C-808

VOLUME 15 1974

MELANDERIA

WITH THE AUTHOR'S COMPLIMENTS

WASHINGTON STATE ENTOMOLOGICAL SOCIETY

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MELANDERIA

The late Dr. A. L. Melander, who was prominent in Northwestern entomology for nearly a quarter century (1904-1926), discovered an interesting new dolichopodid fly while he was collecting along the Washington coast. The labella of the fly were modified into thickened, sharp, mandible-like structures, actually used as a substitute for mandibles. The insect was named *Melanderia mandibulata*, new genus and species, by Dr. J. M. Aldrich (Proc. Ent. Soc. Wash. 24(6): 145-148, 1922) who was then at the University of Idaho. The peculiar morphological modification was described in detail by R. E. Snodgrass (Proc. Ent. Soc. Wash. 24(6): 148-152, 1922) who likewise had an early association with the entomology of Washington. It is fitting, then, that we name our publication MELANDERIA, not only to honor the entomologist whose work has left such an imprint on the entomology of our State, but also to honor his two colleagues in Northwestern entomology.

-- Dr. M. T. James

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Editorial Policies for Melanderia

1. We will follow the AIBS *Style Manual for Biological Journals* with slight modification. Specific changes are that only "one" will be written out, all others will be numerals, that we will place a comma between the author(s) and date when these occur in parentheses, and that we will write a doubly numbered phrase as follows: "2, 4-oz samples."

2. Manuscripts will only be accepted from members of the Washington State Entomological Society, but subject matter will not be limited to the Pacific Northwest.

3. Manuscripts suitable for publication in *Melanderia* should be essentially monographic in nature. Normally, they should be not less than 60 double-spaced typewritten pages (including graphs, tables, and figures). This provides a minimum of about 20 pages per volume of *Melanderia*. Shorter articles will be considered for publication, but will usually take longer to publish because of saving up 2 such items to prepare one issue of *Melanderia*. We will usually advise that shorter papers be submitted elsewhere.

4. Illustrations (charts, photographs, figures, graphs) should be drawn to scale for the 8 1/2 x 11 in. format used in *Melanderia* or a part thereof.

5. The abstract for a 60-page manuscript should not exceed one typed page (about 600 words).

6. Submitted articles must not be submitted for publication elsewhere.

7. Common names of insects will follow the usage and rulings of the Entomological Society of America.

8. The order and family (subfamily where necessary) will be given for each subject in the title of the paper.

9. Each author will be requested to submit a brief abstract for publication in *Biological Abstracts*

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POLLINATION ECOLOGY OF THE FRONT RANGE OF THE COLORADO ROCKY MOUNTAINS

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ABSTRACT

Pollination ecology of plants considered primarily adapted to bumble bees (*Bombus* Latr. spp.) was studied in the Front Range of the Colorado Rocky Mountains from the Plains (1770m) to the high Alpine (4330m). Observations and insect collections were made at 23 study sites during the period 1966-1969. Blooming phenology appeared related to vertical geographic distribution and seasonal thermal patterns with local deviations. Colonies of *Bombus* pollinators below timberline appear to develop in response to thermal stimuli, while those above timberline may be more responsive to photoperiodic stimuli. Both plants and pollinating insects exhibit differences in vertical distribution ranges of individual species.

A large proportion of pollinators foraged for nectar only, and analyses of corbicular loads of pollen revealed individual pollen-gatherers tend to be monolectic for proper pollen. Precise morphological correlations between corolla tube or spur length and tongue length of nectar-foraging insects could not be established. Insect exclosure studies revealed all but two of 29 species highly dependent on insect pollinators. Cinematographic and stereophotographic studies of pollinating insect behavior revealed close coadaptations between some flowers and their pollinators. Adaptations appeared related phenologically to *Bombus* castes more than morphologically and behaviorally to certain insect species. The concept of convergence between plant species in attracting pollinators is developed in relation to phenological and ethological considerations. Although most of the plant species were dependent primarily upon *Bombus* pollinators, less frequent occurrence of other pollinators, including hummingbirds, on their flowers suggests that adaptations between flowers and their pollinators are labile. Current status of flower-insect interaction represents but one stage in continuing coadaptive evolution. In this stage bumble bees play a very significant role in the reproductive success of flowering plants.

