NATURAL POLLINATION OF CALIFORNIA LILIES

By

James S. Davis

A Thesis presented to the General Faculty of The Claremont Graduate School in partial fulfillment of the requirements for the degree of Master of Arts

We certify that we have read this thesis and approve it as adequate in scope and quality for the degree of Master of Arts:

Richard M. Straw
______________________ Thesis Examiner

______________________ Faculty Reader

Verne Grant
______________________ Faculty Adviser

Date Nov. 27, 1956

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

INTRODUCTION

In the past the general tendency has been to designate species on the basis of morphology alone. For purposes of rapid recognition, identification, and discussion there is no better way. But a plant is more than its morphology, and recently the trend has been to consider as much of the totality of a plant as possible or feasible before describing it as a new species.

This totality, of course, includes edaphic and climatic requirements, physiological processes, methods of pollination, and in fact all such factors that go into the make-up of that which we designate as an individual. It is perhaps true that to consider these "hidden" or less obvious factors of a plant is to detract from the ease of recognition and general effectiveness of the taxonomic species, but many feel that in so doing a more accurate perception of the objective species is approached, if such can be said to exist. In addition, valuable aid is given to the plant hybridizer by showing natural affinities and relationships. Why should not a unique physiological process or behavior pattern be given proper consideration in species designation? One answer is simply that so much less is known about such factors than about the more obvious morphological characters.

Also, the significance of the various characters differs according to their relative importance in the evolutionary development of the plant. For example, a change from whorled leaves to scattered leaves can be said not to have the same degree or the same kind of significance as a change from butterfly pollination to bee pollination; a single mutation of a pleiotropic gene in a plant is often enough to alter its morphology to such an extent that it could justifiably be called a new species under the older system of classification, even if the new morphological characters had little or no adaptive significance. It is hardly likely, however, that a single mutation of a gene could result in the transition of a fragrant flower adapted to the life cycle of a night flying moth to that of a non-fragrant flower that has adapted itself to the preferences of a pollen gathering bee. Yet how many taxonomists consider the pollinator of a plant when a new species designation is made?

Thus, it can be seen that we can not justifiably designate phylogenetic species from herbarium specimens or even from plants grown in the botanic garden; we must go out into the field and study these organisms where they evolved. A plant growing in the botanic garden is out of context. It is not a typical representative of the species because of the pampering the plant receives by being placed in a disease and insect free habitat that permits the survival of many non-typical individuals which would otherwise be eliminated in nature.

It has also been reported (Rappley, 1950), and somewhat substantiated by this report, that the activities of plants grown in the wild differ from those removed to the botanic garden. Lilies growing in the wild have very little competition with other flowers for the attention of their pollinating agent, but lilies growing amidst the profusion of bloom found in the garden suffer a considerable reduction in seed production. A reduction often as high as 50% was found in the Rancho Santa Ana Botanic Garden (other factors may be involved here also such as the preponderance of one or two clonal types with incompatibility factors operating). Also, the garden may be outside the range of the natural pollinator and the plants must rely on pollinators other than the usual one. For these reasons, this thesis concerns itself with the pollinators found in the natural habitats of many of the species of the genus Lilium found in California.

It is with this outlook in mind that the following work was begun on the Pacific Coast lilies in an effort to contribute to the existing knowledge of the life histories of these very interesting plants.

THE PROBLEM

It is known that a pollinating system can be a very effective reproductive isolating mechanism (Grant, 1949), and since very little has been published on the natural pollination of the Pacific Coast lilies, it was decided to investigate this phase of reproduction in as many species as possible with the time allotted. An attempt was made to see if the California species were isolated from each other by reason of the pollinator, by reason of habitat preference, or simply by geographic isolation. What is there in nature that keeps them apart?

Reports (Preston, 1933; Griffiths, 1931; Woodcock and Stern, 1950; Purdy, 1895; et al.) indicate that all Pacific Coast lilies can be freely hybridized in the garden and hybrids such as the Bellingham Hybrids (which are hybrids of *Lilium parryi* x *L. pardalinum* x *L. humboldtii*) are listed by dealers, indicating the successful nature of some of the interspecific crosses. Also, many hybrid swarms have been seen in nature by the author and reported by Dr. Albert Vollmer, Mr. Frank Ford, and Dr. S. L. Emsweller (personal communication). These appear, however, to be exceptional, rather infrequent, and not involving the extreme floral forms such as *Lilium washingtonianum*, or *L. rubescens*. Furthermore, it is felt that many of the hybridizing experiments of the earlier workers and of the "home" hybridizers were not carried out under strict scientific control, hence caution and qualification should be used if generalizations are made regarding the inter-fertility of these lilies. Many of these reports were not accompanied by detailed measurements and descriptions of either parent or hybrid. Figures were not given as to the number of seeds produced in each pod and the character distribution of each seed after it reached maturity to eliminate the possibility of the subjective selection of an extreme recombination type from an interclonal cross and confusing it with the supposed progeny of an interspecific cross.

A list of the hybrids of California species that have been reported in the lily literature indicates some widespread interspecific compatibility but by no means does it indicate 100% crossability. Figure 1 summarizes diagrammatically these crossing relationships.

L. humboldtii	x _L. washingtonianum_ (Preston, 1933)
______________	x _L. roezlii_ (_vollmeri_) (Stout, 1933)
______________	x _L. kelloggi_ (Stout, 1933)
______________	x _L. pardalinum_ (Griffiths, 1933)
______________	x _L. parryi_ (Griffiths, 1933)
L. pardalinum	x _L. parryi_ (Griffiths, 1933; Stern, 1938)
______________	x _L. roezlii_ (_vollmeri_) (Stern 1938)
______________	x L. _washingtonianum_ (Stern, 1938; Purdy, 1942)
______________	x _L. kelloggi_ (Emsweller, 1937)

