inner ring flower. Overall, hummingbirds minimize flight distance within inflorescences, as allowed by the frequency of available transitions. Pyke (1981a) also noted that birds tended to move between closest flowers on inflorescences.

How do hummingbirds interpret distance? I mostly used Euclidean distances between flowers to examine hummingbird flights. However, birds may actually travel farther than implied by these distances. For instance, birds often flew in an arc between flowers that I have characterized with a linear distance between the flower tips. In addition, although flight duration increased in direct proportion to distance for racemes and umbels, a decelerating relation was observed for panicles (Fig. 3.17). If birds flew longer flight paths on panicles than those calculated, especially for the shortest distances, the flight duration of birds might well vary in direct proportion to distance. Hainsworth et al. (1983) found that birds had longer inter-flower flight durations on a three-dimensional arrangement of flowers, even though adjacent flowers were closer than those of a two-dimensional arrangement. Again, a difference between the distance perceived by hummingbirds and measured distances might explain this observation. Thus, the three-dimensional arrangement of flowers seems to influence the time, and perhaps the distance flown, as birds orient prior to a flower visit.

Hummingbirds also do not appear to be vertically constrained in their movement. Within racemes, they moved equally upwards and downwards, which resulted in frequent departures from both top and bottom whorls (Figs. 3.1b and 3.5a). On panicles, birds also moved equally up and down between branches (Fig. 3.12). As well, transitions between the upper and lower branches in routes *b* and *c* on panicles occurred with equal frequency (Fig. 3.9).

Hummingbirds may also follow a general departure rule. The probability of a bird remaining at an inflorescence after it revisited a flower decreased as the number of flowers already probed increased (Fig. 3.21). Hainsworth et al. (1983, Fig. 3) also found birds became more likely to leave an inflorescence after revisiting a flower as the number of flowers they had already visited increased. According to the marginal-value theorem, birds should depart an inflorescence when their rate of return falls below that expected for a flower. If this was the case in my arrays, intake rate in the last flower visited before a bird departed should have fallen below the rate for flowers visited previously on an inflorescence. However, when I examined the foraging paths taken through different architectures, three points were clear (Fig. 4.1). First, the rate of intake was generally consistent throughout an architecture as the bird foraged. Second, when the rate of return fell, it was mostly due to a revisited flower, which provided no reward, as all unvisited flowers offered the same nectar volume. Third, departures resulted after this drop (as predicted by the marginal-value theorem), but only when the bird had visited many flowers. Because birds rarely revisit flowers, they seem to leave before their rate of intake decreases, which does not follow the marginal-value theorem. This "premature" departure may be a result of memory of flowers visited and the path taken. Because birds generally minimize the distance they fly between flowers, they maintain a fairly consistent rate of intake. As well, hummingbirds may leave inflorescences either when they cannot remember where they have been or when their route through the

Figure 4.1. Examples of the rate of net energy gain per flower as an individual bird foraged on a a) raceme, b) panicle, and c) umbel. Numbers represent the flower position visited along the bird's foraging route (see Fig. 2.1).

a) raceme

b) panicle

c) umbel

Time (s)
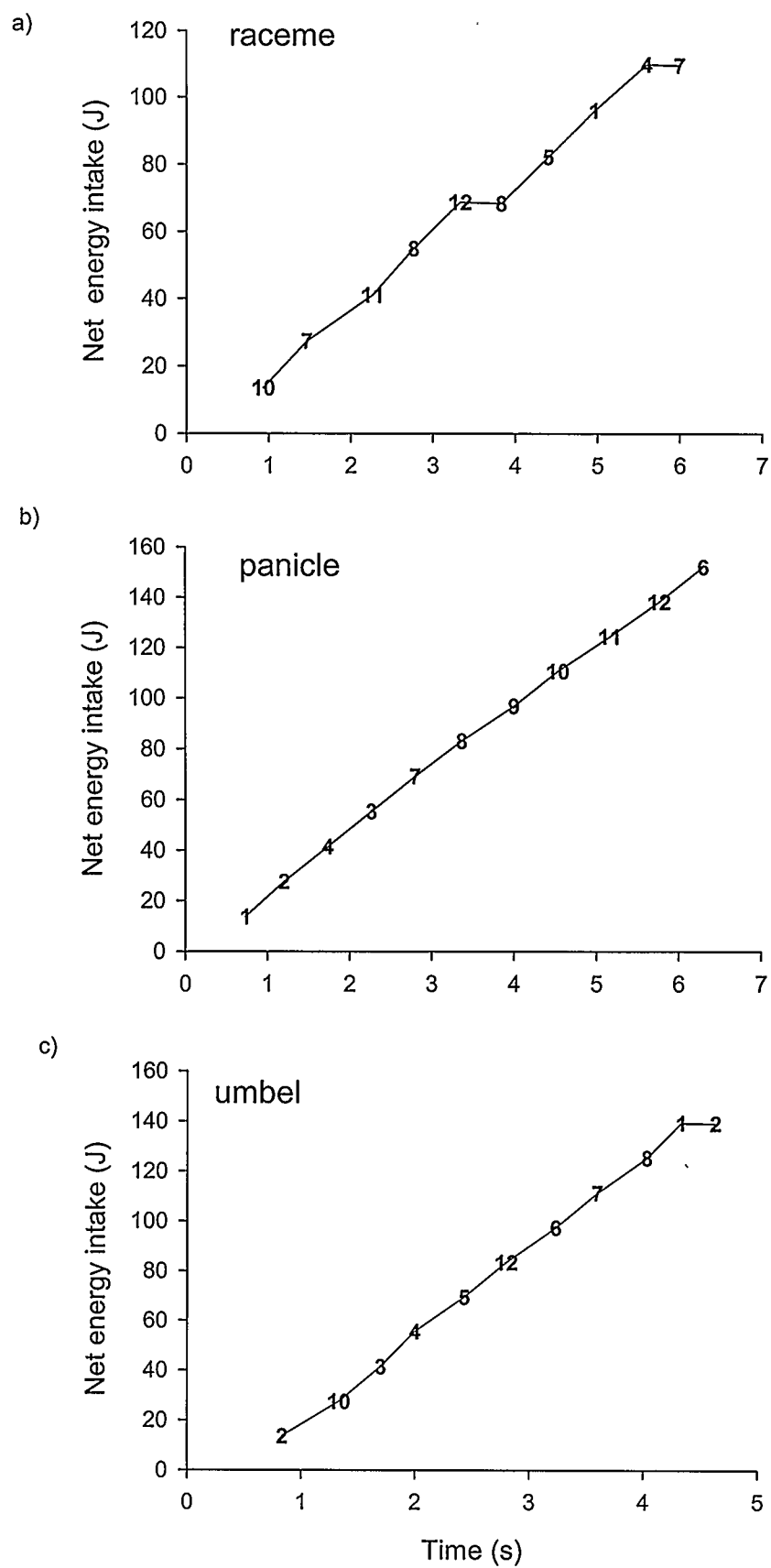
inflorescence has left flowers unvisited, but not close enough to warrant a costly flight to such a flower rather than moving to the next unvisited inflorescence. These behaviours would both reduce the chance of a revisit and maintain a constant rate of intake.