INTRODUCTION

Working in the Pike's Peak region of the Colorado Rocky Mountains, Clements and Long (1923) carried out what is probably the first serious attempt, after brief observations by Kenoyer (1916a, 1916b), to study the ecology of pollination mechanisms and native insects that exhibit close coadaptive relationships. They demonstrated that bumble bees (*Bombus* Latr. spp.) are highly selective of flowers on which they forage and closely adapted to floral color, form, and function. Since Clements and Long studied only a relatively small number of plant species, this study investigates the pollination ecology of as many plant species as possible on the East Slope of the Colorado Rocky Mountain Front Range exhibiting dependence on bumble bee pollinators.

Bumble bees and functionally related flowers were chosen because of several considerations. Firstly, the operation of pollination mechanisms reflecting coadaptation with form and behavior of bumble bee pollinators is simple enough to suggest the manner in which the insect-flower interrelationship may become established and continue to evolve. Secondly, bumble bee queens inseminated at the end of one season hibernate during the winter, while all other castes die and the old nest disintegrates. In the following spring these queens establish new colonies usually in abandoned rodent nests. Annual cycles of colony development and plant blooming present a suitable situation in which to study the phenological implications of pollination ecology. Therefore, bumble bees and flowers related to them functionally were the most promising organisms for study based on recent investigations by the author (Macior, 1964, 1965, 1966, 1967, 1968a, 1968b, 1968c, 1969, 1970a, 1970b, 1970c, 1973).

The study area was chosen on the basis of: (1) transition from temperate lower altitudes to extremes of the high alpine, (2) knowledge of biota, and (3) reasonable access to all habitats. Facilities of The University of Colorado Institute of Arctic and Alpine Research (INSTAAR) and its research areas including Niwot Ridge were used during the 1966 and 1967 seasons. The study was continued on Mt. Evans at the southern end of the Front Range in 1968 and 1969. The vegetation is well known ecologically (Marr, 1961) and taxonomically (Harrington, 1964; Weber, 1967). Plant nomenclature in this study follows that of Weber (1967). Bee fauna of the Front Range was studied early in this century by Cockerell (1907, 1919, 1928), Cockerell and Robbins (1910), and Hicks (1925). Since no regional taxonomy of bumble bees of the Front Range is available at present, nomenclature for *Bombus* species and those of *Psithyrus*, an inquiline of bumble bee colonies, follows that of Mitchell (1962) and Stephen (1957) unless specific authorities are cited.

STUDY AREA

Colorado Front Range is the easternmost extension of the Rocky Mountain system in North America. Although it is continuous with the Continental Divide, it may be considered extending from Long's Peak in Rocky Mountain National Park southward to Gray's Peak, Torrey's Peak, and Mt. Evans. The study area includes the East Slope of the Front Range between Niwot Ridge and the Indian Peaks northwest of Nederland and Mt. Evans and South Park to the southwest. Eastward it extends to the plains in the Denver-Boulder area.

Traversed by many deep, narrow canyons, the East Slope rises in a series of steps of ridges parallel to the Continental Divide. Interspersed through the Front Range are several parklands, or level areas mostly west of the

Divide and separated from the continuous plains below and to the east of it.

Weather patterns of the area are directly related to topography. Prevailing westerly winds deposit moisture on the West Slope and leave the East Slope in a rain shadow. Strong winds and topographic irregularities at higher elevations are responsible for varied patterns of snow deposition on the alpine meadows. These, in turn, like the differences in exposure of canyon slopes to insolation at lower elevations, determine the amount of soil moisture available during periods of plant growth. Mean temperatures and diurnal changes (Tables 1 and 2) during the growing season tend to decrease with increasing elevation, but local habitats exhibit significant differences from the general pattern. In the alpine meadows air temperatures above the ground surface vary greatly from those at ground level. Intense solar radiation penetrating a thinner atmospheric layer at these high altitudes provides a distinct thermal activity zone or microclimate in the ground cover.