L. pardalinum x L. parvum (Beane, 1952; Vollmer, 1955)

______________ x L. maritimum (Grove, 1933; Purdy, 1895)

______________ x L. bolanderi (Woodriff, 1950)

______________ x L. occidentale (Stryker, 1951)

______________ x L. kelleyanum (Beane, 1952)

______________ x L. columbianum (Purdy, 1942; Griffiths, 1931)

L. washingtonianum x L. parryi (Preston, 1933; Stern, 1938)

____________________ x L. maritimum (Preston, 1933)

____________________ x L. columbianum (Shride, 1942; Emsweller, 1953)

____________________ x L. roezlii (vollmeri) (Simmonds, 1939)

L. parryi x L. roezlii (vollmeri) (Grove, 1932; Woodcock, 1950)

__________ x L. kelloggi (Stout, 1933)

__________ x L. parvum (Wyatt, 1954; Simmonds, 1939)

__________ x L. occidentale (Amsler, 1950; Wyatt, 1954)

__________ x L. fresnense (Woodcock, 1950)

__________ x L. nevadense (Woodcock, 1950; Wyatt, 1948)

L. columbianum x L. rubescens (Sturgeon, 1952)

______________ x L. bolanderi (Vollmer, 1942, 1955)

______________ x L. roezlii (vollmeri) (Emsweller, 1937)

L. rubescens x L. bolanderi (Stern, 1938)

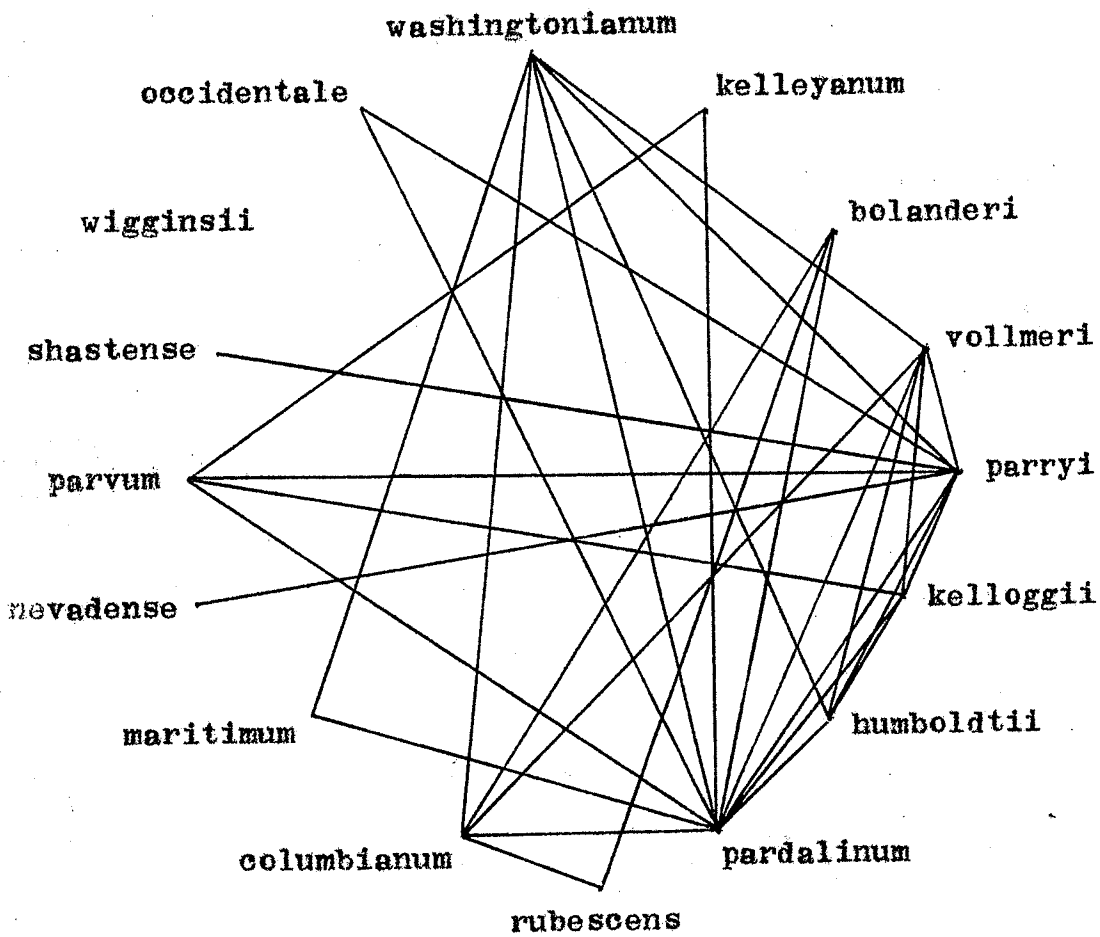
L. parvum x L. kelleyanum (Beane, 1952; Vollmer, 1955)

__________ x L. kelloggii (Stout, 1933; Emsweller, 1937)

L. kelloggii x L. roezlii (vollmeri)(Stout, 1933; Vollmer, 1955)

Figure 1

Reported Hybrids
between California Species of *Lilium*



It is possible that this list is incomplete and that exhaustive searching would perhaps reveal a greater range of crosses, but it indicates the direction of work that has been done. For instance, crosses between L. kelleyanum, L. columbianum, L. maritimum, and L. occidentale have perhaps never been tried because of the general lack of horticultural interest in these species. Hence, Figure 1 could be misleading in that it does not indicate relative hybridizing affinities but rather only the crosses that have been reported.

Whether the California species will or will not cross in the garden, the fact remains that many of them will not cross in nature and the purpose of this investigation was to find out if pollinating agents are responsible for this isolation.

PROCEDURE

The solution of this problem consisted of patient observation, capture, and identification of all animals whose activities on the flowers resulted in the transfer of pollen from one plant to the stigma of another. Of course, it was not conclusive evidence of cross-pollination merely to have seen an insect traveling from flower to flower unless that insect was actually seen to make good contact with the stigma and anther repeatedly, indicating a repetitious feeding pattern. Upon capture and microscopic examination of an insect it was considered important to have seen and identified lily pollen in sufficient amounts to insure ample deposition of the pollen on the stigma. This phase of the study is very important since several insects were seen to touch shedding anthers, but when captured not one grain was found adhering to any part of their bodies. Such occurrences may add to the significance of the great variation found in the sculpturing and chemical composition of pollen grains.

As stated earlier, this work had to be done in the field, and since some of these species are nearing extinction and others are highly restricted in their distribution it was necessary to execute a rather carefully planned procedure in order to: (1) find a location where each species could be found, (2) be there at the time they were blooming, and (3) find them in sufficient quantities to make watching and other experimental work feasible.

Unfortunately, wild lilies are the prize prey of every horned or antlered animal, picnic party, or logging trip that ventures near the habitats of these fine plants, all of which made lily hunting a problem in itself.

CLASSIFICATION

The seventy or eighty species of *Lilium* *L.*, exclusive of *Cardiocrinum* Lindley, *Notholirion* Wallich ex Voigt, and *Nomocharis* Franchet, have been divided into four sections according to the commonly accepted classification of Wilson (1925) based on the shape and poise of the flower. This classification is but a modification of the earlier systems of Endlicher (1836) and Baker (1871) which originally included only the Eastern Asiatic lilies, but later (Elwes, 1880) came to include the Pacific Coast lilies also. These sections of Wilson are:

Section I, *Leucolirion*. The trumpet or funnel-shaped lilies. The Pacific Coast lilies that fall into this section are *L. parryi* S. Wats., *L. bolanderi* S. Wats., *L. rubescens* S. Wats., and *L. washingtonianum* Kellogg. The balance of the species in this section are of Asiatic distribution except *L. candidum* L., which is European.

Section II, *Archelirion*. The bowl-shaped lilies, consisting only of *L. auratum* Lindley which is native to Japan and vicinity.

Section III, *Pseudolirium*. The erect-flowering lilies with clawed perianth segments. There are no representatives of this type on the Pacific Coast. The type species for the section is *L. philadelphicum* L., which is native to North America both east and west of the Rocky Mountains but is not found in the three Pacific states.

Section IV, Martagon. The turkscap lilies, so named because of the strongly recurved nature of the perianth segments that resemble a turban.

All of the Pacific Coast lilies not found in the section Leucolirion are of the martagon type, viz.: *L. pardalinum* Kellogg, *L. humboldtii* Roezl and Leichtl., *L. vollmeri* Eastw., *L. kelloggii* Purdy, *L. parvum* Kellogg, *L. maritimum* Kellogg, *L. occidentale* Purdy, *L. kelleyanum* Lemmon, *L. columbianum*, *L. nevadense* Eastw. Hanson, and *L. wigginsii* Beane and Vollmer (1955).

It cannot be said that the martagons are Old World or New World plants since there are many representatives of the martagon type flower wherever lilies grow. The type species of the section, *L. martagon* L., is found all over Europe and Russia north of the Gobi desert, and is the most widely distributed lily within the genus. Its center seems to be European by reason of its greater frequency of occurrence and its wide adaptation to many habitats in and around Europe.

It is generally admitted (Elwes, 1880; Comber, 1949; Woodcock and Stearn, 1950) that the present classification of the genus is strictly one of convenience and quite artificial.

Any classification that separates the Pacific Coast lilies by placing some with the Asiatic species and others with the European species is certainly not phylogentic, as it is well known that the sixteen or so species of California lilies are notedly interfertile and bear many similar vegetative and physiological characters that would tend to isolate them from the Old World species as well as bind them together amongst themselves.

