DYNAMICS OF HUMMINGBIRD MEDIATED POLLEN FLOW IN
A SUBALPINE MEADOW

By
MARY DEE CHYNOWETH PERKINS

B.Sc., University of Oklahoma, 1973

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in
THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA
December, 1977
(c) Mary Dee Chynoweth Perkins, 1977
Abstract

Previous authors have concluded that hummingbird territorial boundaries would restrict pollen flow. I questioned the validity of this on the time scale of a blooming season for a system in which individual plants remained in flower while the territories surrounding them often changed in size and shape. To determine the effects of hummingbird foraging behavior on pollen flow, I studied six components of a hummingbird-plant pollination system: hummingbird territorial behavior, plant blooming time, foraging flight distances, pollen carry over, other pollinators, and plant breeding systems. Using this information I found I could depict pollen flow between two plants as a function of:

1) The flowering times of the plants.
2) The distance between the plants.
3) The amount of time these plants are surrounded by the same territorial boundaries.
4) The number of plants (or flowers) the bird visits before visiting the second plant.

I found that the influence of territorial boundaries on pollen flow is determined not by the boundary of a single territory, but by the influence of all the territorial boundaries surrounding a plant while it is in bloom. Within these boundaries, the probability of pollen being transferred between two plants is a function of the amount of time they are within the same boundary. The length of hummingbird foraging flights is also a major determinant of pollen flow and the predominance of
short flights between plants may restrict pollen flow probabilities. The restriction imposed by these short flights may be reduced by 1) long pollen carry over distances and 2) the longer flight distances between a perch and a plant.
# Table Of Contents

Abstract ........................................................................................................ i  
LIST OF FIGURES .................................................................................. vi  
LIST OF TABLES .................................................................................... viii  
ACKNOWLEDGEMENTS ......................................................................... ix  
INTRODUCTION ...................................................................................... 1  
THE COMPONENTS OF A HUMMINGBIRD-MEDIATED POLLINATION SYSTEM ................................................................. 5  
Territorial Behavior And Plant Flowering Times ............................. 6  
Foraging Flight Distances ...................................................................... 8  
Pollen Carry Over .................................................................................... 8  
Other Pollinators .................................................................................... 9  
Plant Breeding Systems ....................................................................... 10  
METHODS ............................................................................................ 11  
The Study Area ..................................................................................... 11  
Territorial Behavior ............................................................................ 12  
Foraging Behavior ............................................................................... 15
<table>
<thead>
<tr>
<th>Topic</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Flowering Times</td>
<td>17</td>
</tr>
<tr>
<td>Pollen Carry Over</td>
<td>17</td>
</tr>
<tr>
<td>Other Pollinators</td>
<td>18</td>
</tr>
<tr>
<td>Plant Breeding Systems</td>
<td>21</td>
</tr>
<tr>
<td>RESULTS</td>
<td>22</td>
</tr>
<tr>
<td>Territorial Behavior</td>
<td>22</td>
</tr>
<tr>
<td>Plant Flowering Time</td>
<td>22</td>
</tr>
<tr>
<td>Foraging Behavior</td>
<td>37</td>
</tr>
<tr>
<td>Pollen Carry Over</td>
<td>54</td>
</tr>
<tr>
<td>Other Pollinators</td>
<td>55</td>
</tr>
<tr>
<td>Plant Breeding Systems</td>
<td>59</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>63</td>
</tr>
<tr>
<td>Pollen Flow</td>
<td>63</td>
</tr>
<tr>
<td>The Effect Of Flights To And From A Perch</td>
<td>76</td>
</tr>
<tr>
<td>Pollen Carry Over</td>
<td>78</td>
</tr>
<tr>
<td>Insect Pollinators</td>
<td>81</td>
</tr>
<tr>
<td>Plant Density</td>
<td>83</td>
</tr>
<tr>
<td>Gene Flow</td>
<td>84</td>
</tr>
<tr>
<td>Implications For Other Hummingbird Pollination Systems</td>
<td>86</td>
</tr>
</tbody>
</table>
LITERATURE CITED .................................................. 89
APPENDIX ............................................................. 94
LIST OF FIGURES

Figure 1: Photos And Drawings Of Columbine And Indian Paintbrush. ..............................................13
Figure 2: Photo Of Fuchsia Hybrida. .................................................................19
Figure 3: Changes In Size And Shape Of Territories In Meadow 1. ......................................................23
Figure 4: Changes In Size And Shape Of Territories In Meadow 2. ......................................................25
Figure 5: Changes In Territory Numbers And Size; Meadow 1. ...............................................................27
Figure 6: Changes In Territory Numbers And Size; Meadow 2. ...............................................................29
Figure 7: Flowering Stages In Columbine. ......................................................................................31
Figure 8: Flowering Stages In Indian Paintbrush. ...............................................................................33
Figure 9: Mean Flight Distance Between Patches Of Columbine. .........................................................39
Figure 10: Mean Flight Distance Between Patches Of Indian Paintbrush. ...........................................41
Figure 11: Frequency Distribution Of Distances Between Successively Visited Columbine Patches. ..........43
Figure 12: Frequency Distribution Of Distances Between Successively Visited Indian Paintbrush Patches. ..........45
Figure 13: The Mean Flight Distance To And From Perches. .................................................................49
Figure 14: Relationship Between Territory Size And Two Categories Of Hummingbird Flight Distances. ..............52
Figure 15: Pollen Carry Over For Hummingbirds Visiting Fucshia Flowers. ...............................................56
Figure 16: The Effects Of Changes In Territorial Boundaries On Potential Pollen Flow For A Plant In Meadow 1. ..................................................................................65
Figure 17: Diagramatic Representation Of Pollen Flow For Two Columbine Plants In Meadow 1. .................................69
Figure 18: Diagramatic Representation Of Pollen Flow For Two Indian Paintbrush Plants In Meadow 2. ........................72
Figure 19: Changes In The Number Of Columbine Flowers And Indian Paintbrush Inflorescences In Meadow 1. ...97
Figure 20: Changes In Number Of Columbine Flowers In Meadow 2. ........................................................................99
Figure 21: Changes In The Number Of Indian Paintbrush Inflorescences In Meadow 2. ..............................................101
LIST OF TABLES

Table I. Length Of Flowering Time For Columbine ..........35
Table II. Length Of Flowering Time For Indian Paintbrush ..36
Table III. The Influence Of Territorial Boundaries On
Hummingbird Foraging .....................................38
Table IV. Probability Of Pollen Flow For Columbine And
Indian Paintbrush ...........................................48
Table V. Relationship Between The Number Of Flowers In A
Patch To Those On A Plant ....................................51
Table VI. Probability Of Pollen Flow For Columbine And
Indian Paintbrush Based On Pollen Carry Over To The
Tenth Flower Visited ............................................58
Table VII. Seed Set Data For Columbine ....................61
Table VIII. Seed Set Data For Indian Paintbrush ..........62
Table IX. Times Of Insect Visitor Activity ....................95
Table X. Number Of Patches, Flowers And Inflorescences
(Indian Paintbrush) Visited In A Flight ....................96
"The journey need not be alone at all moments. We can and do spark one another, and carry each other on."
Paulus Berensohn

My advisor Lee Gass introduced me to Grizzly Lake and its hummers, and helped me overcome my flatlander ways. Lee has always been there with questions, ideas and support. Fred Ganders, Judy Myers, and Jamie Smith offered helpful advice along the way and assisted considerably by reading the manuscript and helping with revisions. Kurt Cehak gave long hours of help with mapping territories and with other tedious data collecting. Carl Whitney patiently helped with computer programming and provided much needed moral support. I thank Ethen Perkins for wanting to read this story and encouraging me to write it. He gave his love and encouragement throughout, suggested revision in the drafting of the manuscript, gave botanical advice and helped in the field work. Rachel Ruth Perkins has been a wonderfully rewarding diversion during the last year. Many others have knowingly and sometimes unknowingly given me help and support, and I thank them here also. Of course, without the hummingbirds and the plants none of this would have been possible.
INTRODUCTION

Pollen dispersal is of major importance in the completion of the sexual phase of flowering plant life cycles. Transfer of pollen and seed dispersal are the means by which plant genes move through populations, and sexual reproduction and consequent genetic recombination change or maintain the genetic makeup of a population. (Stebbins 1950, Grant 1958, 1971, Faegri and van der Pijl 1966, Proctor and Yeo 1972, Covich 1974, Macior, 1974).