4.2 Maximization of rate of net energy intake

Hummingbirds confronted by a choice of inflorescence types do not consistently choose types that would maximize their net rate of energy intake, even though they use movement rules within inflorescences that should minimize energy expenditure. Umbels offered a higher rate of net energy intake than either panicles or racemes, yet birds did not prefer umbels when foraging in mixed arrays. In contrast, previous studies indicate that birds should choose to maximize their rate of net energy intake over many scales (e.g., Hixon et al. 1983, Montgomerie et al. 1984, Tamm 1989, Houston and Krakauer 1993).

Wolf and Hainsworth (1983) posed the question of whether hummingbirds can discriminate among energy intake rates and, if they can, do they use the information in selecting patches of plants or plant species. Only Hainsworth et al. (1983) have examined this question in the context of inflorescence structure. The hummingbirds they studied achieved a more consistent average rate of intake on a three-dimensional arrangement of flowers, even though they visited fewer flowers than on linear designs. The linear design, effectively a two-dimensional raceme, provided a higher rate of intake initially, but it decreased considerably with increasing visits due to an increased likelihood of revisits. My study also found that birds visited fewer flowers on more complex architectures (racemes and panicles), but the likelihood of a revisit was not different between inflorescence types. Thus, the consistency in the rate at which birds ingest energy did not differ between architectures (Fig. 4.1).

My mixed array of architectures could represent three 'plant species', all with the same reward per flower and floral cues, growing interspersed with each other. Birds visited these inflorescences in the proportions available. Likewise, Kodric-Brown and Brown (1978) found that hummingbirds visited *Ipomopsis aggregata* and *Penstemon barbatus* indiscriminately in proportion to their occurrence. These species displayed flowers in loose racemes at comparable heights with similar nectar rewards. My architectures differ in flower arrangements and in that umbels presented flowers higher than the other inflorescences (Fig. 2.2). However, hummingbirds in my experiment visited umbels as frequently as racemes and panicles. Thus, the height difference of umbels did not appear to affect their choice.

Mitchell (1989) explained the partial preferences of foraging hummingbirds for poor and rich feeders in terms of levels of information available to the forager. He characterized foragers as "myopic" if they knew the location and expected quality of only one resource, or as "periscopic" if they had knowledge of multiple resources. In his experiment, periscopic birds exploited poor flowers that neighboured rich ones more often than isolated poor flowers, presumably because of differences in travel costs. Due to the design of my mixed array (Fig. 2.2), the closest inflorescences were never the same architecture as the one on which the bird had just foraged. Thus, when a bird was foraging on an umbel, the closest options were lower rewarding racemes and panicles. If these birds were periscopic, they might choose to visit a raceme or panicle in the vicinity, even though it offered a lower rate of net energy intake. If this was the case, a different spacing regime, a multiple hexagonal pattern, with equal distances between all architectures might result in preference for umbels. Similarly, if much greater distances separated inflorescences, birds might choose umbels over the other architectures since the cost of travel to a poor inflorescence would be higher.

Although hummingbirds did not choose the most rewarding inflorescence, their movement patterns may have allowed them to maximize their rate of net energy intake within inflorescences (Fig 4.1). The lack of choice between inflorescence types may also be governed by hummingbirds having a periscopic view of the landscape, whereby they minimize flight costs as they visit rewarding patches. However, the scale of the patch may not be the same for the birds as I considered for the experiment. Because each flower in a mixed array had the same reward, the entire array could have been a highly rewarding patch, rather than each inflorescence being a patch that differed in reward quality (based on rate of net energy intake). Either the birds ignored differences between the inflorescence types, accounted for them in their foraging behaviour, or were unable to detect differences in rate of intake at the inflorescence level.