Recently a new classification of the genus *Lilium* by Comber (1949) has been proposed based on fifteen characters such as type of germination, leaf arrangement, bulb scales, seed morphology, bulb shape and habit, petiole type, stigma type, stem roots, and number of stems per bulb. This classification agrees remarkably well with the existing geographical distribution of the genus and provides us with a good stepping stone toward a phylogenetic analysis of these plants.

This new classification cannot be applied quantitatively, nor can any classification, because of the variations in magnitude of these characters mentioned above, and also because of the fact that the phenomenon of parallel evolution makes it impossible to infer that similarity implies relationship. For instance, it is felt (Comber, 1949) that the nodding characteristic found in weak-stemmed plants with cup-shaped flowers occurs in many distantly related lilies as a protective mechanism against filling up with rainwater and snapping. If this is true, then the nodding character is valueless as a phylogenetic indicator even though it may be good as an artificial taxonomic character. Much of the life history of every species must be known before the satisfying stage of phylogenetic inquiry is reached.

The new classification by Comber divides the genus into two sub-genera Cardiocrinum Endl. and Eulirion Reichenbach. The Eulirion are divided in turn into seven rather than four sections. Of these, only section 2, Pseudolirium Endl. amend. is of interest here, since it includes exclusively the American species. This section is held together by the general presence of: (1) hypogeal germination, (2) delayed germination in all but four species, (3) whorled leaves, (4) jointed bulb scales in all except subsection 2a, (5) seeds heavy--comparative average weight within each species, (6) perianth segments smooth, not papillose, (7) bulbs more or less rhizomatous, not erect, (8) stems erect, not stoloniferous. This section falls naturally into four subsections still based on as many of the above fifteen characters as possible. They are:

Subsection 2a. These are the lilies with sub-rhizomatous bulbs (dry land lilies) whose bulb scales are large and entire. Included are Lilium humboldtii Roezl and Leichtl., L. columbianum Hanson, L. kelloggii Purdy,

L. washingtonianum Kellogg, L. rubescens S. Wats., and L. bolanderi S. Wats. All are restricted to the Pacific Coast.

Subsection 2b. Here we find the wet land or creek lilies whose bulbs are rhizomatous and with small bulb scales. The seeds of this group are very similar also, and again the distribution is confined to the Pacific Coast. In this group are Lilium pardalinum Kellogg, L. vollmeri Eastw., L. nevadense Eastw., L. occidentale Purdy., L. maritimum Kellogg, L. parvum Kellogg, and L. parryi S. Wats. Although Comber (1949) was not aware of the recently discovered Lilium wigginsii Beane and Vollmer (1955), it is certain that it also falls into his subsection 2b. The same can be said for Lilium kelleyanum Lemmon.

Subsection 2c. These are all Atlantic Coast lilies with stoloniferous bulbs and light seeds.

Subsection 2d. Only Lilium philadelphicum L. and L. catesbaei Walter are found in this group by reason of their almost erect bulb, erect flowers, and light seeds. Both are east of the Rocky Mountains.

Comber's classification deals only with the species of Lilium and is not extended to subspecies or varieties. Of the California lilies it may be noted that the older system of classification divides Lilium humboldtii into three varieties, one of which is restricted to the central and northern areas of the Sierra Nevada range and is designated as the type. The other two are limited to the mountain ranges of southern California and are called L. humboldtii var. ocellatum Kelloggi, and L. humboldtii var. bloomerianum Purdy. When the common term Humboldt Lily is used in this report it refers to Lilium humboldtii and its variety ocellatum but not the variety bloomerianum (unless otherwise specified) since the latter was not included in this study. The difference between L. humboldtii and its variety ocellatum does not justify a distinction, at least as far as their reproductive habits are concerned.

The identification of the species used in this report was made by Dr. Albert M. Vollmer from mounted specimens collected by the author, as well as from a description of the habitat and exact geographic location.

POLLINATION

The general flower type of the genus Lilium is adapted to, or has evolved with, the feeding habits of medium to large butterflies, moths, and/or hummingbirds, in contrast to bees, long-tongued flies, promiscuous insects, wind or water. The factors that indicate this conclusion are: (1) the presence of nectar grooves comparable in length to the tongues of large butterflies and hummingbirds, (2) the inaccessibility of nectar to short tongued insects, (3) the distance separating the stigma from the nectaries prohibiting small nectar gathering insects from pollinating to any extent (possible exceptions in L. parvum, L. bolanderi, L. kelleyanum, and L. maritimum), (4) the distance separating the stigma from the anthers prohibiting pollen gathering insects from pollinating (minor exceptions to be discussed later), and (5) the distance from the landing platform (recurved perianth segment) to the stigma being too great in most species for small insects to effect pollination.

With these conditions in mind, the question now becomes, "Are today's lilies pollinated by the same agents as those responsible for the evolution of that floral type?" If so, which of the many species of moths, butterflies and hummingbirds in California are the active pollinators, and if not, which ones have taken over that function? If another type of insect is pollinating a lily that is already adapted to a moth or butterfly, is it successful?

To begin with, it is known that a plant that has as many asexual reproductive mechanisms as do the lilies, e.g., bulbs, scales, bulblets, bulbils, etc., does not need to reproduce by seed, in fact if a clone is well adapted to its habitat genetic recombination might detract from the already achieved optimum effectiveness of that clonal type. The only recombination that would be needed would be if some aspect of the habitat were to change which rendered that clone less suited than before. However true this may be, the fact remains that an abundance of seed is produced year after year by the California lilies. Further, bagging experiments indicate that this seed is the product of cross-pollination (inter-clonal) rather than of self-pollination or apomixis--a conclusion that could be expected since self-fertilization is rare or absent in long lived perennials with rhizomes (Stebbins, 1950).

Seed set of any kind, however, would prove favorable in Lilium if the clone should become infested with some virus or other type of disease that is not transmitted through the seed, but even here a new disease-free habitat would be needed. So it is then, that while seed production may or may not be favorable to the clone, it does occur and appears to be of an interclonal nature in the California species.

Lilium humboldtii var. ocellatum

The flowers of Lilium humboldtii var. ocellatum are of the strongly recurved martagon type whose color ranges from yellowish orange to dark orange and whose general floral morphology is quite similar to that of L. pardalinum (see Plate 1). The flowers are neither horizontal nor are they nodding but assume a position intermediate between these two positions. The perianth segments are marked (except at the tip) with deep maroon spots surrounded by a crimson area, which gave rise to the varietal name ocellatum. It is one of the largest of the Pacific coast lilies, being exceeded only by L. washingtonianum, L. parryi and one variety of L. pardalinum. There is no noticeable fragrance nor is there an abundance of nectar produced in this lily as is the case with L. washingtonianum and L. rubescens.

This lily was studied for pollinators in four canyons in the San Gabriel Mountains (Los Pinetos, Evey, Coble and Palmer) as well as at the Rancho Santa Ana Botanic Garden. In each case the pattern of pollination was the same. These plants are all self-pollinated (not to be confused with self-fertilized) often before the flowers are fully open and always within two days after opening. In the drier locations pollen was found shedding within closed perianth segments, and in the wetter locations the anthers would remain closed until the first dry hour after the flower opens.

For the first twenty-four hours or so after anthesis the style is straight and not in contact with the anthers, but after still another day of drying the style begins to curve upward until it makes contact with one of the six shedding anthers. It does not stop curling here, however, but continues until the stigma is outside the ring of anthers. Even before it touches one of the anthers the wind or an insect will cause pollen to fall from one of the top anthers to the stigma below or even from a flower higher on the inflorescence. All of this is of no value to the plant, however, because self-fertilization will not occur in this species except infrequently at the end of the season, producing seed of questionable viability.