A wide variety of mechanisms including wind, water and the visitations of various insects, birds, and mammals have been identified as means of pollen dispersal. Plants are often highly specialized to increase the effectiveness of a particular system of pollination. These adaptations are apparent in the wide range in floral morphology seen, from the fairly inconspicuous flowers of wind pollinated grasses to the showy flowers of some orchids (Knuth 1908, Percival 1965, Faegri and van der Pijl 1966, Proctor and Yeo 1972).

For successful pollination by an animal, the plant must accomplish three things. First the potential pollinator must be attracted, usually by a specific food reward (nectar or pollen). The presence of a food source and the correct procedure for obtaining it may be cued by a variety of floral signals including color, shape, and patterning of the flowers. Non-visual signals include various odors, or even tactile signals in the form of tongue and body guides (van der Pijl 1960, 1961, Percival 1965, Faegri and van der Pijl 1966, Proctor and Yeo 1972, Macior 1971). Second, the visitor must visit more
than one individual of the same species. This can be accomplished if the visitor does not become satiated at the first flower and picks up signals from the second that indicate where more food may be found (Heinrich and Raven 1972, Covich 1974, Heinrich 1975). Third, the shape of the flower and precise positioning of the reproductive parts must be such that the pollen deposited on the visitor is in a location where it will contact the stigma of the next flower visited (Percival 1965, Faegri and van der Pijl 1966, Proctor and Yeo 1972).

Specific animal pollinators possess adaptations which exploit the resources provided by a plant. These may be structural adaptations such as a tongue whose length corresponds to the length of a corolla tube, or a body shape which fits neatly into a flower (Percival 1965, Faegri and van der Pijl 1966, Proctor and Yeo 1972). The adaptations may also be behavioral, in the case of a visitor foraging at a time when the flower is open (Wolf 1970, Mosquin 1971, Heithaus 1974), or whose feeding behavior is especially effective in extracting food with the least amount of effort (Percival 1965, Faegri and van der Pijl 1966, Proctor and Yeo 1972).

In coadapted systems the specific mechanisms by which the plant and its pollinator interact reflect the characteristics of the specific individuals involved. Highly coadapted pollination systems reduce pollen wastage by ineffectual and often unreliable pollinators and guarantee a food source that is free from competition by non-adapted animals (eg. Mosquin 1971, Macior 1971, 1974).

Whatever the mechanism of pollen transport, a major
question concerns the effect of the pollen dispersal mechanism on pollen flow and thus on gene flow and the genetic makeup of the population. Variations in pollinator behavior will affect gene flow in different ways. The genetic significance of pollen flow (hence pollinator behavior) will also depend very much on the breeding system of the plant population. A pollinator that flies from flower to flower on one plant before going on to the next, or forages in a restricted area, may restrict outcrossing in the population, while a wide ranging forager may increase outcrossing (Stebbins 1950, Grant 1971, Proctor and Yeo 1972). A pollinator that forages in a restricted area may cause more inbreeding in a plant species that is self compatible than in one that is obligately outcrossing.

In order to determine the full effect of pollinator behavior on pollen and gene flow it is important to consider each individual plant-pollinator system as a whole. This is especially important in coadapted systems, where the foraging behavior of the animal visitor is often highly influenced by various plant components such as attractiveness, plant density, and the presence of other visitable plant species (e.g., Levin 1969, Levin and Kerster 1969a, 1969b, Levin and Anderson 1970, Macior 1971, 1974).

Hummingbirds are pollen vectors for many New World plant species, and the coadaptation of hummingbirds and many of the plants they visit is well documented (Grant and Grant 1966, 1968). Typical hummingbird plants, most often perennial species, produce copious amounts of nectar which is often located at the base of a long tube. In order to feed, the bird
must brush against the stigmas and anthers of the flower while gathering nectar thus pollinating the flower (Percival 1965, Faegri and van der Pijl 1966, Grant 1966, Grant and Grant 1966, 1968, Proctor and Yeo 1972). The birds have long narrow bills, tongues adapted for licking nectar, and the ability to hover, all of which aid the bird in feeding from these flowers (Bent 1940, Percival 1965, Grant and Grant 1968, Proctor and Yeo 1972). So as the birds forage they disperse pollen within the plant populations.
What are the effects of hummingbird foraging on pollen dispersal? In order to answer this question, I studied the interactions between the following components of a plant-hummingbird system: territorial behavior, plant flowering times, foraging flight distance, pollen carry over, other pollinators, and plant breeding systems.

Hummingbird foraging behavior is a complex set of behavioral patterns influenced by many factors such as floral nectar production, plant density, the presence of other birds and the energy required for foraging (Béné 1945, Grant and Grant 1968, Wolf 1969, Wolf et al. 1972, Linhart 1973, Schemske 1975, Gass et al. 1976, and others). In considering foraging behavior as the major means of pollen dispersal I concentrated on two major areas within the foraging behavior complex: 1) the relationship of territorial behavior to foraging behavior, and 2) how far a bird flies between flowers and plants on a foraging flight.
Territorial Behavior And Plant Flowering Times


How do these territories affect pollen dispersal in the plant population? Two studies have concluded that pollen flow in plant-hummingbird pollination systems would be restricted to a territory, thus limiting outcrossing in the plant population (Grant and Grant 1968, Linhart 1973). Grant and Grant (1968) based their conclusions on observations that an individual Costa's hummingbird (Calypte costa) spent the major part of its foraging time within its territory, and that very few other individuals intruded into the territory during their study. Linhart (1973) studied the dispersal of marked pollen for both territorial and non-territorial hummingbird species. For strongly defended territories he found that there was a sharp decline in pollen movement at the territorial boundary. In an
area where territories were not as strongly defended and where he noted flights by intruders into territories, pollen dispersal again dropped sharply at the territory boundary but marked pollen was found as far as 100 m from its source. These studies provide strong evidence for the restriction of pollen flow by territorial behavior.

The observation period in both of these studies was quite short, two days in the study done by Grant and Grant and three to five days in Linhart's study. Possibly due to such short observation times the authors did not account for the fact that territorial boundaries may change during the course of a flowering season. In fact their conclusions implicitly assume that territories do not change.

Gass (1974, Gass et al. 1976) showed that the numbers and sizes of territories within his study areas changed considerably throughout the season. He found that as the number of flowers in a meadow increased, the number of territories increased and their sizes decreased. Boundary changes also occurred when birds arrived at or left a meadow. Thus I felt it important to consider the relationship between territorial behavior and pollen flow for the major part of a flowering season.

If plants remain in flower longer than territorial boundaries remain unchanged, the restriction of outbreeding predicted by the previous studies would be reduced. Theoretically, if a plant remains in flower throughout a sequence of changes in territorial boundaries, the restrictions imposed by a single set of boundaries may be less significant on a long term time scale. Therefore, it is important to determine
when and for how long the plants in the area flower.

**Foraging Flight Distances**

What are the dynamics of pollen dispersal within feeding territories? As a bird moves from flower to flower and plant to plant feeding on nectar it is also dispersing pollen: the length of these flights is the basic building block for pollen movement within territories and plant populations. If the flowers visited are close together pollen flow will be restricted whether territorial boundaries restrict foraging or not. The longer the flights the greater the effect of territorial boundaries. Knowledge of the dynamics of the bird's foraging flights is essential in understanding pollen flow dynamics in a plant-hummingbird system.

**Pollen Carry Over**

Is all the pollen picked up from one flower deposited on the next flower the bird visits or does some of this pollen remain on the bird to be deposited on the third, fourth, fifth, or fiftieth flower visited? Foraging flight distances provide an estimate of the potential for pollen movement. However, pollen flow distances derived from this measure will be greatly affected by pollen carry over distances.

Previous studies of pollinator mediated pollen flow have either ignored the question entirely (e.g. Levin and Kerster 1968, Beattie 1976) or made a rather vague assumption as to how
far pollen is "carried over" (Kerster and Levin 1968, Levin and Kerster 1969a,b; Levin et al. 1971). The problem is not in failing to realize that the pollen carry over question must be asked, but in finding an experimental technique that would provide the information needed to answer it. In only one case that I know of (Levin and Berube 1972) were any experiments done to determine the extent of pollen carry over. In that study carry over of butterfly dispersed Phlox pollen was estimated for conspecific pollen by determining the number of pollen tubes in the styles after pollination (Levin and Berube stated that these plants were self-incompatible and that the number of tubes is indicative of outcross pollen). For interspecific crosses, direct pollen counts could be made because of differences in pollen size between the species. Pollen carry over in these experiments did not extend beyond the fifth flower visited (Levin and Berube 1972).