4.3 Context dependence of foraging rules

The general rules that hummingbirds follow while foraging within inflorescences were modified by context. Irrespective of architecture, birds visited more flowers on the first inflorescence of a bout. Why would they do this when their rate of intake appears consistent, regardless of number of flowers visited? One explanation might be that birds used different foraging paths on each inflorescence in a sequence, taking a route that maximized the number of flowers visited on the first inflorescence and then changing where they start their bout on subsequent inflorescences. This change might leave some flowers 'orphaned', so that the cost to visit them would be higher than that of moving to the next inflorescence. Alternatively, birds might have a higher tendency to visit 'orphaned' flowers on the first inflorescence. This seems unlikely because energy intake increases consistently throughout an inflorescence visit and would decline (and result in departure) if these 'orphaned' flowers were visited. Another explanation may be that hummingbirds use the first inflorescence to sample the environment. Hummingbirds

sample their environment even when such behaviour may not be profitable (Tamm 1987). Birds may gain information on the first inflorescence that they visit thoroughly and use it subsequently during that bout and in future bouts (Valone 1992). Alternatively, birds may use the first inflorescence to meet their immediate energy needs and then reduce the number of flowers visited on subsequent inflorescences as they approach satiation and as meal size increases flight costs (DeBenedictis et al. 1978). Visits to these later inflorescences may provide information of patch quality for the future.

The arrival and departure patterns of hummingbirds to inflorescences also can be context dependent. Arrival positions on racemes differed between pure and mixed arrays (Fig. 3.25a). Birds arrived at the lower two whorls less often in mixed arrays than in pure arrays. This change may be due to an increase in the overall height distribution of flowers in mixed arrays (Fig. 2.2). Because most flowers in the array were higher than those presented by racemes, birds may not have descended as frequently to the lower whorls of racemes. The positions form which hummingbird departed panicles also differed between array types (Fig. 3.25b). Birds left from the top and bottom branches in mixed arrays, whereas they tended to depart from the top branch in pure arrays. Hummingbirds may differ in their response to panicles in mixed arrays because they changed the direction of their route through the inflorescence, or they responded to the vertical level of flowers on the next inflorescence. For example, when birds departed from the lower branches of panicles for a raceme, they arrived equally at the four whorls.

The density of flowers on an inflorescence may also play a role in hummingbird foraging. Birds typically arrived at panicles in both mixed and pure arrays at the bottom two branches (Fig. 3.6). This preference may have been a response to the greater apparent density of flowers on these branches. Hummingbirds preferentially visit inflorescences with many flowers (Wolf and Hainsworth 1990) and the greatest apparent size (Pyke 1981b). Clusters of flowers on the bottom branches of my panicles may have

increased the size and attractiveness of the inflorescence, which could result in hummingbirds selecting those branches first.

Foraging routes within an inflorescence could also be context dependent. On umbels, flights between the inner and outer rings involving flowers 1 or 5 did not reflect the symmetrical pattern observed for transitions involving flowers 3 or 7 (Fig. 3.14). Why did this occur? The differences in movement patterns may be due to the orientation of the umbels, as they were presented at an angle rather than horizontally. Transitions from flowers 3 or 7 were probably symmetric because, for the most part, they are vertical transitions and cost the same regardless of the actual transition. However, flowers 1 or 5 are oriented more horizontally, so perhaps it was easier (memory) or less costly (more future movements could be downward, especially because flowers 1 and 5 were common arrival points at an umbel) for a bird to translate its movement up and in rather than down and in, which occurred infrequently.

Foraging routes within inflorescences seem to have been little affected by context. In all architectures, routes generally involved the closest flower available. In panicles, birds flew from flower 9 to 12, but not from flower 12 to 8 (Fig. 3.9). Why was there a difference if birds respond to the closest option? Usually, birds move in a sequence of flowers 7, 8 and 9. Each transition in that sequence is the closest option, and thus when a bird reaches flower 9, it can either go to flower 10 or 12. However, from flower 12, flower 8 is the closest option. Thus, foraging routes depend on the path the bird takes and the general movement rules used.

4.4 Differences between the sexes

Foraging differences between female and male hummingbirds could result from morphological differences and/or behavioural demands. Male rufous hummingbirds have lighter bodies but higher wing loading than females (Calder 1993), which should result in

a higher cost of hovering, but greater maneuverability in flight (Chai and Dudley 1999). Such differences should result in males visiting more flowers per inflorescence than females to limit flight costs. In contrast, males visited two fewer flowers per inflorescence, on average, than females.

Alternatively, male and female hummingbirds may also experience different energy demands from behaviour. Females are solely responsible for incubation and parental care (Calder 1993), so they may require more energy to sit on the nest or provision offspring. They might accumulate as much energy as possible to stay on the nest longer or satiate offspring. Males vigorously defend territories and frequent, short foraging bouts may allow them to remain vigilant for much of the time. Females seemed more driven to accumulate energy in my arrays. They visited 60% more flowers than males during foraging bouts and more flowers per inflorescence. They also visited most inflorescences in the pure arrays, unlike males. The sexes also differed in the number of flowers visited per inflorescence, depending on the inflorescence's sequence in a bout. Both sexes visited fewer flowers on the second inflorescence than they had on the first inflorescence, but females increased the number of flowers they visited on the last inflorescence, whereas males did not. Males may not need to top-up their energy before returning to their perch. Females may visit more flowers on the last inflorescence to fill more of their crop before leaving to care for young. Because hummingbirds develop spatially structured expectations about the quality of their environment (Sutherland and Gass 1995), females may revisit more inflorescences because of an expectation of constant reward and their energetic demands.