Cross-pollination (inter-clonal pollination, outcrossing), on the other hand, occurs through the medium of several agencies of varying importance. Of least importance are the honey bees (Apis mellifica Apidae) whose numbers were small and whose activities were such as to effect pollination only infrequently. Rather than collect the fresh pollen from the young anthers these bees seemed to prefer the pollen from week-old anthers in which the pollen had turned from a creamy yellow through brown or pinkish brown then finally to bright yellow. By this time the flowers had already been successfully outcrossed by some other more efficient pollinator.

The pollen sacs on the legs of some of these bees were removed and the pollen stained and compared microscopically with pollen of known lily identity. The sacs contained no pollen other than that of *Lilium*--a finding that could be expected from the known habits of these bees (Grant 1950b).

A smaller number of bumblebees (*Bombus* *sp.* *Bombidae*) were observed, but showed considerably more vigor and collected fresh pollen rather than old. Both bees came in contact with the stigma only by accidently knocking into it or resting momentarily, and hence can be considered of negligible importance. It is strange that these bees should go from flower to flower collecting pollen when there is more available pollen on two or three anthers than either of them could possibly carry.

Another pollinator of this lily is the Fritillary Butterfly (*Argynnis* *sp.* *Nymphalidae*). This butterfly is remarkably similar in its color and markings to the Humboldt Lily; in fact, when this butterfly is resting on the blossom it is so well camouflaged that it could easily go unnoticed by the casual observer. This is quite often the case with flowers that have evolved in response to the pollinating activities of one insect (Knuth 1906), and at one time the Fritillary Butterfly may have played a more important role than today. This is rather doubtful unless the feeding habits of this insect were different in the past, or the flowers of this lily were of a smaller size and shape.

This insect lands on a perianth segment of the semi-pendulous flower with its head facing the central portion of the flower and with its wings horizontally outstretched. Using the nectar grooves it thrusts its tongue down to the nectar at the base of the flower. In so doing its wings change from the horizontal or outstretched position to a point about halfway to the vertical or closed position. When they are at this position they sometimes touch the anthers if the stamens have had time to spread enough. The insect then moves to another segment of the same flower and repeats this process until it is near the top of the flower where the stigma is found, and if the style has curled out past the ring of anthers the tips of the butterfly's wing may touch the stigma. Many times it will not touch it, however, because: (1) the degree of recurvature of the perianth segments is often greater in some plants than in others, thus increasing the distance between the landing platform and the anthers and stigma, (2) variations in the length of the style (3.3 cm to 4.8 cm) and filament (4.0 cm to 5.0 cm) can increase this distance also, and (3) often the insect will not use the two uppermost perianth segments which are the only two that properly orient it for contact with the stigma.

A more convincing fact of the meager role the Fritillary Butterfly plays in the pollination of var.

ocellatum is revealed when the butterfly is placed under the microscope and no or very few pollen grains are found anywhere on the insect's body. Secondly, these butterflies were found in only two canyons (Los Pinetos and Evey) both of which contained running water, and were not seen at all in the other three locations.

The hummingbird (Calypte sp.) might be called a constant or dependable secondary pollinator of the Humboldt Lily. At all locations this bird was present and actively obtaining nectar from the flowers. These birds hover in front of the flower, insert their beaks, and extract as much nectar as possible from one flower before going to the next. The bird's wings would repeatedly batter the anthers and when operating on the uppermost perianth segments its chest would touch both anthers and stigma. On numerous occasions they would grab on to anther and/or style with their feet and use these structures for support while still flapping their wings. Sometimes the wings would stop momentarily and the style and stamens would prove strong enough to support their weight. On one occasion a bird visited thirty-five individual flowers of the Humboldt Lily before going to another species, such as Eriophyllum sp. or or Salvia sp. These birds were seen feeding at all hours of the day and even until quite dark.

It is believed that the genus Lilium co-evolved with some other pollinator than the hummingbird because of: (1) the absence of the birds in the Old World--the alleged birthplace of Lilium, (2) the presence of a superior ovary in contrast to the usually protected inferior ovary of typical bird flowers (Grant, 1950a), and (3) the presence of a sweet fragrance in two-thirds of the California species--a characteristic usually not found in bird plants (Grant, 1953).

The most efficient pollinator of the Humboldt Lily that was observed is the Swallowtail Butterfly (Papilio sp., Papilionidae). This butterfly lands on the lily and clambers over the reproductive structures in a vigorous and clumsy manner. Upon alighting it makes no use of the perianth segments as landing platforms (unlike the Fritillary Butterfly), but uses the six stamens and one style for that purpose. With its head facing each perianth segment it dips in for the nectar then rotates on its axis to the next segment rather than revolving in an orbit as in the case of the Fritillary Butterfly. It seems, however, that this butterfly prefers not to be upside down since it was never seen to rotate more than ninety degrees to the right or left, thus neglecting the nectar of the lowermost segments. The Swallowtail Butterfly was seen at all locations but by far the greater number were at the locations that had running streams nearby, and the least of all at the botanic garden.

The amount of lily pollen found on the Swallowtail Butterfly was quite variable. It seems that when it picks up pollen on its legs, abdomen, and the lower surfaces of the hind wings it loses it all rather easily in flight except for that which clings to the veins of the hind wings. These veins are of a sticky nature and rather prominently embossed, thus providing additional surface area capable of collecting pollen.

The validity of this pollinating mechanism was tested by capturing a swallowtail and dusting its hind wings and feet with several ripened lily anthers. Under the dissecting microscope the abundant pollen grains were seen to be uniformly distributed, but after one quick breath of air all the grains had been blown off except those that adhered to the sticky veins. The next step (still under the microscope) was to touch the remaining pollen grains with a mature and immature stigma from the Humboldt Lily. It was found that the mature stigma could wipe the veins clean with a single stroke, whereas the immature stigma would do no better than any blunt object of a non-sticky nature.

The fact that Swallowtail Butterflies (the species) are known to pollinate other flowers besides lilies does not make them promiscuous pollinators. If an individual butterfly went from lily to _Dicentra,_ then to _Salvia_ as the hummingbirds did, it could certainly be called promiscuous, but of all the Swallowtail Butterflies observed none changed flowers in the middle of a feeding flight, and not one had pollen grains of any other species except that of Lilium. All Swallowtail Butterflies observed went to two or three flowers then flew over the mountain or upstream so fast that they could not be followed to see what their next flower was. The fact remains, nevertheless, that since lilies are so few and far between a Swallowtail Butterfly has to be promiscuous in order to maintain its migration flight.

This report of pollination of Lilium humboldtii var. ocellatum by the Swallowtail Butterfly substantiates an earlier observation by Dr. Verne Grant (unpublished) in which these butterflies were seen feeding on this lily at approximately two hour intervals in Coble Canyon of the San Bernardino Range.

At the beginning of this investigation it was felt that these Humboldt Lilies were pollinated by night flying hawkmoths because of their morphological similarity to Lilium martagon L. which is pollinated by night flying species of Sphingidae (Knuth, 1906), but after watching from dusk until well after dark at all locations for two summers no hawkmoths were seen feeding on any of these lilies, although in the two canyons that had running water several were seen flying about.

Lilium humboldtii, *L. pardalinum*, *L. vollmeri*

These three lilies are grouped together because their flowers are so similar that few insects or taxonomists could tell one from another if a bouquet were made of all of the many floral variations of each of these species. *Lilium pardalinum* is characterized by the red tips of the perianth segments, but in areas in the southern and central part of California the flowers are almost or entirely yellow or orange (Woodcock and Stearn, 1950). Likewise the Humboldt Lily when growing near water may have the red tip of *L. pardalinum*, and one can never be sure which is which unless other characters of the plant or the location are known.