Other Pollinators

Hummingbirds may not be the sole pollinators of the plants in a system. It is important to note the presence and behavior of other potential pollinators since they could be contributing to pollen movement within the populations even though their overall influence may be considerably smaller than that of the hummingbirds.
In order to relate the dynamics of pollen flow to gene flow in a plant population, the specific breeding systems of the plants must be known. It is impossible to correlate pollen flow with gene flow in a population without knowing whether or not plants are self incompatible. For example, if a plant is self incompatible the pollen transferred from one flower to other flowers on the same plant will not be effective in producing seed, only the pollen transferred from another plant will be successful in fertilizing an ovule and thus be the important determinant of gene flow.

A description of the interactions between the components discussed above probably would not portray a completely accurate picture of the total dynamic interactions occurring in nature. However, they would provide enough information about the system to allow description of the major effects of hummingbird foraging on pollen flow.
METHODS

The Study Area

This study was done in July and August 1975 in two subalpine meadows (altitude 2200-2500 m), located on talus slopes above Grizzly Lake in the Salmon-Trinity Alps Primitive Area of northern California. The meadows are small; meadow 1 is roughly 500 m² and meadow 2 roughly 1300 m². The meadows are quite steep (30-40°) and surrounded by granite outcrops. The outcrops provided excellent vantage points from which observations of the hummingbirds could be made. These are the same as meadows 1 and 2 described by Gass (1974, Gass et al., 1976).

The hummingbirds visiting these meadows were migrating female and juvenile Rufous hummingbirds (Selasphorus rufus). These birds winter in central Mexico and may migrate as far north as Alaska each spring to breed. Following the breeding season they return to Mexico visiting flowering meadows of the Coast, Cascade-Sierra and Rocky Mountain ranges during the trip (Bent 1940, Grant and Grant 1967, 1968, Phillips 1975). This southward migration usually occurs in two major waves with the males preceding the female and juvenile birds (Phillips 1975). During migration the birds stop and set up feeding territories in subalpine meadows along the route. It is not clear how long the birds remain in one area but they may hold territories from less than a day to several weeks before moving on (Gass and
Lynch, in preparation). They usually begin to arrive at the Grizzly Lake meadows in early July and are gone by early September. This coincides with the flowering times of the plants in these meadows (Gass 1974, Gass et al. 1976).

In the Grizzly Lake meadows the birds fed predominantly on Indian paintbrush (Castilleja miniata) and columbine (Aquilegia formosa). These are perennial species that exhibit the morphology of typical hummingbird flowers (Fig. 1) and flower abundantly in the study areas. Although the predominant plant species visited by hummingbirds in meadow 1 was columbine and in meadow 2 was Indian paintbrush, both species were present in both meadows.

Because of the heavy snowfall prior to the 1975 field season, flowering was delayed almost a month. Consequently my observations did not begin until the last week of July. Most of the data for this thesis were gathered during August of that year.

Territorial Behavior

To determine changes in size, shape, numbers and positioning of territories in the meadows, I noted perch locations, foraging flights and where chases of intruders occurred for each territory holder in each meadow approximately every three days. With this information the boundary of a territory could be defined and plotted on scale maps of the meadows. Most days the territorial boundaries in a meadow could be determined in about two hours. The areas of territories were
Figure 1: a. Columbine (*Aguilegia formosa*) b. Indian paintbrush (*Castilleja miniata*)
determined later by weighing paper cutouts of each and converting this measurement into square meters. After the territorial boundaries were determined the number of flowers in each meadow was counted. Counts of the number of inflorescences were made for Indian paintbrush and of the number of individual flowers for columbine. These techniques were the same as those used by Gass in his 1974 and 1976 studies (Gass et al. 1976).

Foraging Behavior

I recorded the location and sequence of patches (roughly equivalent to an individual plant, see below) visited on each foraging flight on large scale maps of the meadows, and gathered three types of information from each flight. First, I determined whether the flight was entirely within, outside of, or across territorial boundaries. Second, to determine flight distances I calculated the straight line distance from patch to patch within each foraging flight. I also calculated the distance from the last patch visited in a flight to the perch and from the perch to the first patch visited. During a foraging flight a bird seldom forages in a straight line and may even circle back to feed a second time at the first patch it visited. Thus the maximum distance of potential pollen dispersal for a flight may not always be the same as the distance between the first and last patches visited. The data presented are based on the maximum potential pollen flow distance in all cases. Probabilities of potential pollen flow for a specific distance were derived from data over the duration of the study by
determining the total number of visits within that specific distance and dividing this by the total number of visits observed. Finally, I recorded information on foraging behavior within a patch by recording the number of flowers and/or inflorescences and the number of potentially visitable flowers and/or inflorescences for each patch.

From my observation posts I could not positively determine whether a patch was equal to an individual plant. To determine how well the patches corresponded to a single plant, I recorded the number of flowers (columbine and Indian paintbrush), or inflorescences (Indian paintbrush) with visitable flowers for each of fifty randomly chosen plants located along transects through each of the meadows. I determined the flight distance between flowers or inflorescences within a patch by measuring the distance from a randomly chosen flower or inflorescence on each plant to its nearest neighbor.

I gathered data on columbine and Indian paintbrush visits for both meadows. The final analyses were based on data gathered for the predominant species in each meadow.
Plant Flowering Times

I determined the duration of flowering of thirty marked individuals of each species. Half were observed for the entire study season. The others were added to this group about halfway through the season so that any differences in flowering time during the season could be accounted for. All the plants had some flowers in bloom at the start of the study. I checked these plants about every three days and recorded whether or not they still had flowers in bloom. I assumed that if a bird visited a flower, pollen could be transferred to and from that flower. Thus I defined the flowering time of a plant as the time during which any of its flowers were at a stage that a hummingbird would visit. I determined which stages were "visitable" by following the flowering sequence for each species, dividing this sequence into a number of distinct stages, and recording which of these stages I observed hummingbirds visiting (Figs. 7, 8).

Pollen Carry Over

To determine the extent of hummingbird mediated pollen carry over I did a series of experiments in the laboratory in which live hummingbirds with no pollen on them visited a single intact fuchsia flower (*Fuchsia hybrida*) and then visited a series of emasculated flowers. As the bird fed on these flowers I recorded the sequence of feeding; a bird was allowed to make more than one jab into a flower to feed but was not allowed to return to a flower after having visited another. I presented ten
flowers as pollen "sinks" in four experiments and in two experiments I used twenty flowers. The stigmas of the flowers visited were removed and cleared using 10% KOH and then squashed on microscope slides to spread out the tissue. Total pollen counts were made for each stigma and also for ten stigmas of unvisited flowers to test my assumption that stigmas were indeed pollen free prior to an experiment. Four Rufous hummingbirds (females and juvenile males) were used in the experiments, which were performed in the aviary where these birds were kept.

Fuchsia flowers were used because the experiments were done in October, when neither columbine or Indian paintbrush were in flower. Fuchsia is a domesticated plant that flowers abundantly in autumn and hummingbirds are known to visit its bright pinkish-red blossoms (Fig. 2). Pollen is released abundantly in sticky strands from the anthers and the single large stigma becomes receptive before the anthers mature.

**Other Pollinators**

In order to obtain information about non-hummingbird visitors to columbine and Indian paintbrush I observed the behavior of various insect visitors and then collected them for later identification. I also monitored the presence of these visitors in the meadows at various times of day.
Figure 2: Fuchsia (*Fuchsia hybrida*)
In order to determine whether columbine or Indian paintbrush were self-compatible I did a series of bagging experiments. Tables VII and VIII summarize the field experiments that were done. Flowers of columbine or inflorescences of Indian paintbrush were bagged while still in bud and then pollinated by hand as they came into flower; any flowers not used in the experiments were clipped off. When the seeds in these experimental flowers had begun to develop the capsules were collected, as were a random sample of seed capsules from the population. Later I counted the number of good seeds per capsule for each flower. I judged a seed as being "good" if it was large and fairly normal in shape. I did not attempt to germinate the seeds. I did not do any experiments using emasculated Indian paintbrush flowers because they could not be emasculated without damaging the flowers.