4.5 Why did hummingbirds not visit all flowers?

On average, hummingbirds did not visit all flowers on an inflorescence. It is not clear whether birds can remember all of the flowers they have visited on an inflorescence,

even within a bout (Waser and McRobert 1998, Healy and Hurly 2001). Thus, hummingbirds may be limited by their memory of where they have been within an inflorescence. However, hummingbirds have a remarkable spatial memory (Gass and Sutherland 1985, Sutherland and Gass 1995, Healy and Hurly 2001), and revisits occur rarely, although they increase with the number of flowers already visited on an inflorescence (Fig. 3.20). When a revisit occurs, a bird is likely to depart an inflorescence, especially if most of the flowers have been visited. It seems as though either the foraging path or memory generally prevents revisits until the total number of flowers visited is high.

Valone (1992) found that hummingbirds remembered the last few flowers visited but not those visited earlier in an array. If that was also true for my experiment, a bird's foraging route may be important in reducing the frequency of revisits (see Dreisig 1985). However, I observed hummingbirds visiting 'orphaned' flowers that were excluded from their route, especially on racemes and panicles. This implies that birds can remember flowers that they missed previously on an inflorescence and that complex architectures may facilitate this ability. Perhaps birds can use the greater relative distance between flowers on racemes and panicles, compared to umbels, to assist their memory.

Birds visited fewer flowers on the three-dimensional inflorescences than on umbels, even though they seem more able to remember their route or flower locations. How do these seemingly contradictory observations complement each other? Birds seem to use energetics and memory while foraging. Using general movement rules, birds minimize flight durations and follow a route dependent upon their arrival position. Thus, on two-dimensional umbels, a bird should visit many flowers, as the cost of moving between them is low. However, when a bird has visited many flowers on a three-dimensional architecture, it must eventually decide whether to continue foraging and risk a memory error, or to leave. 'Orphaned' flowers may not be worth the energetic cost

much of the time, even if the bird can remember where they are located. Thus, particular flowers within three-dimensional inflorescences may have higher probabilities of not being visited depending on their location in an inflorescence and hummingbird foraging routes.

4.6 General foraging

Overall, hummingbirds foraged similarly on both pure and mixed arrays. In mixed arrays, birds visited approximately five of sixteen inflorescences and 39 flowers in a bout. Waser and McRobert (1998) found that birds visited between 4 and 5 *Ipomopsis aggregata* plants and between 30-40 flowers per bout. Birds in Wolf and Hainsworth's (1991) study visited five inflorescences per bout. Thus, hummingbird foraging behaviour does not appear to differ between natural plants and my artificial inflorescences.

While I did not explicitly examine search behaviour within mixed arrays, birds moved between the closest adjacent inflorescences and usually followed rows or columns. This was close to the directional search which Baum and Grant (2001) observed and simulated for uniformly rewarding patches. However, Wolf and Hainsworth (1990) found that hummingbirds used area-restricted search between clumped *I. aggregata* inflorescences. Spatial distribution of the patches may result in these different search tactics.

4.7 Hummingbirds are not feathered bees

My study has demonstrated that although hummingbirds follow general foraging rules (see Section 4.1), they behave very differently from bumble bees while foraging on inflorescences. Previously, the only contrast possible of pollinator foraging involved the behaviours of these pollinators on racemes, which are well documented (e.g. compare Wolf and Hainsworth 1986 to Best and Bierzychudek 1982). My study agrees with the evidence available for hummingbird movement patterns on racemes (Pyke 1978c, 1981a,

Devlin and Stephenson 1985, Wolf and Hainsworth 1986). Hummingbirds start visits at any position within racemes, move up and/or down, and depart from top or bottom flowers. They tend to move laterally or down between inflorescences. This pattern is in direct contrast to the stereotypic pattern of bees. Bumble bees start visits at the bottom of racemes, move upwards, visiting most flowers, and depart from the top (reviewed in Jordan 2000). They subsequently fly downwards to the next inflorescence.

On panicles, bumble bees also have an overall upward movement pattern (Jordan 2000), although they follow less consistent paths as they move among flowers on branches. In contrast, hummingbirds forage more predictably on panicles than on racemes. They followed three general routes through my panicles, treating the inflorescence as an edge. Unlike bees, as birds foraged along a branch, they never crossed over the branch to access the nearest flower on the other side. Although the routes followed by hummingbirds and bumble bees within inflorescences differ, the arrivals and departures of hummingbirds, like those of bees, tend to be to the bottom and from the top branches of the panicle, respectively.

Hummingbirds also exhibit different foraging patterns from bumble bees on umbels. Although both bumble bees and birds arrive on the outer flowers, birds almost always depart from them as well. In contrast, bumble bees depart equally from inner and outer flowers (Jordan 2000). After arriving at an outer flower, bumble bees frequently move to an inner flower, taking them across the umbel. Hummingbirds are more likely to remain on the outer ring of flowers for several flowers as they move around the umbel before visiting inner flowers.

Inflorescence architecture also affected the number of flowers visited by bumble bees and hummingbirds differently. Architecture affected the number of flowers visited by bumble bees only weakly (Jordan 2000). On average, they visited less than one flower more on umbels than on panicles, with racemes not differing from either of these

types. In contrast, inflorescence architecture strongly affected the number of flowers visited by hummingbirds, as they visit more flowers on umbels than on racemes or panicles (Fig. 3.19).