Lilium vollmeri has a typical *L. pardalinum* flower as far as color is concerned and differs in no morphological way that would be of concern to a pollinating agent. These groups are separated (in this thesis only) from *L. humboldtii* var. *ocellatum* only because the latter was worked on far more extensively by reason of its restriction and abundance in southern California.

Here, as in *L. humboldtii* var. *ocellatum*, Swallowtail Butterflies and hummingbirds were seen on each of the three species and at almost every location, occurring with the same frequency and feeding pattern as described earlier.

In Nevada City (Nevada County, California) there is a section of irrigation ditch approximately fourteen miles long which has four species of lilies growing along its banks--Lilium humboldtii and L. pardalinum found at the lower end, and L. washingtonianum and L. parvum at the upper end above a forebay. Year after year a tri-hybrid swarm between L. pardalinum x L. humboldtii x L. parvum is found, usually near the lower end of the ditch. Lilium washingtonianum always maintains its identity in this area although its location along the ditch will change periodically.

In the summer of 1955 pure stands of Lilium washingtonianum and L. parvum were found only at the extreme upper end above the forebay, and the tri-hybrid swarm was near the lower end growing in full sunlight. The swarm consisted of a rather compact hedge of lilies growing on both sides of the bank for about a quarter of a mile. It then graded into a stand of "pure" Lilium pardalinum at the extreme lower end growing in the shade which, in turn, graded into a "pure" stand of L. humboldtii growing from four to fifty feet away from the water, also in the shade.

The lower end of this ditch was watched for eight days and nights at the height of the blooming season during which time hundreds upon hundreds of Fritillary Butterflies (Argynnis sp.) were seen each day gathering nectar from morning until dark from all of the lilies in this area regardless of their ancestral lineage. Their feeding habits were identical with those seen on L. humboldtii var. ocellatum in the San Gabriel Mountains. The amount of lily pollen found on these butterflies was the same also--practically none. This was most amazing since on several occasions only those insects that were actually seen touching the shedding anthers were captured and placed under the microscope, yet no lily pollen could be found except for a few grains scattered here and there that could be easily removed by holding the wing with a pair of forceps and shaking it to simulate flight. Furthermore, these insects are so dainty and careful when feeding that it seems as though they wish to avoid contact with the reproductive parts of the flower. Since there are so many of them and they feed for so long each day without visiting any other species of flower (few others were available) it seems that they must effect considerable cross-pollination, in spite of the non-adhesive nature of their wings. It must be remembered that these insects were captured with a butterfly net which could account for much of the loss of lily pollen. It is possible also, that their wings are somewhat more adhesive at an earlier stage in the insect's adulthood before so many scales are lost as a result of usage.

About every half hour or so a Swallowtail Butterfly would fly by and very efficiently pollinate three or four flowers, then fly about one hundred yards or so down the stream before landing on another lily, whereas the

Fritillary Butterfly would go pretty much from plant to plant. Occasional hummingbirds fed here also.

All three of these pollinators indiscriminately fed upon the creek lilies (L. pardalinum), the dry land lilies (L. humboldtii) as well as the hybrids that contained much of the yellow flower color of L. parvum. Individual insects were followed to establish this fact.

The extreme or typical forms of L. pardalinum and L. humboldtii in this area differ from each other in three ways that would be of concern to an insect: (1) L. humboldtii has nectar grooves that consist of linear invaginations of the basal portions of the adaxial epidermal surfaces of the perianth segments, while nectar grooves in L. pardalinum are of a definite morphological structure resulting from a deepening and lateral bunching together of these invaginations producing linear flaps capable of lateral movement or yield--perhaps an accommodation for variations in tongue diameter or delicacy, (2) L. pardalinum produces much more nectar than L. humboldtii, and (3) L. pardalinum has the red tipped perianth segments that are (for the most part) absent in L. humboldtii. These differences, however, appear to be of no concern to the pollinators mentioned above, because individual insects visited both types with equal frequency. Here also, no night flying creatures were active on these flowers.

Plate 1

Swallowtail Butterfly on Lilium pardalinum

The only insect that was seen to visit the dry land lilies and not the creek lilies was a small bee (Halictus sp. Andrenidae) whose activities seem to be confined to the morning hours. These bees experienced much difficulty obtaining pollen from the anthers that were still wet from the heavy morning dew, the outer layer of moist pollen grains forming a crust around the anther. After about a half-minute of this frustration the bees would fly back about six to nine inches from the anther and at full speed fly directly into the anther, opening it up by the force of the impact and exposing the now available pollen supply. It seems, however, that they can make no distinction between anther and stigma (both are purplish) hence they go through the same procedure on the stigma, thus depositing an abundant supply of pollen at the proper place. These bees were not found all up and down the ditch but only in areas where they apparently had a nest, but in these areas they were superb pollinators. Every available spot on their bodies contained pure lily pollen.

Occasionally a small bee (Megachile sp., Megachilidae) gathered pollen from Lilium pardalinum rather industriously and if these bees had been as abundant as the Halictus bees, they could be rather important also. Their bodies were coated with approximately 50 per cent lily pollen and 50 per cent pollen from another unidentified species. Reports of this bee as a lily pollinator are also found in older botanical literature (Blanchan, 1927; Weed, 1895) dealing with other areas.

Lilium washingtonianum, *L. parvum*

These two lilies are treated together because they grow together at the location in which they were studied the most, i.e., at the upper end of the ditch above a forebay in Nevada City, Nevada County, California.

Certain varieties of *Lilium washingtonianum* are the largest of all the California lilies, with perianth segments often exceeding 9 cm. They tend to appear much larger than the rest of the lilies (except *L. parryi*) because of the non-recurved nature of the perianth segments that form a tubular corolla which flares open at the tip. The flowers are pure white for the most part, often with a few reddish or purplish dots deep in the corolla tube. Some flowers may have a purplish tinge to the perianth that becomes even more purple with age. This is known as the variety *purpurascens*. Nearly all Washington Lilies carry their flowers in a horizontal position, and all are extremely fragrant.

Lilium parvum, on the other hand, is a non-fragrant very small creek or alpine lily, with dainty ascending bell-shaped flowers whose colors range from pure yellow at the lower elevations to dark red at the higher locations. All have maroon spots.

In botanical literature L. washingtonianum is usually described as a dry land lily found on open dry ridges or pine forests. Around Nevada City it is found under those conditions, for the most part, but many plants are also found growing a few inches away from plants of L. parvum both of which are often found six inches above the level of the water in the ditch. No intergrade or hybrid between these two species has ever been seen by the lily enthusiasts in this area, and no other species of lily is to be found in this area, the closest being the tri-hybrid swarm, mentioned above, twelve miles downstream.

In this section above the forebay relatively few Argynnis or Fritillary Butterflies are to be found, and rather than feeding on the lilies they are observed to fly just over the tops of these plants without feeding at all. Many individuals were followed along the course of the waterway, and while they would periodically rest on a twig of some kind, they would refrain from taking food from any plant and would not stay in this area longer than the length of time it took to fly through.

Lilium parvum, in this area, was found to possess the usual complement of minor or secondary pollinators, mostly Hymenoptera (Andrena sp., Bombus sp., Halictus sp.), but also some Coleoptera (Anoplodera sp., Cerambycidae), all of which can account for considerable seed set. One small bee

(*Chlorohalictus* *sp.*, *Andrenidae*) gathered pollen from *L. parvum* while another individual gathered nectar from *L. washingtonianum* and neither individual performed any other function while under observation.