To determine the timing of stigmatic receptivity I removed stigmas of flowers at various developmental stages and stained them with lactophenol cotton blue (Sass 1958). Blue staining of the stigmatic surface, presence of pollen grains or morphological changes were considered to be indications of receptivity. The slides were made permanent using Hoyer's mounting medium (Alexopoulos and Beneke 1952).
RESULTS

Territorial Behavior

I expected marked changes in the size, number, shape and positioning of territories in each meadow during the season as in Gass 1974, and Gass et al. 1976. The occurrence and extent of these changes during my study are quite clear (Figs. 3-6). In meadow 2 the mean size of territories was inversely related to the number of territories in the meadow (Fig. 6). Because not all of meadow 1 came into flower at once, territory formation was restricted to the densely flowered upper part of the meadow at first, and the territories formed there were small. Thus the relationship of average territory size and numbers of territories is not simple for this meadow.

Plant Flowering Time

Figures 7 and 8 are drawings of the basic flowering stages for each species. The hummingbirds visited columbine from the time the buds began to open (stage 3) until the old flowers had only a couple of spurs remaining (stage 6). They visited Indian paintbrush from stage 3 to stage 5. Indian paintbrush flowers beyond stage 5 were dry and produced little or no nectar.

Plants of both species remain in flower for at least a month (Tables I and II). The flowering time may even be longer than this because all the plants on my transects were in flower.
Figure 3: Changes in size and shape of territories in meadow
1. The major rock outcrops have been drawn in. Shaded areas indicate territories.
Figure 4: Changes in size and shape of territories in meadow 2. Symbols as in Fig. 3.
Figure 5: Changes in territory numbers (a) and size (b) in meadow 1.
Figure 6: Changes in territory numbers (a) and size (b) in meadow 2.
Figure 7: Flowering stages in columbine. Hummingbirds visit stages 3-6. Anthers begin to dehisce at stage 4. Stigmas become receptive at stage 5 (arrows indicate stigmas). Nectar is present at stages 3-6. All measurements indicate average lengths in millimeters.
Figure 8: Flowering stages in Indian paintbrush. Hummingbirds visit stages 3-5. Anthers begin to dehisce at stage 4. Stigmas are receptive by stage 4 (see text p. 59). Nectar is present at stages 3-5. All measurements indicate average lengths in millimeters.
# Table I
Length of flowering time for Columbine

<table>
<thead>
<tr>
<th>Date</th>
<th>Group 1</th>
<th>Group 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>31 July</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>2 Aug</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>5 Aug</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>9 Aug</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>12 Aug</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>16 Aug</td>
<td>10</td>
<td>15</td>
</tr>
<tr>
<td>19 Aug</td>
<td>7</td>
<td>14</td>
</tr>
<tr>
<td>22 Aug</td>
<td>7</td>
<td>13</td>
</tr>
</tbody>
</table>
### Table II
Length of flowering time for Indian paintbrush.

<table>
<thead>
<tr>
<th>Date</th>
<th>Group 1</th>
<th>Group 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>30 July</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>2 Aug</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>5 Aug</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>8 Aug</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>9 Aug</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>12 Aug</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>15 Aug</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>19 Aug</td>
<td>11</td>
<td>15</td>
</tr>
<tr>
<td>22 Aug</td>
<td>8</td>
<td>15</td>
</tr>
</tbody>
</table>
when I began monitoring them and the majority were still in flower at the end of my study season.

Foraging Behavior

My observations confirmed the conclusions of Grant and Grant (1968), Linhart (1973) and others (eg. Stiles 1971, Wolf et al. 1972) that hummingbirds tend to restrict their foraging to within their territories (Table III). In territories containing *Delphinium cardinale* (Grant and Grant 1968) 88% of the flights observed were entirely within territories. In my study 89% of the flights in the columbine meadow (meadow 1) and 97% of the flights in the Indian paintbrush meadow were entirely within territorial boundaries.

A foraging flight as I've defined it begins with a flight from a perch to a patch of flowers. The bird feeds from one or more flowers then may fly to one or more other patches and feed. Finally it flies back to a perch. During a flight a bird may also chase other birds or bees or hawk for insects. I found it convenient in determining foraging flight distances to divide a foraging flight into three stages:

1) The flight from a perch to a patch (or a patch to a perch).

2) Flights between patches.

3) Flights between flowers within a patch.

The majority of flights between patches were less than 2 m in length (Figs. 9-12). The mean flight distance between patches in foraging flights was $1.8 \pm 0.09$ m (standard error) for columbine
<table>
<thead>
<tr>
<th></th>
<th>Meadow 1</th>
<th>Meadow 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flights entirely within territorial boundaries</td>
<td>.892(431)</td>
<td>.970(195)</td>
</tr>
<tr>
<td>Flights entirely outside of any territory</td>
<td>.017(8)</td>
<td>.005(1)</td>
</tr>
<tr>
<td>Flights which crossed territorial boundaries</td>
<td>.091(44)</td>
<td>.025(5)</td>
</tr>
<tr>
<td>Total flights</td>
<td>483</td>
<td>201</td>
</tr>
</tbody>
</table>

Numbers indicate proportion of total flights observed. Numbers in parentheses indicate number of flights.
Figure 9: Mean flight distance between patches of Columbine. Bars indicate standard errors.
Figure 10: Mean flight distance between patches of Indian paintbrush. Bars indicate standard errors.
Figure 11: Frequency distribution of distances between successively visited Columbine patches.
Figure 12: Frequency distribution of distances between successively visited Indian paintbrush patches.
territories, and 1.9±0.16 m for Indian paintbrush territories. This tendancy of most of the flights to be short has been found in studies of flight distances of insect pollinators (eg. Levin and Kerster 1968,1969a,b; Beattie 1976). Calculations of pollen flow probabilities based only on foraging flight distances indicate a very high probability of short distance (about 2 m pollen dispersal (Table IV)). The data (Fig. 13) for flight distances between a perch and a patch for meadow 1 is less constant over the season than the between-patch flight distances (Fig. 9). The increase in this flight distance towards the end of the season may correspond to an increase in territory size at this time. Within patches a mean of 3.0±0.1 columbine flowers, or 3.3±0.2 Indian paintbrush inflorescences (7.5±0.5 Indian paintbrush flowers) were visited.

For both columbine and Indian paintbrush the number of flowers in a "patch" was greater than the number on a plant (Table V). The extensive rhizome system of columbine made it difficult to determine precisely what a "plant" as a genetic individual was, thus my determination of flowers per plant for columbine may be an underestimate.

I hypothesized that as territory size increased or decreased so would the length of foraging flights. There was no correlation between the length of flights between patches and territory size (Fig. 14), but there was a positive correlation between territory size and perch to patch flight distance (Fig. 14) indicated by my data. This implies that it is on the level of the perch to patch flight where the influence of territory size is manifested, but more data are needed to
Table IV
Seasonal probability of pollen flow for Columbine and Indian paintbrush based on hummingbird flight distances.

<table>
<thead>
<tr>
<th>Distance (m)</th>
<th>Columbine</th>
<th>Indian paintbrush</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-2</td>
<td>.67</td>
<td>.67</td>
</tr>
<tr>
<td>2-4</td>
<td>.26</td>
<td>.23</td>
</tr>
<tr>
<td>4-6</td>
<td>.03</td>
<td>.06</td>
</tr>
<tr>
<td>6-8</td>
<td>.03</td>
<td>.02</td>
</tr>
<tr>
<td>8-10</td>
<td>.01</td>
<td>.01</td>
</tr>
<tr>
<td>10-12</td>
<td>--</td>
<td>.01</td>
</tr>
<tr>
<td>12-14</td>
<td>--</td>
<td>.005</td>
</tr>
</tbody>
</table>
Figure 13: The mean flight distance to and from perches. Bars indicate standard errors.
### Table V
Relationship between the number of flowers in a patch to those on a plant.