Finally, like bumble bees, hummingbirds use some general foraging rules. Both pollinator groups tend to move between neighboring flowers and inflorescences while foraging. Bees incorporate vertical directionality in their foraging (Waddington 1983), whereas hummingbirds seem to be much more inconsistent in movement direction. Bees use simple departure rules when leaving inflorescences such as threshold nectar rules or amount of nectar reward (Hodges 1985, Cresswell 1990). Both bees and birds should depart an inflorescence when the rate of energy intake declines. However, birds in my experiment maintain a consistent rate of intake within inflorescences, even when they choose to leave the inflorescence. Wolf and Hainsworth (1986) found that hummingbirds departed after visiting an empty flower, whereas Pyke (1978c) concluded that birds used an optimal rule based on inflorescence size, flowers visited and nectar reward. It is not clear whether birds in my experiment behaved differently because they encountered flowers with fixed nectar volumes, but they leave after revisiting a flower when they have visited many flowers on an inflorescence.

4.8 Architecture modifies behaviour

My study has demonstrated that inflorescence architecture can modify foraging behaviour in several ways. I have demonstrated that the spacing of flowers on an inflorescence can influence the number of flowers visited and the order and speed with which they are visited. Birds and bees (Jordan 2000) visit more flowers on umbels, a denser inflorescence. Hummingbirds also visit flowers on umbels more quickly than on racemes or panicles. Larger or apparently larger inflorescences are more attractive to pollinators (Wolf and Hainsworth 1990, Pyke 1981b, respectively). Plants can vary this

attractiveness by adjusting the number of open flowers and their spacing. Many inflorescences have few open flowers, but developing and finished flowers may also serve to make the display more attractive (Gori 1983). The spacing and number of flowers can have two effects on pollinators: earlier departures (fewer, more widely spaced flowers) and easier routes through the inflorescence to create a more consistent path (Dreisig 1985).

Even though hummingbirds tend to treat inflorescences as edges, their arrivals and departures can be manipulated. More flowers, spaced closely together, increase the proportion of arrivals to the lower branches of panicles. As well, birds arrived at exterior flowers first. Regardless of the consistency of the route, birds often departed panicles from the uppermost branch. These results suggest that architecture can modify behaviour, but some aspects do not change with context. In mixed arrays, the relative heights of flowers on racemes, compared to the rest of the array, changed the arrival pattern of hummingbirds, but foraging behaviour within racemes did not change. As a result, hummingbird departure patterns did not change. On the other hand, the location of arrivals to panicles did not change in mixed arrays, but foraging routes were modified so that birds departed from both the top and bottom branches.

Overall movement within an inflorescence can be modified by architecture. On racemes, birds leave from the top and bottom of the inflorescence, whereas hummingbirds tend to arrive at the bottom of panicles and leave from the top. Panicles modify birds' foraging in a manner that creates a more consistent pattern between inflorescences.

Architecture appears to change the consistency in the foraging paths that hummingbirds use. Hummingbirds do not use a consistent route on either racemes or umbels, whereas they forage on panicles using three linear routes (Fig. 3.10b). The direction of these routes still depends on the position at which the bird arrives and the

initial direction it chooses. However, selection for improved mating may result in the evolution of inflorescence designs that impose more consistent foraging paths (see below).

The relative consistency of foraging paths on similar architectures also depends on the pollinator's response. Wolf and Hainsworth (1983) suggested that the three-dimensional organization of plants either confuses or facilitates a foraging bird. If it confuses the bird, the bird may depart earlier and have a less consistent foraging pattern within the inflorescence. They suggested that the racemose design of *I. aggregata* does just this, whereas *Leonotis nepetifolia* facilitates sunbird visitation. *Leonotis* produces verticillate cymes, with whorls of flowers (paw) at intervals along a vertical stalk (Gill and Wolf 1977). Sunbirds, which perch, visit most flowers at one paw, by rotating around it, before flying horizontally to the next stalk, rather than upwards to the next paw. In direct contrast to this observation, hummingbirds move vertically between whorls on the verticillate cyme of *Salvia spathecea* in an inconsistent manner (pers. obs.). Thus, inflorescence design can impact different pollinators in different ways, with contrasting consequences for plant mating systems (Lange and Scott 1999).

4.9 Opportunity for plants to control mating by manipulating pollinator foraging

Hummingbird foraging behaviour appears more plastic than that of bees, which begs the question: "If behaviour is plastic, is it harder or easier to manipulate behaviour through architecture and thus control mating opportunities?". Plants take advantage of the stereotypic foraging pattern of bumble bees. In bee-pollinated plants with vertical inflorescences, flowers typically mature upward from the bottom of the inflorescence, which likely reflects bee foraging patterns (Bertin and Newman 1993, Harder et al. 2000). Because bees move upwards on an inflorescence, they remove pollen from the top flowers and deposit it on the lower female flowers of the next individual, thereby

promoting cross-pollination, rather than geitonogamous self-pollination (Best and Bierzychudek 1982, Barrett et al. 1994). In contrast, hummingbirds do not follow the same foraging pattern on racemes. As a result, racemose plants may suffer higher rates of selfing, loss of outcrossing opportunities and perhaps inbreeding depression. Thus, vertical protandry may not be an effective strategy for hummingbird-pollinated plants, which may select for alternate flowering patterns within inflorescences.

How have plants adapted to inconsistencies of hummingbird foraging? One means that plants have adopted is to synchronize the sexual phase of dichogamous (temporal separation of sexual phases) flowers within inflorescences, as in *Delphinium cardinale* (pers. obs.) and *Bomarea acutifolia* (Snow and Grove 1995). Thus, plants increase their outcrossing potential and eliminate the chance of geitonogamy.