The peculiar feature about the *Chlorohalictus* bees concerns the fact that on the bodies of all the bees captured (both pollen and nectar gatherers) were found abundant quantities of scales from the Swallowtail Butterfly. The pollen gatherers of *L. parvum* had much pure lily pollen and many scales, while the nectar gatherers of *L. washingtonianum* had relatively little pollen and a proportionately smaller number of scales. These scales were most carefully compared side by side with those removed from several of the captured Swallowtail Butterflies and there was no question as to their identity. How did these scales get on the bodies of the bees? They could not have come from the butterfly net as forceps were used in their capture. They could have come from the killing jar, but this same jar was used over and over again at every location and no scales were found on any other insect. If the flower constancy of bees can be trusted in this case, it must mean that the Swallowtail Butterfly visits both *L. parvum* and *L. washingtonianum*, but in the five days and nights spent camping at this location, not one Swallowtail Butterfly was seen anywhere in this area. The only other two possibilities are that both bee and butterfly visit a third flower or they come in direct contact with each other in battle or nesting habits in some way which seems rather remote. Another fact that tends to confirm the first hypothesis is the four large bumble bees (Bombus edwardsii) that were captured clambering all over the anthers and stigmas of L. parvum after first crawling down to the base of the style for nectar. Scales from the Swallowtail Butterfly, some pine pollen, some lily pollen, and much unidentified pollen of two species were scraped from two large thick clumps confined to the hind legs.

Field observations by Dr. Verne Grant indicate that butterflies in general are not a factor in the pollination of Lilium parvum since many species were observed flying over the tops of this lily without paying any attention to this plant. However, Dr. Grant did not see Swallowtail Butterflies in this area at the time of observation. He did see Rufus Hummingbirds (Selasphorus rufus) pollinating this lily with apparent effectiveness and in the same manner described earlier.

The beetles of the family Cerambycidae (Anoplodera sp. and Strangalina sp.) while numerous, confined their activities to nectar gathering on L. washingtonianum, and very little pollen was found on their bodies because of the hard glossy nature of their exoskeleton as well as their infrequent contact with stigma or anther.

Regarding the Washington Lilies growing at other locations (open pine forests and hot dry ridges), similar Hymenoptera (*Halictus sp.*, *Andrena sp.*) were captured while gathering pollen, but no butterfly scales were included in the pollen samples removed from their bodies. It is felt that the most important pollinator of the Washington Lily is yet to be seen. It is doubtful that the tongue of the Swallowtail Butterfly is long enough to touch the nectar of the average flower of this species as the distance from the base of the ovary to the stigma averages 8.2 cm. Since the Swallowtail Butterfly lands on the stigma and dips into the corolla tube its tongue would have to be longer than the tongue adapted to the Humboldt Lily, whose pistil length averages 5.8 cm. Hawkmoths, on the other hand, gather nectar while in flight and the style could bend under the pressure of the moth's body. The extreme fragrance of the Washington Lily is another indication of hawkmoth rather than butterfly pollination. No hawkmoths, hummingbirds or butterflies were seen pollinating this lily, however.

One interesting character of *L. washingtonianum* and *L. parvum* is the speed with which the pollen is lost from the anthers after anthesis. On the second day after opening there is no pollen to be had from either of these flowers, while *L. humboldtii* retains (or sheds) its pollen for as long as ten days or more. This could well be a factor to insure cross-pollination if the stigmas were not receptive on the first day. The receptiveness or non-recepetiveness of these plants is not known, but it is known that the stigmas are sticky just as soon as the flowers have opened.

Lilium rubescens

This lily, known as the Redwood Lily, is similar to the Washington Lily in that it also is a dry land lily that occasionally has its "feet in the water" in certain locations. In the wet places are found the same or similar insects that were found on the Washington Lily, such as the Strangalina and Anoplodera beetles (Cerambycidae), two species of Halictus bees, and one fly, Eulonchus tristis Loew (Cyrtidae) that account for at least some of the seed set, but in the dry locations where most of the plants are found these insects are very few and probably account for very little of the seed set. One interesting point is the presence of a small green (unidentified) spider that is found on approximately 50 per cent of the flowers of the Redwood Lily and on many of the Washington Lilies when these plants are growing in the dry area and the absence of the spider when they grow in the moist locations. This spider, along with its young, spins a very scant web in the corolla tube and waits for a nectar-loving insect to seek the over-abundant supply of nectar which is often found running down the pedicel.

The many hours spent watching this lily were very unrewarding and discouraging since nothing except the minor insects noted above visited this flower, yet it was always felt that a primary pollinator would be found feeding on this flower by reason of its extremely sweet fragrance and its characteristic form and color.

Lilium kelloggii

The only insect seen feeding on *Lilium kelloggii* was the *Anoplodera* beetle, but since this lily could be found in only one location and with but a few widely separated flowers in bloom at the time of observation, a discussion of the pollinators of this flower must await further data.

Lilium kelleyanum

Lilium kelleyanum, on the other hand, was found at many locations and in abundant numbers. This plant has a small tightly recurved flower that is similar in size, color, and spotting (light yellow to light orange with maroon spots) to that of *Lilium parvum*. However, *Lilium kelleyanum* has nodding, recurved fragrant flowers while *L. parvum* has ascending, bell-shaped, non-fragrant flowers. Another outstanding characteristic of *L. kelleyanum* that is missing in all other California lilies is the corona or ring of anthers that is formed by the failure of the filaments to recurve. Also the fragrance of this species is unlike that of L. parryi, L. washingtonianum, or L. rubescens not only because it is weak, but also because it differs in quality being less pleasurable to smell and less fragrant at night as is the case with the other species mentioned above.

At all locations numerous Swallowtail Butterflies were actively feeding on these plants with their same familiar methodical clusiness. A noticeable difference between these Swallowtail Butterflies and those found on L. humboldtii is that the lily pollen was more abundantly located on the legs and underside of the abdomen of insects captured from L. kelleyanum while pollen from L. humboldtii adheres only to the veins of the wings. It is not known why the pollen of L. kelleyanum should stick to the legs and abdomen of the Swallowtail Butterfly while the pollen of L. humboldtii does not. Perhaps the pollen itself is stickier or the insects' legs are different in some respect because of the higher altitude of Walker Lake in Mono County (7,926 ft.) where these plants were studied. Of course, much more pollen comes in contact with the butterfly's feet and abdomen with this flower than with the Humboldt Lily because of the tighter ring of anthers and shorter filaments (2.0 cm. compared to 4.5 cm. in Lilium humboldtii).

Toward the upper end of Walker Lake an apparent tri-hybrid swarm was found between Lilium kelleyanum, L. parvum, and L. pardalinum. In this swarm all possible combinations of color, form, and fragrance were found such as yellow fragrant flowers with red tips to orange non-fragrant flowers without red tips. These variations, however, had no apparent effect on the feeding habits of the Swallowtail Butterflies who fed indiscriminately on all of these forms. This butterfly was the only insect that came near these flowers other than a few honey bees. These flowers were not watched at night because of their remoteness from the nearest available base camp, so nothing can be said regarding night pollinators.

Lilium bolanderi

Since the time factor in watching for pollinators was one that required much consideration, it was decided to omit this lily from this phase of the study. However, while emasculating and bagging these flowers several Anoplodera beetles were found obtaining nectar at the base of the corolla tube.

Lilium occidentale, L. columbianum, L. maritimum

These are coast lilies, or mostly so, and all the time these lilies were watched the wind was blowing much fog in from the ocean around Patrick's Point (Humboldt County). Such climatic conditions inhibit the feeding flights of insects, and as a result the time spent in this area watching for pollinators was not at all fruitful. In fact, the weather was so wet and foggy that the flowers of several plants of *L. columbianum* were seen to open but the anthers did not start to shed pollen for three days.

At two locations large hybrid swarms between *L. columbianum* and *L. occidentale* were found which contained all manner of variations and intergrades.