**COLUMBINE**

<table>
<thead>
<tr>
<th>Date</th>
<th>Mean number of flowers/plant (N=50)</th>
<th>Mean number of flowers/patch (Total season)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 Aug</td>
<td>8.0±1.01</td>
<td>12.69±0.51 (N=520)</td>
</tr>
<tr>
<td>15 Aug</td>
<td>8.2±0.95</td>
<td></td>
</tr>
<tr>
<td>22 Aug</td>
<td>7.0±0.88</td>
<td></td>
</tr>
</tbody>
</table>

**INDIAN PAINTBRUSH**

<table>
<thead>
<tr>
<th>Date</th>
<th>Mean number of flowers per inflorescence (N=50)</th>
<th>Mean number of inflorescences per plant (N=50)</th>
<th>Mean number of inflorescences per patch (Total season)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 Aug</td>
<td>4.4±0.68</td>
<td>4.2±0.47</td>
<td>14.25±0.91 (N=162)</td>
</tr>
<tr>
<td>15 Aug</td>
<td>4.9±0.54</td>
<td>4.1±0.45</td>
<td></td>
</tr>
<tr>
<td>22 Aug</td>
<td>4.5±0.55</td>
<td>3.6±0.43</td>
<td></td>
</tr>
</tbody>
</table>
Figure 14: Relationship between territory size and two categories of hummingbird flight distances.

\( x = \) Flights between a perch and the first or last patch visited \( r = 0.91 \) \( p = 0.0045 \)

\( \Delta = \) Flights between patches \( r = 0.45 \) \( p > 0.1 \)
\[ Y = 2.166 + 0.7874E-02 \times X \quad N = 7 \]
\[ Y = 1.771 + 0.8245E-03 \times X \quad N = 7 \]
Pollen Carry Over

My working hypothesis for the pollen carry-over experiments was that pollen would carry over farther than the first flower visited, and would be deposited in decreasing numbers of grains on consecutive flowers visited. Pollen was consistently deposited even to the tenth flower visited, but there was no regular pattern of decline in the amount of pollen deposited on consecutive flowers visited (Fig. 15). In the two experiments in which twenty flowers were presented as pollen sinks there was no decline in the amount of pollen deposited even to the twentieth flower. The range in amount of pollen deposited was high, probably due in part to variability in the feeding position of a bird. Pollen is deposited by fucshia in large quantities on a restricted area of the bird's throat, thus the amount of pollen deposited on a stigma is determined by the directness of contact of the anthers on this pollen deposition site. None of the birds in these experiments were consistent in the way they touched the stigmas of the flowers they visited and in some cases birds probed flowers without touching the stigmas at all.

I calculated pollen flow probabilities based on pollen carry over to the tenth flower visited, a conservative estimate (Table VI). These data indicate an increase in the probability of longer distance (past two meters) pollen flow due to pollen carry over (compare with values in Table IV). It is interesting
to note the differences in the effect pollen carry over has on pollen flow probabilities for columbine and Indian paintbrush. Because seven Indian paintbrush flowers were visited per patch as compared to three columbine flowers, pollen carry over does not extend past the second Indian paintbrush patch visited, thus pollen flow probabilities at longer distances do not drastically increase. It is clear that a large number of flowers blooming per plant may have the effect of decreasing the overall distance of pollen flow in a population.

Other Pollinators

My observations of insect visitors to columbine and Indian paintbrush are by no means exhaustive. The most prevalent insect visitors to columbine in these meadows were bumblebees (Bombus sp.). Individuals gathered pollen while clinging to the anthers, and gathered nectar by crawling up the bundles of filaments into spurs. These bees have also been recorded in other studies as frequent visitors to columbine (Grant 1952, Macior 1966, Chase and Raven 1975).

The other frequently seen visitors to columbine were Syrphid flies (Syrphidae). These flies would cling to the anthers for long periods of time, possibly feeding on pollen. I also observed them crawling up into the spurs of the flowers, presumably to feed on nectar. The Syrphids probably do disperse some pollen although I feel that they contribute in only a minor way to pollen flow in these populations. They do not carry much pollen on their bodies, have little contact with stigmas, and
Figure 15: Pollen carry over for hummingbird visited fucshia flowers. Bars indicate ranges and standard errors.
FLOWER NUMBER

NUMBER OF POLLEN GRAINS
Table VI
Seasonal probability of pollen flow for Columbine and Indian paintbrush based on hummingbird flight distances.

<table>
<thead>
<tr>
<th>Distance (m)</th>
<th>Columbine</th>
<th>Indian paintbrush</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-2</td>
<td>0.28</td>
<td>0.51</td>
</tr>
<tr>
<td>2-4</td>
<td>0.35</td>
<td>0.29</td>
</tr>
<tr>
<td>4-6</td>
<td>0.24</td>
<td>0.08</td>
</tr>
<tr>
<td>6-8</td>
<td>0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>8-10</td>
<td>0.04</td>
<td>0.02</td>
</tr>
<tr>
<td>10-12</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
<td>12-14</td>
<td>0.01</td>
<td>--</td>
</tr>
</tbody>
</table>

Probabilities are based on pollen carry over to the tenth flower visited and the fact that a bird visits three columbine and seven Indian paintbrush flowers per patch.
they remain on flowers for long periods of time (up to an hour or more) before moving on, all of which will reduce their effectiveness as pollinators. Chase and Raven (1975) also noted Syrphid visitors to columbine.

Two taxa of insect visitors are probably effective pollinators of Indian paintbrush. The first and most frequently observed was a large bee (family Megachilidae) and the other was a small solitary bee (family Halictidae). Individuals of both types fed on nectar by probing head downward into the tubes of flowers while oriented so that their abdomens contacted the anthers and stigma. The Megachilid carries pollen in a layer of hairs on its abdomen and manipulates the anthers with its legs and abdomen while in this head downward position, presumably collecting pollen. The Halictids seemed to gather pollen with their hind legs in a similar manner although they lack the pollen storing abdominal hairs.

**Plant Breeding Systems**

Columbine flowers are clearly self-compatible, since there is no significant difference between the number of seeds set between selfed or outcrossed flowers (Table VII). Even flowers from which insects were excluded (class 5) set good seed. During floral development of columbine the anthers mature well ahead of the stigmas, which mature at flowering stage 6 (Fig. 7); at this point the styles protrude below the dried up anthers and the lobes of the stigmatic surfaces open up. At this stage the stigmas stained with lactophenol cotton blue, and the stigmas of
unbagged flowers were covered with pollen grains that showed evidence of pollen tube growth, all of which indicated that the stigmas were receptive.

Indian paintbrush is apparently an obligately outcrossing species, since very little if any seed was set unless the flowers were outcrossed (Table VIII). My evidence concerning stigmatic maturity in Indian paintbrush flowers is somewhat conflicting. The stigmas of fairly small immature flowers (flowering stage 2; Fig. 8) stained with lactophenol cotton blue as did those of later stages (flowering stages 3-6; Fig. 8). There was no pollen present on the stigmas of the immature flowers though, which leads me to question either their receptivity or the applicability of the lactophenol cotton blue test in this case. The first anthers mature at flowering stage 4 which is also the stage where I can be certain that the stigmas are mature (pollen grains and tubes are present). Thus, I can conclude that these plants may be somewhat protogynous but further evidence concerning receptivity of younger stigmas is needed to prove this point.
Table VII
Seed set data for Columbine.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Number of plants</th>
<th>Number of flowers</th>
<th>Mean number good seeds per capsule</th>
<th>X²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flowers selfed (with own pollen)</td>
<td>12</td>
<td>23</td>
<td>13.4±1.49</td>
<td>1.39 NS</td>
</tr>
<tr>
<td>Flowers selfed (with pollen from same plant)</td>
<td>10</td>
<td>22</td>
<td>14.5±1.53</td>
<td>1.08 NS</td>
</tr>
<tr>
<td>Outcrossed</td>
<td>9</td>
<td>21</td>
<td>14.1±1.53</td>
<td>1.19 NS</td>
</tr>
<tr>
<td>Emasculated then outcrossed</td>
<td>6</td>
<td>14</td>
<td>8.0±1.01</td>
<td>3.84 NS</td>
</tr>
<tr>
<td>Bagged only</td>
<td>11</td>
<td>17</td>
<td>14.1±1.12</td>
<td>1.19 NS</td>
</tr>
<tr>
<td>Emasculated only</td>
<td>4</td>
<td>10</td>
<td>1.6±0.88</td>
<td>9.59*</td>
</tr>
<tr>
<td>Wild control</td>
<td>16</td>
<td>16</td>
<td>23.6±1.19</td>
<td></td>
</tr>
</tbody>
</table>