Nectar distributions are another way plants can modify bird behaviour. *Lobelia cardinalis* presents a top-down nectar gradient within its raceme (Devlin and Stephenson 1985). Birds respond to this gradient by arriving in the middle of the inflorescence and moving upward much of the time. An increase in the consistency of movements within the inflorescence results in greater outcrossing potential.

Schemske (1980) suggested that the large nectar production of *Combretum farinosum* satiates territorial hummingbirds, which establish territories on a plant or portion thereof, and therefore provide low outcrossing potential for individual plants. Satiation reduces the advantage of territory defense and enables transient birds to increase the outcrossing potential of the plant. Floral development in this plant is also synchronized, but flowers are simultaneously hermaphroditic. The inflorescence is dense rows of flowers on a liana. Applying the results of my studies, birds would move along the rows of flowers, likely in one direction. However, if birds are satiated quickly on the inflorescence, the number of flowers visited is reduced and self-pollination potential is also reduced in this manner.

Variability in nectar rewards in a plant may result in a more complex foraging pattern, for example on racemes (Wolf and Hainsworth 1983). Thus, if a bird's rate of energy intake is reduced or it probes an empty flower, earlier departures from the plant may result. This response may minimize geitonogamy and increase the outcrossing potential. Hummingbirds learn complex patterns less well than simple ones (Sutherland and Gass 1985). The ability to learn patterns of rewards may be important if the pattern is repeated within and between inflorescences of a plant species (Hurly and Healy 2002), as in bee-pollinated plants (see also Devlin and Stephenson 1985). Thus, plants may manipulate pollinator behaviour using a combination of architecture, reward schedules and attractive display. Likewise, pollinator foraging behaviour can impact plant mating and a shift in pollinators may have evolutionary consequences for plant architecture.

LITERATURE CITED

Baker, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. Biotropica 7:37-41.

Barrett, S. C. H., L. D. Harder, and W. W. Cole. 1994. Effects of flower number and position on self-fertilization in experimental populations of *Eichhornia paniculata* (Pontederiaceae). Functional Ecology 8:526-535.

Baum, K. A., and W. E. Grant. 2001. Hummingbird foraging behavior in different patch types: simulation of alternative strategies. Ecological Modelling 137:201-209.

Bertin, R. I., and C. M. Newman. 1993. Dichogamy in angiosperms. Botanical Review 59:112-152.

Best, L. S., and P. Bierzychudek. 1982. Pollinator foraging on foxglove (*Digitalis purpurea*): a test of a new model. Evolution 36:70-79.

Biernaskie, J. M., R. V. Cartar, and T. A. Hurly. 2002. Risk-averse inflorescence departure in hummingbirds and bumble bees: could plants benefit from variable nectar volumes? Oikos 98:98-104.

Brown, G. S., and C. L. Gass. 1993. Spatial learning association by hummingbirds. Animal Behaviour 46:487-497.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer-Verlag, New York.

Calder, W. A. 1993. Rufous hummingbird (*Selasphorus rufus*). *In* Poole, A., and F. Gill (eds.). The birds of North Amercia, No. 53. The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C. Pp. 1-20.

Campbell, D. R., N. M. Waser, and G. T. Pederson. 2002. Predicting patterns of mating and potential hybridization from pollinator behavior. American Naturalist 159:438-450.

Caraco, T., W. U. Blanckenhorn, G. M. Gregory, J. A. Newman, G. M. Recer, and S. M. Zwicker. 1990. Risk-sensitivity: ambient temperature affects foraging choice. Animal Behaviour 39:338-345.

Cartar, R. V., and L. A. Real. 1997. Habitat structure and animal movement: the behaviour of bumble bees in uniform and random spatial resource distributions. Oecologia 112:430-434.

Chai, P., and R. Dudley. 1999. Maximum flight performance of hummingbirds: capacities, constraints, and trade-offs. American Naturalist 153:398-411.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129-126.

Corbet, S. A., I. Cuthill, M. Fallows, T. Harrison, and G. Hartley. 1981. Why do nectar-foraging bees and wasps work upwards on inflorescences? Oecologia 51:79-83.

Cresswell, J. E. 1990. How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot *Monarda fistulosa* (Lamiaceae)? Oecologia 82:450-460.

Cresswell, J. E., J. L. Osborne, and S. A. Bell. 2002. A model of pollinator-mediated gene flow between plant populations with numerical solutions for bumblebees pollinating oilseed rape. Oikos 98:375-384.

DeBenedictis, P. A., F. B. Gill, F. R. Hainsworth, G. H. Pyke, and L. L. Wolf. 1978. Optimal meal size in hummingbirds. American Naturalist 112:301-315.

Devlin, B., and A. G. Stephenson. 1985. Sex differential floral longevity, nectar secretion, and pollinator foraging in a protandrous species. American Journal of Botany 72:303-310.

Dreisig, H. 1985. Movement patterns of a clear-wing hawkmoth, *Hemaris fuciformis*, foraging at red catchfly, *Viscaria vulgaris*. Oecologia 67:360-366.

Dukas, R., and L. A. Real. 1993. Effects of recent experience on foraging decisions by bumble bees. Oecologia 94:244-246.

Gass, C. L., and R. D. Montgomerie. 1981. Hummingbird foraging behavior: decision-making and energy regulation. *In* Kamil, A. C., and T. D. Sargent (eds.). Foraging behavior: ecological, ethological and psychological approaches. Garland STPM Press, New York. Pp. 159-194.