Lilium wigginsii

This recently named lily (Beane and Vollmer, 1955) grows in a wet habitat similar to that of *L. parryi*, and while the area was swarming with all kinds of insects, none, other than a few honey bees, fed upon these plants. Hummingbirds were more abundant here and appeared rather efficient as pollinators.

Upon examination it was found that many of these plants had diseased anthers, yet there was no evidence of the entry of an insect into the bud.

Lilium parryi

This yellow marsh or creek lily, often called the Lemon Lily, is pollinated by night flying hawkmoths (*Celerio lineata*) of the family *Sphingidae* and apparently by nothing else. These moths are superbly efficient, extremely rapid, and highly erratic in their pollinating habits. They pollinate at late dusk and night, but apparently not in the dark early morning hours, perhaps because the heavy morning dew makes flying difficult. At any rate, they were never seen later than 4 A.M., but were seen at 12:30 A.M. They are extremely few in number and no two were seen at one time, but rather at half to one hour intervals. They pollinate _L. parryi_ and _L. parryi_ var. _kessleri_, both of which grow in similar habitats in the San Gabriel Mountains at elevations of from 6,000 to 10,000 feet. The only difference in the feeding habits of the hawkmoths when feeding on the two varieties is that it is more difficult for the moths to feed from var. _kessleri_ than from the type as indicated by the numerous attempts to steal nectar from the side of the flower of the former. Variations in the size of the moths could account for this, however.

These lilies are good examples of a typical hawkmoth moth flower because: (1) their flowers begin to open at 6 or 7 P.M. and are fully opened by 8:30 or 9 P.M.; (2) the anthers do not start to shed until after the flowers are fully opened; (3) the stigma is exserted beyond the anthers by 6 to 20 mm.; (4) they are extremely fragrant at night; (5) they have bright clear yellow corollas with no nectar guide lines, and (6) their tubular corollas are so constructed as to discourage all pollinating agents other than the Lepidoptera.

Several humming birds visited the var. _kessleri_ and their feeding pattern was noticeably different from those feeding on *L. parryi* in that they would never feed on var. *kessleri* while on the wing, but would land on the peduncle and enter the corolla tube from the side, apparently well aware of the fact that they could not obtain nectar in their usual manner.

Unlike the Fritillary Butterfly or the hummingbird, the hawkmoth prefers to use the uppermost perianth segments only, hence a single feeding thrust is all that is required to pick up and deposit pollen in the proper places. There is no wasted effort here as in the other pollinators mentioned.

At one large stand of *L. parryi* var. *kessleri* there were four flower buds that were seen to open while under observation. Their stigmas were perfectly free of pollen and after a pollen covered bumble bee (*Bombus sp.*) vigorously landed on the stigma it was found that the stigmas were still perfectly free of pollen. This bee was captured and under the microscope it was noticed that its sticky abdomen did not readily release the adhering pollen, indicating the meager role this insect plays in the pollination of this lily.

Pollination of Old World Species

Lilium martagon L. is an unpleasant smelling turkscap type lily that is adapted for pollination by moths and to a lesser degree by butterflies. Nocturnal hawkmoths hover

over these flowers and first touch the under side of their bodies to the stigma projecting beyond the anthers and then the pollen covered anthers (Knuth, 1906). They are pollinated not only by the family Sphingidae but also by members of the family Noctuidae (Muller, 1883). The action of the hawkmoths on these turkscap lilies is noticeably different than in the case of the trumpet lilies such as L. parryi in that the hawkmoth never alights on the flowers of the latter but feeds like a hummingbird. In the Alps and in the gardens at Kiel (Germany) the hummingbird hawkmoth (Macroglossa stellatarum L.) as well as ten other species of Lepidoptera were seen to fly continuously from flower to flower and pollinate a large number of these plants (Knuth, 1906).

Lilium bulbiferum L. is odorless, but brilliantly colored lily that is pollinated by butterflies (Knuth, 1906) or simply by diurnal lepidoptera, according to Muller (1883). Muller tells of butterflies of the genera Polyommatus and Argynnis that are of the same color as the flower of this species visiting these flowers in the Alps. Knuth mentions visits by the peacock Butterfly Vanessa io L. at the gardens in Kiel.

Lilium candidum L. is another good example of hawkmoth flower in that it is only slightly fragrant during the day and quite strong at night when the flowers open. The white color, exserted stigma, and the lack of a suitable landing platform are further indication of hawkmoth pollination. Hawkmoths, however, have never been seen visiting this flower in spite of the many hours of watching in the warm summer evening (Knuth, 1906).

DISCUSSION

It has been shown that the Swallowtail Butterfly plays a rather important role in the pollination of four (possibly six or more) of the native species of *Lilium* of California, from the very large flowers of *L. humboldtii* var. *ocellatum* to the relatively small flowers of *L. kelleyanum*, using the same feeding pattern in each case. It has also been shown that many of the same minor or secondary pollinators (*Halictus*, *Andrena spp.*) are active on several species of lilies, and probably many of the lilies are visited by hummingbirds.

Knowing this, it would seem that there would be many natural hybrids produced where these species grow together if their isolating mechanisms were only of an ethological nature. It appears that there are isolating mechanisms working here other than those of an ethological nature. It has been said (Grant, 1949) that two processes are responsible for permitting two interfertile species to grow together and still not produce fertile hybrids: (1) no available habitat for the hybrid, and (2) non-production of hybrids due to non-pollination.

Applying this information to the situation along the ditch at Nevada City where *L. parvum* and *L. washingtonianum* grow side by side, we find that neither of these two explanations seems entirely satisfying (assuming that these species can be crossed successfully in the botanic garden under strict control). The explanation that there is no available habitat seems invalid since both species are found growing in the same habitat. The explanation concerning the non-production of hybrids due to non-pollination is, for the most part, tentatively true since only secondary pollinators (Halictus sp., Andrena sp.) were actually seen visiting both flowers. But there seems to be a third isolating mechanism working here that may be even more important than those mentioned above, and is explained by saying that these two species have reached a point in evolution that may be called the "point of optimum adaptation," and to hybridize two species that have reached this point is to detract from an already achieved optimum effectiveness. It is like the cacophony produced when two beautiful melodies are played simultaneously.

Assume that there are two species that can produce viable hybrids in the botanic garden. These species would be called interfertile species. Assume also that they are adapted to the same habitat, as in the case of the L. washingtonianum and L. parvum under discussion. Now, if these species had different germination mechanisms, different disease-resistant qualities, different periods of stigma receptiveness, or different methods of asexual reproduction, and each of these characters worked well together when in combination but worked poorly when recombined, then there could be no hybridizing in nature even if they were in the same habitat. But, in the botanic garden these characters could be of little or no consequence since the caretaker pampers his plants until the desired results are obtained.

This pampering in the botanic garden might be called "hybridizing the habitat" by those who wish to retain or apply the concept to plants taken "out of context," but it seems like an error to call two plants interfertile when they will cross only in the botanic garden or even only when the embryos are dissected and cultured to maturity in the laboratory. This is not what Anderson (1949) meant by the term "hybridizing the habitat" even though he indicated that human beings were the greatest habitat hybridizers. Also, to say that there is no available habitat seems like an oversimplification---a sort of a catch-all phrase that really does not explain anything. It is true that if the habitat is altered, there will be some F_2 hybrids that will find a niche, but these will only be the extreme recombination types and even then the new habitat would have to be disadvantageous to either or both of the parental stocks or else the hybrids would be swamped out of existence by numerical superiority or engulfed by backcrossing. Such seems to be the situation with <u>Lilium washingtonianum</u> and <u>L. parvum</u>.