* = significant at P<.05
All experiments tested against wild control.
Table VIII
Seed set data for Indian paintbrush.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Number of plants</th>
<th>Number of flowers</th>
<th>Mean number good seeds per capsule</th>
<th>( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flowers selfed (with own pollen)</td>
<td>5</td>
<td>27</td>
<td>0.10 ± 0.10</td>
<td>44.87*</td>
</tr>
<tr>
<td>Flowers selfed (with pollen from same plant)</td>
<td>5</td>
<td>29</td>
<td>0.29 ± 0.29</td>
<td>44.59*</td>
</tr>
<tr>
<td>Outcrossed</td>
<td>5</td>
<td>31</td>
<td>110.4 ± 8.78</td>
<td>1.03 NS</td>
</tr>
<tr>
<td>Emasculated then outcrossed</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Bagged only</td>
<td>20</td>
<td>147</td>
<td>0.0</td>
<td>--</td>
</tr>
<tr>
<td>Emasculated only</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Wild control</td>
<td>25</td>
<td>75</td>
<td>90.0 ± 7.10</td>
<td>--</td>
</tr>
</tbody>
</table>

* = significant at \( P < .05 \)
All experiments tested against wild control.
DISCUSSION

Pollen Flow

In the previous chapters I discussed each of the components of this system as separate entities. Here I will discuss the dynamics of pollen flow for this system based on these components and the interactions between them. Initially I set out to determine the influence territorial boundaries have on pollen flow. I hypothesized that because territorial boundaries change rapidly over time while the plants they encompass remain in flower, the constraints on outcrossing proposed by Grant and Grant (1968) and Linhart (1973) would be less severe. I found, as those authors did, that birds confined the majority of their foraging flights to their territories (Table III). However, the spatial arrangement of the territories changed frequently and on as short a time scale as part of a day (Figs. 3-6), and most of the plants remained in flower throughout these changes.

Each individual plant is surrounded by dynamically changing territorial boundaries which may enclose or exclude different plants at different times in the season. A given plant will usually be within some hummingbird's territory, but because the territorial boundaries change, so will the plants which are potential pollen sources. The plant will continue flowering throughout these changes and thus it may be giving or receiving pollen from a larger and different pool of plants than those enclosed by a particular territory on a particular day.
On initial consideration one might conclude that the breeding pool for a particular plant is delimited by the largest territory that the plant was in. However, since the shapes of territorial boundaries are irregular the boundary of the breeding pool would be a composite of the boundaries of all the territories in which a given plant was included. Within the breeding pool surrounded by this composite boundary, the probability of pollen being transferred from one plant to another is a function of the amount of time that these two plants are enclosed by the same territorial boundaries (Fig. 16).

My results suggest that pollen does not move randomly throughout a territory. It is necessary to consider characteristics of a bird's foraging behavior beyond the fact that hummingbirds restrict their visits to within territorial boundaries. The key element is the distance a bird flies between the flowers it visits. The majority of flights are from flower to flower or inflorescence to inflorescence within patches. If a patch is equal to a plant, visits within patches result mainly in self pollination. Since a patch is somewhat larger than a plant (Table V) the amount of self pollination may not be as great. The distance of cross pollination should be determined by the distance flown between patches. Between patch flight distances remain at about two meters regardless of territory size (Figs. 9, 10). This short patch to patch flight distance in combination with the extent of within patch visitation favors pollen dispersal to near neighbors. This trend is independent of territory size and there is a high probability of pollen
Figure 16: The effects of changes in territorial boundaries on potential pollen flow for a plant in meadow 1.  
1. Plant (x) surrounded by a single territory.  
2. Composite of all the territories which surrounded this plant during the study. Shaded areas indicate the largest territory that this plant was in.  
3. The shading indicates the amount of time which plants were within the same territorial boundaries as plant x.  
Eg. Plant x was within the same boundary as A for 14% of the time, and plant B for 57%.
movement at distances considerably smaller than a territory. This would reduce the influence of territory boundaries on pollen flow. Their major influence would be near boundaries, where pollen flow would be restricted in direction because of the fact that birds seldom cross boundaries when foraging.

My laboratory experiments indicate that pollen is transferred considerably further than the first flower visited; this factor will increase the probability of pollen flow at greater distances (Table VI). Because the potential pollen flow distance increases due to pollen carry over, the influence of territorial boundaries on pollen flow will be more pronounced than I indicated above.

The composite picture of pollen flow I get from interrelating these components is depicted by Figures 17 and 18. The underlying maps in each Figure depict pollen flow probabilities based only on the interactions of changing territorial boundaries. The overlays depict pollen flow probabilities based on hummingbird flight distances (as modified by pollen carry over). These probabilities are based on foraging flight distances from data on all the foraging flights in a meadow recorded during the study (Table VI). Since local differences in topography and plant density may modify local distribution of foraging flights, these data can only provide an approximation of the probability of pollen flow for an individual plant.

Pollen flow probabilities which incorporate the influence of hummingbird foraging flight distances, an approximation of pollen carry over, and the effect of combined territorial
boundaries may be derived by multiplying the probabilities based on each factor (from Figs. 17 and 18) for a plant at any point in the meadow. This is assuming that two plants are capable of pollen transfer and that previously deposited pollen has not already fertilized the ovules. For example, plant 1 (Fig. 17a) would have a probability of .30 of exchanging pollen with plant x. Plant 2 would only have a .05 probability. Even though the probability of pollen flow for both plants based on foraging flight distances is quite high (.35), the probability of pollen flow between plant 2 and plant x is greatly reduced because plant 2 was within the same territorial boundaries as plant x for only 14% of the study season. The overall pollen flow probability between plant x (Fig. 17b) and plant 3 is .25 and between plant x and plant 4 is .17. This indicates how the high probability of short distance foraging flights will reduce pollen flow despite the high (.71) pollen flow probability based on territorial boundary location.

Although the present data are imprecise for some local situations and individual plants, it is clear that pollen flow for plants in different areas of a meadow is quite different due to the location of territorial boundaries. Here again the influence of local differences in topography and plant density can be seen. The location and size of territories is influenced by topography (e.g., rock outcrops which influence where plants grow, perch locations, etc.), and plant density (see correlation between plant density and territory size in Gass 1974, Gass et al. 1976). Plant x in Fig. 17a was located at the edge of territories throughout most of the study, thus the pool of
Figure 17: Diagramatic representation of pollen flow for two columbine plants in meadow 1. Inset map indicates location of each plant. Circles indicate intervals of 2 m from the plant. Numbers indicate the probability of a plant being visited at that distance based on pollen carry over to the tenth flower visited (Table VI). Shading as in Fig. 16. See text for discussion.
Figure 13: Diagramatic representation of pollen flow for two Indian paintbrush plants in meadow 2. Inset map indicates location of each plant. Circles indicate intervals of 2 m from the plant. Numbers indicate the probability of a plant being visited at that distance based on pollen carry over to the tenth flower visited (Table VI). Shading as in Fig. 16. See text for discussion.
potential sources for this plant changed considerably with each change in territorial boundaries. Plant x in Fig. 17b was located in the middle of territories and thus the members of its breeding pool did not vary much with territorial changes. In general, because of the frequency of changes in territorial boundaries in these meadows, territory edge plants have the opportunity for pollen exchange between a wider range of plants than mid-territory plants. The dynamics of territorial boundary changes in a meadow will produce a range from exclusively "edge" plants to exclusively "middle" plants. The extent of diversity of breeding pools for these plants will be governed by this range.

I have depicted pollen flow in these meadows based on four factors:

1) How long the plants are in flower.
2) The distance between the plants.
3) How long two plants are surrounded by the same territorial boundaries.
4) The number of plants (or flowers) which the bird visits before visiting the second plant in consideration.

Each factor alone will not give an accurate prediction of pollen flow. Probabilities based on interrelating these four factors provide insight into overall pollen flow dynamics. However, they lack precision in their predictions since they do not account for the effects of local variability in foraging flight distances. An important next step should be to define an index of this variability to incorporate in these calculations. Two other general problems must also be studied. First, a more
accurate field measure of pollen carry over for both species is needed. Second, the extent and importance of the influence of long perch to patch flights on foraging flight distances must be assessed.