Gass, C. L., and W. M. Roberts. 1992. The problem of temporal scale in optimization: three contrasting views of hummingbird visits to flowers. American Naturalist 140:829-853.

Gass, C. L., and G. D. Sutherland. 1985. Specialization by territorial hummingbirds on experimentally enriched patches of flowers: energetic profitability and learning. Canadian Journal of Zoology 63:2125-2133.

Gilbert, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. *In* Gilbert, L. E., and P. H. Raven (eds.). Coevolution of animals and plants. University of Texas Press, Austin, Texas. Pp. 210-240.

Gill, F. B. 1988. Trapline foraging by hermit hummingbirds: competition for an undefended, renewable resource. Ecology 69:1933-1942.

Gill, F. B., and L. L. Wolf. 1977. Nonrandom foraging by sunbirds in a patchy environment. Ecology 58:1284-1296.

Gori, D. F. 1983. Post-pollination phenomena and adaptive floral changes. *In* Jones, C. E., and R. J. Little (eds.). Handbook of experimental pollination biology. van Nostrand Reinhold, New York. Pp. 31-49.

Goulson, D. 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. Perspectives in Plant Ecology, Evolution and Systematics 2:185-209.

Green, R. F. 1984. Stopping rules for optimal foragers. American Naturalist 123:80-90.

Hainsworth, F. R., T. Mercier, and L. L. Wolf. 1983. Floral arrangements and hummingbird feeding. Oecologia 58:225-229.

Harder, L. D., and S. C. H. Barrett. 1996. Pollen dispersal and mating patterns in animal-pollinated plants. *In* Lloyd, D. G., and S. C. H. Barrett (eds.). Floral biology: studies on floral evolution in animal-pollinated plants. Chapman and Hall, New York. Pp. 140-190.

Harder, L. D., S. C. H. Barrett, and W. W. Cole. 2000. The mating consequences of sexual segregation within inflorescences of flowering plants. Proceedings of the Royal Society of London B Biological Sciences 267:315-320.

Harder, L. D., N. M. Williams, C. Y. Jordan, and W. A. Nelson. 2001. The effects of floral design and display on pollinator economics and pollen dispersal. *In* Chittka, L., and J. D. Thomson (eds.). Cognitive ecology of pollination. Cambridge University Press, Cambrige, Pp. 297-317.

Healy, S. D., and T. A. Hurly. 2001. Foraging and spatial learning in hummingbirds. *In* Chittka, L., and J. D. Thomson (eds.). Cognitive ecology of pollination. Cambridge University Press, Cambridge. Pp. 127-147.

Heinrich, B. 1979. Resource heterogeneity and patterns of movement in foraging bumblebees. Oecologia 40:235-245.

Heyneman, A. J. 1983. Optimal sugar concentrations of floral nectars – dependence on sugar intake efficiency and foraging costs. Oecologia 60:198-213.

Hixon, M. A., F. L. Carpenter, and D. C. Paton. 1983. Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. American Naturalist 122:366-391.

Hodges, C. M. 1985. Bumble bee foraging: energetic consequences of using a threshold departure rule. Ecology 66:188-197.

Houston, A. I., and D. C. Krakauer. 1993. Hummingbirds as net rate maximizers.

Oecologia 94:135-138.

Huntingford, F. A. 1993. Can cost-benefit analysis explain fish distribution patterns? Journal of Fish Biology 43 (Supplement A):289-308.

Hurly, T. A., and S. D. Healy. 2002. Cue learning by rufous hummingbirds (*Selasphorus rufus*). Journal of Experimental Psychology: Animal Behavior Processes 28:209-223.

Iwasa, Y., T. J. de Jong, and P. G. L. Klinkhamer. 1995. Why pollinators visit only a fraction of the open flowers on a plant: the plant's point of view. Journal of Evolutionary Biology 8:439-453.

Jennrich, R. I., and M. D. Schluchter. 1986. Unbalanced repeated-measures models with structured covariance matrices. Biometrics 42:805-820.

Jones, E. G. 1993. Throat patterns of female rufous hummingbirds. North American Bird Bander 18:13-14.

Jordan, C. Y. 2000. The consequences of inflorescence architecture for bumble bee behaviour and plant mating. Masters Thesis. University of Calgary, Calgary, Alberta.

Kadmon, R., and A. Shmida 1992. Departure rules used by bees foraging for nectar: a field test. Evolutionary Ecology 6:142-151.

Keasar, T., A. Shmida, and U. Motro. 1996. Innate movement rules in foraging bees: flight distances are affected by recent rewards and are correlated with choice of flower type. Behavioral Ecology and Sociobiology 39:381-388.

Kirk, R. E. 1995. Experimental design: procedures for the behavioral sciences. Brooks/Cole, Pacific Grove, CA.

Kodric-Brown, A., and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. Ecology 59:285-296.

Lange, R. S., and P. E. Scott. 1999. Hummingbird and bee pollination of *Penstemon pseudospectabilis*. Journal of the Torrey Botanical Society 126:99-106.

Liang, K. Y., and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. Biometrika 73:13-22.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute Inc., Cary, NC.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models, 2nd edition. Chapman and Hall, London.

McNamara, J. M., and A. I. Houston. 1980. The application of statistical decision theory to animal behavior. Journal of Theoretical Biology 85:673-690.

Miller, R. S. 1985. Why hummingbirds hover. Auk 102:722-726.