Another reason for the non-establishment of hybrids in the case of L. washingtonianum and L. parvum could be that the intermediate flower type between the (presumably) hawkmoth flower of L. washingtonianum and the (presumably) butterfly pollinated flower of L. parvum cannot be effectively pollinated by either hawkmoth or butterfly. Under these conditions the hybrid could only survive in nature if a pollinator intermediate in tongue length and feeding pattern were brought in from an outside area, but even this could be called "hybridizing the habitat."

This idea of the non-intermediate pollinator seems to be the case with the non production of hybrids between Lilium parryi and L. humboldtii. These two species will certainly cross in the garden as evidenced by the many beautiful plants obtained using these and L. pardalinum as parent stocks; the Bellingham Hybrids are fine examples. The two species grow in the same canyon along Doane Creek in the Palomar Mountains and bloom at the same time, but no evidence of hybridization could be found (Grant, unpublished data). Grant reports that Swallowtail Butterflies flew over the tops of L. parryi and paid no attention to the flowers, yet these butterflies are the most important pollinators of L. humboldtii. Hawkmoths, on the other hand, fly right over the tops of L. humboldtii. If a colony of Bellingham Hybrids could be planted along Doane Creek and observed over the years for the presence of F_2 variation and intermediate pollinators, it might solve this problem.

SUMMARY

The recognized need for additional information on the life histories of the California species of *Lilium* initiated this study of the pollination mechanisms of these plants.

It was found that the chief pollinator of *Lilium humboldtii*, *L. humboldtii* var. *ocellatum*, *L. pardalinum*, *L. vollmerii* and *L. kelleyanum* is the Swallowtail Butterfly (*Papilio sp.*). In addition the Fritillary Butterfly (*Argynnis sp.*) must also account for considerable seed set in *L. humboldtii* and its variety *ocellatum* as well as *L. pardalinum*. The chief and perhaps sole pollinator of *L. parryi* is the hawkmoth, *Celerio lineata*, of the family *Sphingidae*.

Other minor pollinators, such as several species of wild bees, hummingbirds, and beetles are responsible for much pollination, especially in swampy or other localized areas, but certainly none of these is responsible for the evolution of the floral type of any of the California species of *Lilium*.

ACKNOWLEDGEMENTS

I wish to use this space to extend my gratitude to my adviser, Dr. Verne Grant, for originally suggesting the problem, to Dr. R. A. Fleck for determination of the insects captured, and to Mr. Frank Ford for assistance in locating many of the southern species.

Particular appreciation goes to Dr. Albert M. Vollmer, for without his many years of devotion to the study of the Pacific Coast lilies much of this thesis would have resulted in complete failure owing to the difficulty of locating many of these lilies in the wild state.

To my wife I offer a warm thanks not only for assistance in the field and with the manuscript, but for many happy hours of patient companionship during the preparation of this thesis.

LITERATURE CITED

Anderson, Edgar, 1949. Introgressive hybridization. John Wiley and Sons, Inc. 109 pp.

Baker, J. G., 1871. A new synopsis of all the known lilies The Gardner's Chronicle, pp. 104, 201-202, 479-480, 708-709, 903, 1033-35, 1325, 1422, 1650-51.

Beane, L., 1952. On the taxonomic status of some of the Pacific Coast lilies. The Lily Yearbook of the No. Am. Lily Soc. 25-28.

________ and Albert M. Vollmer, 1955. Some undescribed lilies from California. Cont. Dudley Herb. 4: 355-360.

Blanchan, Noltje, 1927. Nature's Garden. Doubleday, Page and Co. New York, 415 pp.

Comber, Harold F., 1949. A new classification of the genus Lilium. The Lily Yearbook of the Royal Hort. Soc. 173-193.

Elwes, H. J., 1880. A monograph of the genus Lilium. Taylor and Francis. London.

Emsweller, S. L., 1937. Improvement of flowers by breeding. U.S.D.A. Yearbook of Agric. 890-998.

________, 1946. Lily breeding at the Plant Industry Station, Beltsville, Maryland. The Lily Yearbook of the No. Am. Lily Soc. 11-15.

________, 1953. The lily research programme at the Beltsville Station. The Lily Yearbook of the Royal Hort. Soc. 11-21.

Endlicher, S., 1836. Genera Plantarum. 141. Vienna.

Grant, Verne, 1949. Pollination systems as isolating mechanisms in Angiosperms. Evol. 3: 82-97.

________, 1950a. The protection of the ovules in the flowering plants. Evol. 4: 179-201.

________, 1950b. The flower constancy of bees. Bot. Rev. 16: 379-398.

________, 1953. Article on pollination. Encyclopedia Americana.

Griffiths, David, 1931. Hybridity in the genus Lilium. Am. Soc. Hort. Sci. Proc. 28: 62-66.

_______, 1933. Hybrid lilies. USDA Agric. Cir. No. 299.

Grove, A., 1932. Hybrid lilies, Gardner's Chronicle, 117.

_______, 1933. Hybrid lilies, Gardner's Chronicle, 6.

Knuth, P., 1906. Handbook of flower pollination. 3 vol. trans. Ainsworth Davis, Oxford.

Muller, Herman, 1883. The fertilization of flowers. Macmillan and Co., London. 669 pp.

Preston, Isabella, 1933. Hybridization in lilies. The Lily Yearbook of the Royal Hort. Soc. 173-193.

Purdy, Carl, 1895. Luther Burbank's hybrid lilies. Garden and Forest 8: 328-329.

_______, 1942. The Burbank hybrid lilies. The Lily Yearbook Am. Hort. Soc. 60-62.

Rappleye, R. D., 1950. Pollination studies on Lilium regale. The Lily Yearbook of the No. Am. Lily Soc. 84-88.

Shride, C. L., 1942. Lilium columbianum in Washington. The Lily Yearbook of the No. Am. Lily Soc. 17-18.

Simmonds, A., 1939. List of names of hybrid lilies. The Lily Yearbook of the Royal Hort. Soc. 40-51.

Stebbins, G. L., 1950. Variation and evolution in plants. Columbia Univ. Press, New York. 643 pp.

Stern, F. C., 1938a. Hybrid lilies. The Lily Yearbook of the Royal Hort. Soc. 42-56.

_______, 1938b. Hybrid lilies for the garden. The Lily Yearbook of the Royal Hort. Soc. 80-85.

Stoker, F., 1950. Lily group dinner. The Lily Yearbook of the Royal Hort. Soc. 151-152.

Stout, A. B., 1933. Sterilities in lilies. The Lily Yearbook of the Royal Hort. Soc. 142-171.

Strycker, D. W., 1951. Experiences with lilies on the Oregon Coast. The Lily Yearbook of the No. Am. Lily Soc. 19-22.

Sturgeon, Wade, 1952. Hybrids by guess or by gosh. The Lily Yearbook of No. Am. Lily Soc. 116-119.

Vollmer, A. M., 1955. Hunting lilies in California. The Lily Yearbook of the Royal Hort. Soc. 53-64.

Weed, C. L., 1895. Ten New England blossoms and their visitors. Riverside Press, Cambridge, 142 pp.

Wilson, E. H., 1925. The lilies of Eastern Asia. Dulan and Co., London. 110 pp.

Woodcock, H. B. D., and W. T. Stearn, 1950. Lilies of the world. Charles Scribner's Sons, New York. 431 pp.

Woodriff, Leslie, 1950. Results of lily breeding in Oregon. The Lily Yearbook of the No. Am. Lily Soc. 95-97.

Wyatt, O. E. P., 1948. Awards to lilies. The Lily Yearbook of the Royal Hort. Soc. 89.

_______, 1950. The hybridizing of lilies. The Lily Yearbook of the Royal Hort. Soc. 11-21.

_______, 1954. Hybridization of lilies. The Lily Yearbook of the Royal Hort. Soc. 107-117.