East Slope of the Colorado Front Range is conveniently divided into five vegetation zones at progressively higher elevations, namely, (1) the Plains (to 1770m) including grazed grasslands and erosional tablelands, or mesas, rising to 1880m; (2) the Foothills (1880-2440m) with *Pinus ponderosa* forests interspersed with mesic meadows; (3) the Montane (2440-2745m) with forests of *Picea engelmannii* and *Pinus contorta*, *Picea pungens* in cooler canyons, *Populus tremuloides* woodlands, grasslands, and marshy meadows; (4) the Subalpine (2745-3475m) with *Picea engelmannii-Abies lasiocarpa* forests, marshy meadows, *Populus tremuloides* woodlands, and extensive parklands; and (5) the Alpine (3475-4330m) above timberline with a great diversity of plant associations. In all vegetation zones local, artificial disturbance of the native climax vegetation has provided disclimax succession areas in which unusually large and diverse populations of herbaceous species occur. Some adventive species have also been naturalized in these areas. Repercussions of this disturbance may be expected on the normal coadaptive interrelationships of plants and their insect pollinators. Disturbance is caused by excessive grazing, land development, road construction, and mining. Twenty-three study sites from these vegetation zones are described in Table 3.

In the Plains Zone an unusual concentration of *Astragalus bisulcatus* made possible mass collections of *Bombus* queens reflecting the relative frequency of species in the plains.

Fallow fields in the Foothills Zone provided an opportunity to study interactions of the native legumes, *Astragalus* and *Oxytropis* with the adventive *Melilotus* and *Trifolium* species.

In the Montane Zone a disturbed roadside of a new land development near Nederland displayed one of the richest and most heterogeneous temporary plant associations indicating the ability of native plants to invade newly exposed areas rapidly.

Subapline Zone includes the greatest diversity of habitats. Blooming periods for each habitat differ mutually not only on the basis of elevation, but also in relation to soil moisture and exposure to insolation. Parkland vegetation in the Subalpine was studied at Jefferson in South Park at two adjacent sites. A mesic to wet, grazed and mowed meadow supported abundant *Dodecatheon*, *Pedicularis*, and *Thermopsis*, while a drier, overgrazed rangeland was occupied almost exclusively by *Oxytropis sericea*.

In the treeless Alpine Zone the most marked seasonal bloom was in the temporary snowfield meadows formed in troughs of solufluction terraces where *Trifolium parryi* bloomed together with *Erigeron melanocephalus* and *E. simplex*. High alpine tundra on Mt. Evans presented a habitat in which a high degree of reproductive and phenological coadaptation between plants and their pollinators was observed.

RESULTS

PHENOLOGY AND ALTITUDINAL DISTRIBUTIONS

Atmospheric temperature records from 2288 to 4319m in the Front Range (Tables 1 and 2) indicate a general reduction in temperature coupled with a progressive decrease in diurnal temperature variation with increasing altitude. Above timberline these trends appear less marked and may be over-shadowed by extreme differences based upon local topography. Mean diurnal differences on a south-facing slope at 3965m, for example, were much higher than on any other alpine recording site, all of which were nearly level. Compared with each other, sets of data for two successive seasons at identical elevations indicate substantial temperature differences from one season to the next. In the Alpine Zone, for example, without exception the 1968 season had earlier temperature maxima and consistently lower mean temperatures than the following one.

The blooming phenology of plant species (Table 4) is related to their vertical geographic distributions. Populations within a species bloom earlier at lower elevations. At any one elevation a local plant community may have all of its species blooming simultaneously or each at a different time.

Seasonal development of the annual colonies of *Bombus* species begins with queens, fertilized at the end of the previous season, emerging from hibernation and

establishing their nests usually in abandoned rodent nests. One or more broods of workers precede the final brood of new queens and males at the end of the season, at which time the nest disintegrates and the colony disperses. The appearance of *B. kirbyellus* males by the end of July in 1966 suggests a shorter colony duration at higher altitudes. With one exception, all castes of these species were collected earlier in 1966, when higher mean temperatures generally occurred earlier and persisted longer than in 1967. Above timberline mean temperatures were consistently higher in 1966 and 1969 than in 1967 and 1968, respectively. However, all castes of alpine *Bombus* species were captured earlier in 1966 and 1968 than in 1967, and 1969. Above timberline inception and development of colonies may not be related directly to changes in atmospheric temperatures.