Mitchell, W. A. 1989. Informational constraints on optimally foraging hummingbirds. Oikos 55:145-154.

Montgomerie, R. D., J. M. Eadie, and L. D. Harder. 1984. What do foraging hummingbirds maximize? Oecologia 63:357-363.

Neter, J., M. H. Kutner, C. J. Nachtsheim and W. Wasserman. 1996. Applied linear statistical models, 4th edition. Irwin, Chicago.

Pyke, G. H. 1978a. Are animals efficient harvesters? Animal Behaviour 26:241-250.

Pyke, G. H. 1978b. Optimal foraging: movement patterns of bumblebees between inflorescences. Theoretical Population Biology 13:72-98.

Pyke, G. H. 1978c. Optimal foraging in hummingbirds: testing the marginal value theorem. American Zoologist 18:739-752.

Pyke, G. H. 1979. Optimal foraging in bumblebees: rules of movement between flowers within inflorescences. Animal Behaviour 27:1167-1181.

Pyke, G. H. 1981a. Hummingbird foraging on artificial inflorescences. Behaviour Analysis Letters 1:11-15.

Pyke, G. H. 1981b. Optimal foraging in hummingbirds: rule of movement between inflorescences. Animal Behaviour 29:889-896.

Pyke, G. H., and N. M. Waser. 1981. The production of dilute nectars by hummingbird and honeyeater flowers. Biotropica 13:260-270.

Pyke, G. H., and R. V. Cartar. 1992. The flight directionality of bumblebees: do they remember where they came from? Oikos 65:321-327.

Schemske, D. W. 1980. Floral ecology and hummingbird pollination of *Combretum farinosum* in Costa Rica. Biotropica 12:169-181.

Schemske, D. W., and H. D. Bradshaw, Jr. 1999. Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). Proceedings of the National Academy of Sciences of the United States of America 96:11910-11915.

Snow, A. A., and K. F. Grove 1995. Protandry, a neuter phase, and unisexual umbels in a hermaphroditic, neotropical vine (*Bomarea acutifolia*, Alstroemeriaceae). American Journal of Botany 82:741-744.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry, 3rd edition. W.H. Freeman and Company, New York.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.

Sutherland, G. D., and C. L. Gass. 1995. Learning and remembering of spatial patterns by hummingbirds. Animal Behaviour 50:1273-1286.

Tadey, M., and M. A. Aizen. 2001. Why do flowers of a hummingbird-pollinated mistletoe face down? Functional Ecology 15:782-790.

Tamm, S. 1987. Tracking varying environments: sampling by hummingbirds. Animal Behaviour 35:1725-1734.

Tamm, S. 1989. Importance of energy costs in central place foraging by hummingbirds. Ecology 70:195-205.

Thomson, J. D., and B. A. Thomson. 1989. Dispersal of *Erythronium grandiflorum* pollen by bumblebees: implications for gene flow and reproductive success. Evolution 43:657-661.

Valone, T. J. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. Animal Behaviour 41:569-577.

Valone, T. J. 1992. Information for patch assessment: a field investigation with black-chinned hummingbirds. Behavioral Ecology 3:211-222.

Waddington, K. D. 1983. Foraging behavior of pollinators. *In* Real, L. (ed.). Pollination biology. Academic Press, Orlando, Florida. Pp. 213-239.

Waddington, K. D., and B. Heinrich. 1979. The foraging movements of bumblebees on vertical "inflorescences": an experimental analysis. Journal of Comparative Physiology 134:113-117.

Waser, N. M. 1982. A comparison of distances flown by different visitors to flowers of the same species. Oecologia 55:251-257.

Waser, N. M., and J. A. McRobert. 1998. Hummingbird foraging at experimental patches of flowers: evidence for weak risk-aversion. Journal of Avian Biology 29:305-313.

Wesselingh, R. A., and M. L. Arnold. 2000. Pollinator behaviour and the evolution of Louisiana iris hybrid zones. Journal of Evolutionary Biology 13:171-180.

Williams, C. S. 1998. The identity of the previous visitor influences flower rejection by nectar-collecting bees. Animal Behaviour 56:673-681.

Williams, N. M., and J. D. Thomson. 1998. Trapline foraging by bumble bees: III. Temporal patterns of visitation and foraging success at single plants. Behavioral Ecology 9:612-621.

Wolf, L. L., and F. R. Hainsworth. 1983. Economics of foraging strategies in sunbirds and hummingbirds. *In* Aspey, W. P., and S. I. Lustick (eds.). Behavioral

energetics: the cost of survival in vertebrates. Ohio State University Press, Columbus, Ohio. Pp. 223-264.

Wolf, L. L., and F. R. Hainsworth. 1986. Information and hummingbird foraging at individual inflorescences of *Ipomopsis aggregata*. Oikos 46:15-22.

Wolf, L. L., and F. R. Hainsworth. 1990. Non-random foraging by hummingbirds: patterns of movement between *Ipomopsis aggregata* (Pursch) V. Grant inflorescences. Functional Ecology 4:149-157.

Wolf, L. L., and F. R. Hainsworth. 1991. Hummingbird foraging patterns: visits to clumps of *Ipomopsis aggregate* inflorescences. Animal Behaviour 41:803-812.

Wolf, L. L., F. R. Hainsworth, and F. B. Gill. 1975. Foraging efficiencies and time budgets in nectar-feeding birds. Ecology 56:117-128.

Wyatt, R. 1982. Inflorescence architecture: how flower number, arrangement, and phenology affect pollination and fruit-set. American Journal of Botany 69:585-594.