The Effect Of Flights To And From A Perch

My data suggest that the component of within flight foraging behavior that is most responsive to changes in territory boundaries is the distance a bird flies to a flower from a perch and to a perch from a flower. These perch-patch and patch-perch flights could be quite important in determining overall pollen flow and degree of outcrossing. Unless a bird wipes its bill or preens excessively while perched (which, from my observations is usually not the case) the pollen from the last flower visited on one flight should carry over to the first plant visited on the following flight. Although these longer flights are only two components of an entire foraging flight, they could significantly increase pollen flow distances.

On the average a foraging flight consisted of visits to about three columbine or Indian paintbrush patches (about eight columbine flowers or 13 Indian paintbrush inflorescences and 21 Indian paintbrush flowers; Table X; Appendix). Each average flight then, consisted of two long perch-patch flights, two short (about 2 m) flights between patches, and five (columbine) or seven (Indian paintbrush) very short (about 10 cm) flights between flowers or inflorescences in a patch. For Indian paintbrush there are an additional 12 very short moves between the flowers on inflorescences. The contribution of the longer
flights to potential pollen flow distances would be 22% (2 of 9 total moves per flight) for columbine and 8.7% (2 of 23 total moves) for Indian paintbrush. It is interesting to note that a large number of simultaneously flowering flowers per plant would decrease the potential distance of pollen flow, as can be seen by comparing the percentages for columbine and Indian paintbrush. The next step in studying hummingbird mediated pollen flow in these meadows is to determine exactly what influence the perch-patch flights have on potential pollen flow distances, by carefully recording data on consecutive flights which are interrupted by perching.

The presence of the long distance perch to patch flights combined with the assumption that pollen carry over continues through at least the tenth flower visited should increase considerably the probability of pollen flow for longer distances, possibly approaching the point where essentially the only limit on this distance is the territory boundary itself. A major question that needs to be answered, though, is what the distance is between the last patch a bird visits before perching, and the first patch visited on the next flight. If the bird returns on the next flight to a patch near the one that ended the last flight, these patch to perch flights may have only a minor effect on pollen flow distance.
Pollen Carry Over

The fuchsia flowers I used in the laboratory experiments exhibit the morphology of typical hummingbird flowers (Percival 1965, Faegri and van der Pijl 1966, Grant 1966, Proctor and Yeo 1972), but they are different in many aspects from the two species I studied in the field. However, I believe the general trends shown in the laboratory experiments can be extended to pollen carry over for columbine and Indian paintbrush. I attempted some crossing and pollen carry over experiments with Indian paintbrush in the field using a stuffed hummingbird to transfer pollen from a single pollen source to a number of "sinks". Even after visiting ten pollen sinks I could often see pollen in the feathers of the stuffed bird and on the stigmas of the plants. All flowers used in these experiments had been bagged in bud and therefore had not been pollinated. I observed very large amounts of pollen on the birds in the field. The pollen present was so clearly visible that it could be used as temporary identifying marks for birds foraging on different species of flowers. The presence of these large amounts of pollen is also indicative of a potential capacity for extensive pollen carry over.

Because both columbine and fuchsia have protruding anthers and stigmas, I feel that the variability in the way the hummingbirds contacted the stigmas of the fuchsia flowers may occur for columbine as well. The hidden reproductive parts and tubular flowers of Indian paintbrush make this type of variability in feeding less likely in that species.
Levin and Berube (1972) experimented with pollen carry over in heterospecific phlox pollen carried on the proboscis of Lepidopterans. In their work, pollen carried over to the fifth flower (for *Phlox pilosa* pollen on *P. glaberrima* stigmas) but most (about 45 grains) of the pollen load was deposited on the first flower and only three grains were deposited on the fifth flower visited. For the reciprocal cross, pollen only carried over to the third flower with a mean of 1.39 grains on the first and 0.17 on the third stigma. Thus probability of pollen flow past flower one is quite small in that system. Pollen flow is probably greater in pollinations between conspecifics, since the floral mechanisms of these two species are not totally compatible (Levin and Berube 1972).

Differences in behavior patterns and general morphology between hummingbirds and insects leads me to hypothesize that in general, hummingbird mediated pollen carry over will be considerably greater than insect mediated carry over. Pollen loads available for transfer should be greater for hummingbirds than insect pollinators. The amount of surface area available to carry pollen on a hummingbird's head, neck and bill is greater than an insect's proboscis or the area of surface hairs on the bodies of some insect pollinators, although the pollen carrying surface area of the larger bees may be comparable to that of the hummingbirds. Since bees often collect and store pollen in specialized hairs in order to provision a nest or hive (Percival 1965, Faegri and van der Pijl 1966, Proctor and Yeo 1972), much of this pollen is essentially unavailable for carry over. In many cases the contact of an insect pollinator with the
reproductive parts of a flower may be more precise than that of a hummingbird, since they often land on a flower and crawl over it while feeding. This would cause any pollen available for transfer on an insect to be depleted more rapidly. The variability in stigmatic contact which may occur when a hummingbird feeds would also extend and increase the variability in the carry over distance.

In using emasculated flowers for the pollen "sinks" I removed one factor which may be very relevant to pollen carry over. Because of the lack of pollen on emasculated flowers, I couldn't tell how the pollen picked up at each flower affects pollen dispersal from the "source" flower. This masking could affect pollen carry over in three ways.

1) If pollen from successive flowers was deposited on the bird in layers, pollen from the source flower would be buried under more recently deposited pollen and would not be available for transfer.

2) If pollen from each source was deposited at random on the bird, pollen from the source flower would be distributed further, but in smaller quantities to each flower within a mixture of pollen from all of the flowers visited.

3) If pollen from each source was deposited on and transferred from different locations on the bird, the source pollen would be distributed as though there was no other pollen present.

An experiment using intact flowers and either dyed pollen or pollen of another species as source pollen would probably
provide some insight into how the interactions of pollen from several flowers will affect pollen carry over.

The experimental technique I used to determine pollen carry over is not perfect. It does give a good indication of the extent of hummingbird mediated pollen carry over though. Much of the previous research on pollinator mediated pollen and gene flow has been weakened because the authors have not been able to integrate determinations of pollen carry over with their data. I feel that the techniques I have used in these experiments can be refined and expanded to provide more answers to the pollen carry over questions for all types of pollinators.

**Insect Pollinators**

It seemed clear that both major insect species visiting Indian paintbrush could be effective pollinators, but they are probably responsible for much less pollen dispersal than hummingbirds. Unlike the homeothermic hummingbirds, these bees are only active for a few hours at midday (Table IX; Appendix). They were not seen foraging when there was a wind, or a drop in temperature, even that caused by cloud cover in the meadow.

*Bombus* that visited columbine were common in the meadows at a wider range of temperatures than the visitors to Indian paintbrush. *Bombus* species are partially homeothermic (Heinrich 1972) which allows them to successfully displace poikilothermic insect pollinators at high altitudes (Heinrich and Raven 1972, Heinrich 1975). However their number was reduced somewhat in cool or windy weather (casual observations).
I can not draw any clear conclusions about the relative contributions of Bombus and hummingbirds to pollen flow. Exclusion experiments, allowing only bees to visit a group of flowers and comparing their seed set to flowers visited by both hummingbirds and bees would provide the needed data to compare the influences of these two pollinators. I found it quite easy to record bee foraging behavior using the same methods I used to record hummingbird foraging. This type of data would also contribute to an understanding of the contributions that bees are making to the movement of pollen in these meadows.

The diversity of insect pollinator species and their behavior is wide (Percival 1965, Faegri and van der Pijl 1966, Proctor and Yeo 1972). As far as I know only Lepidopterans and various bee species have been studied in research on the distance of insect mediated pollen flow (e. g. Kerster and Levin 1968, Levin and Kerster 1968, 1969a, b, 1974; Beattie 1976). These investigators used insect flight distances as indicators of pollen flow as I did in this study, and found that in general flight distances were short (Levin and Kerster 1968, 1969a, b, Kerster and Levin 1968, Beattie 1976). The majority of the hummingbird flights I noted were also short. Unlike insects, the hummingbirds exhibited a high frequency of longer moves, the perch-patch flights. These flights, along with a possible greater pollen carry over distance for hummingbirds leads me to believe that hummingbird mediated pollen flow may extend over longer distances than that observed for insect visitors.
Plant Density

Most research on insect mediated pollen flow indicates that plant density and distribution affect the length of pollinator foraging flights. As density increases, flight distances become shorter (Levin and Kerster 1969a, b, 1974; Beattie 1976).

It is clear from other data that plant density and spacing also influence hummingbird behavior. In non-territorial birds the evidence points to a similar influence of density on pollen dispersal distance to that found for insect pollinators. That is, pollen dispersal distance seems to increase with a decrease in plant density (Linhart 1973, Schlising and Turpin 1971). For territorial birds the determination of whether or not a bird sets up a territory and what size the territory will be, is based to a large extent on plant density (Gass 1974, Gass et al. 1976, Carpenter and MacMillen 1976, Kodric-Brown and Brown 1978).

What is not known is how plant density affects hummingbird flights within territories. I have very little data correlating plant density and hummingbird flight distances for my study area. Total flower counts for each meadow (a very rough indication of density) increase and then decrease during the season (Figs. 19-21; Appendix), and these changes in flower numbers can be correlated with changes in size and numbers of territories in the meadows (as in Gass (1974) and Gass et al. (1976)). My data indicate that the perch-patch flight distance is correlated with territory size (thus at least indirectly with plant density), while the inter-patch flight distances remain
fairly constant regardless of changes in territory size (and plant density). My data do not indicate that the relationship between plant density and hummingbird flight distances within territories is merely the simple inverse relationship that is seen in insects. It indicates a higher level of complexity in this relationship which needs further investigation.

**Gene Flow**

Pollen flow, being the major means of genetic exchange for flowering plants, has often been used as an indicator of gene flow in plant populations. The general prediction for research both on insect and wind mediated pollen dispersal is that most outcrossing occurs only over very short distances, even though both dispersal agents occasionally move pollen over long distances. (e.g. Bateman 1947a,b; Kerster and Levin 1968, Levin and Kerster 1969a,b, Gleaves 1973, Beattie 1976).

My data predict a high probability of short distance pollen dispersal in a hummingbird pollination system which would lead to gene flow restriction in the plant populations. In comparison to wind and insects as pollinators though, there may be a greater proportion of longer distance pollen moves which should increase gene flow.

The effect of hummingbird mediated pollen flow on the movement of genes differs between the two plant species I studied. Columbine is a self compatible species (Table VII). Thus gene flow in the columbine population should be restricted and considerable inbreeding could occur. The fact that the
stigmas of flowers mature after the anthers have lost most of their pollen reduces this inbreeding factor somewhat, but because more than one flower on a plant is likely to be in flower at one time the importance of this reduction is probably minimal.

The potential for self pollination for Indian paintbrush is even higher than that for columbine. This is due to the fact that a bird visits several flowers on each inflorescence and several inflorescences on each plant before flying to the next plant. In my study birds visited more than seven Indian paintbrush flowers per patch as compared to three columbine flowers. However, because Indian paintbrush is self incompatible, the potential for inbreeding is not great.

Further investigation of the relationship between hummingbird mediated pollen flow and gene flow must include a more precise determination of the genetic structure of the plant populations involved. The utilization of genetic markers to monitor actual gene flow in a plant population should provide a good test of the hypotheses derived from knowledge of pollen flow dynamics.
Implications For Other Hummingbird Pollination Systems

Grant and Grant (1968) and Linhart (1973) both concluded that hummingbird territorial behavior restricts pollen flow and contributes to inbreeding in plant populations. I have found that the major restriction of pollen flow in my study area is due not to territorial behavior but to the predominance of short flights within foraging flights. Individual territories are not powerful as restricting mechanisms because of numerous changes in shape, size, and positioning of the territories surrounding a plant which occur throughout its flowering season. They also lose significance in terms of inhibiting pollen flow because the short flight distances will cause high pollen flow within even the smallest territories. Data on pollen carry over and long perch-patch flights indicate that the low probability of longer distance pollen flow based on these short flights may result in a fairly large underestimate of actual pollen flow distances in the population. The power of territorial boundaries as pollen flow restricting mechanisms will increase as the potential pollen flow distance within the territories increases (in light of pollen carry over and long flights between a perch and a patch of flowers).

A large variety of plant species are visited and pollinated by hummingbirds, (Grant and Grant 1966, Stiles and Wolf 1970, Stiles 1975, Gass et al. 1976, and others), and the applicability of my results to other hummingbird pollination systems will be affected by this variety. My conclusions should apply for many other perennial herb populations in which the
plants remain in flower for a similarly long time. If the plants flower for a very restricted time the territorial boundary restriction on pollen flow will be much greater, possibly contributing to increased inbreeding for the population. Of course gene flow will be influenced by the breeding system and means of seed dispersal for each plant species. Pollen and gene flow for a flowering tree or shrub, such as the tree (*Genipa americana* (Rubiaceae)) studied by Stiles and Wolf (1970), may differ extensively from that portrayed for this meadow. In that type of system the number of flowers per plant is much larger than in a small perennial herb, thus it seems that the restriction of pollen flow between plants would be much greater.

It would be interesting to compare pollen flow in this migrating hummingbird system to that of breeding hummingbirds. Breeding territories may be held longer than the feeding territories held by migrants. This would imply a stricter control of pollen flow imposed by the boundaries of a single territory. It seems that here, as with a system in which individual plants flower only for a short period of time, there would be a restriction of pollen flow which may considerably increase inbreeding in the population.

What differences would be caused by strong versus weakly defended territories? I noted few flights by intruders into the territories I observed, but Gass (1974) noted times of high rates of intrusion at certain times of day in some territories for the same meadows. Linhart (1973) found pollen movement at a distance of 100 m from weakly defended territories where he noted visits by intruding birds. Wolf and Stiles (1970) and Wolf
(1975b) noted male hummingbirds allowing females to feed in their territories during the breeding season. It would be interesting to see how much these "intruders" extend pollen flow.

What are the differences in pollen flow between territorial and non-territorial situations? It has been shown that territories restrict pollen flow more than non-territorial situations (Linhart 1973, Schlising and Turpin 1971, present study). Does this also imply that flowers pollinated at the beginning or end of a season, when the low numbers of flowers in an area prevent the establishment of territories, and when any existing territories occupy most of each meadow, will receive more "outcrossed" pollen and thus produce offspring with greater variability than those which are pollinated during the peak of the flowering season? If so what are the implications about gene flow in these populations? If competition is great, would the seeds set at the beginning and end of a flowering season have a higher probability of growth and establishment than the seeds produced in the middle of the season? I hope that this study will provide a good starting point for working on the answers to some of these questions.
LITERATURE CITED


APPENDIX
Table IX
Times of insect visitor activity.

<table>
<thead>
<tr>
<th>Meadow 1</th>
<th>14 Aug 1975</th>
<th>Time</th>
<th>Insect visitors Counted</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>6:40 AM</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>9:40</td>
<td>8 Bombus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11:36</td>
<td>9 Bombus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1:36 PM</td>
<td>3 Bombus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3:36</td>
<td>1 Bombus, 1 Syrphidae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5:36</td>
<td>1 Bombus, 2 Syrphidae</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Meadow 2</th>
<th>15 Aug 1975</th>
<th>Time</th>
<th>Insect visitors Counted</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>6:30 AM</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8:30</td>
<td>2 Megachilidae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10:30</td>
<td>9 Megachilidae, 2 Halictidae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12:30 PM</td>
<td>4 Megachilidae, 3 Halictidae, 1 Bombus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2:30</td>
<td>8 Megachilidae, 5 Halictidae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4:30</td>
<td>0 (Entire meadow in shade at about 4:00 PM)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6:30</td>
<td>0</td>
</tr>
</tbody>
</table>
### Table X

Number of patches, flowers and inflorescences (Indian paintbrush) visited in a flight.

<table>
<thead>
<tr>
<th></th>
<th>Mean number of patches</th>
<th>Mean number of flowers</th>
<th>Mean number of inflorescences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Columbine</td>
<td>$2.9 \pm 0.13$ (203)</td>
<td>$8.6 \pm 0.56$ (154)</td>
<td>--</td>
</tr>
<tr>
<td>Indian Paintbrush</td>
<td>$2.9 \pm 0.15$ (81)</td>
<td>$21.0 \pm 2.27$ (67)</td>
<td>$9.6 \pm 0.98$ (63)</td>
</tr>
</tbody>
</table>

Numbers in parentheses indicate sample size.
Figure 19: Changes in the number of columbine flowers (x) and Indian paintbrush inflorescences (p) in meadow 1.
Figure 20: Changes in number of columbine flowers in meadow 2.
Figure 21: Changes in the number of Indian paintbrush inflorescences in meadow 2.