Vertical distribution of *Bombus* species based upon collection records of foraging individuals is found in Table 5. Collections of pollinating insects were made during peak bloom on 52 species of plants for which bumble bees were the prime pollinators. *Bombus* species were identified by means of a collection determined by R. W. Thorp at The University of Colorado Museum of Natural History and subsequent suggestions by H. E. Milliron. Of the four species with geographic ranges extending east of the Mississippi River, (Mitchell, 1962), *B. fervidus, B. griseocollis*, and *B. nevadensis auricomus* are confined to the Plains and Foothills, while *B. rufocinctus* ranges from the Plains to the Subalpine. Western species include *B. fraternus*, which is confined to the Plains, and *B. huntii, B. morrisoni*, and *B. nevadensis nevadensis* extending into the Montane. *B. californicus, B. centralis*, and *Psithyrus suckleyi* are confined largely, if not entirely, to the upper Foothills and Montane. Vertically wide-ranging species include *B. bifarius, B. flavifrons, B. melanopygus, B. mixtus, B. occidentalis*, and *Psithyrus insularis. Psithyrus* are inquilines of bumble bees and closely related to them. Typically alpine species include *B. frigidus, B. kirbyellus*, and *B. sylvicola*. Peculiarly disjunct vertical distributions of *B. appositus, B. griseocollis, B. huntii, B. morrisoni, B. rufocinctus*, and especially *B. nevadensis nevadensis* in the alpine may result from vertical drift since these species were not found to nest in the alpine meadows. (Table 6)

FORAGING ACTIVITY OF INSECTS

Pollinator activity on flowers is directed to collection of nectar and/or pollen. Differences between total foragers and total pollen foragers collected while foraging on flowers (Table 7) indicate the number of nectar-foraging insects for each plant species. Degree of fidelity of pollen-foragers to one plant species was studied by identifying constituents of corbicular pollen loads carried by pollinators using methods described by Macior (1968a). In general, a large portion of the total foragers gathers only nectar even though pollen is readily available. Of all plant species studied, only *Dodecatheon pulchellum, Lupinus argenteus, Pedicularis groenlandica*, and *P. racemosa* lack nectar. Pollen-gatherers on flowers with nectar collected nectar also. Smaller insects on flowers with long corolla tubes often collected pollen in an inverted position at the corolla apex without contacting nectar at the base of the tube. This was found in *Pedicularis bracteosa, P. grayi*, and *P. sudetica. Bombus* males as well as *Psithyrus* males and females gather nectar only.

Analysis of constituents of corbicular pollen loads carried by foragers indicates *Bombus* species are generally polylectic, but individual foragers are olioglectic or monolectic in certain situations. Foragers collecting only pollen proper to the plant species on which they were captured are distinguished from those collecting proper pollen mixed with one or more foreign pollens and those collecting one or more types of foreign pollen only (Table 7). Pollen-foraging individuals tend to be monolectic for proper pollen. Relatively few individuals collected more than one foreign type together with proper pollen, and the number of individuals collecting foreign pollen only was generally smaller still. Only on *Corydalis aurea, Erysimum amoenum*, and *E. nivale* did foragers completely fail to collect pollen.

Early-blooming plants at any given elevation are pollinated by *Bombus* queens. Plant species blooming later interact with foraging workers. *Bombus* males and new queens are effective pollinators late in the season on flowers where they forage for nectar exclusively. *Erysimum amoenumm, E. nivale, Polemonium viscosum*, and *Primula angustifolia* bloom very early on the alpine tundra and are pollinated exclusively by *Bombus* queens and *Psithyris* females (Tables 4 and 7). Blooming slightly later in their respective habitats and pollinated by these insect casters and relatively small numbers of the earliest *Bombus* workers are *Astragalus bisculcatus, A. striatus, Erysimum asperum, Iris missouriensis, Mertensia viridis, Oxytropis sericea, Pedicularis crenulata* and *Thermopsis divaricarpa*. Blooming earlier but pollinated by large numbers of workers as well as queens, *Dodecatheon pulchellum* offers no nectar. Thus, it is less attractive to *Bombus* queens, all of which must gather both pollen and nectar in establishing their colonies. At mid-season both workers and queens occur on *Castilleja occidentalis, C. sulphurea, Chionophila jamesii, Corydalis aurea, Delphinium ramosum, Melilotus officinalis, Mertensia viridis, Pedicularis bracteosa, P. parryi, Penstemon secundiflorus, P. virens, Phacelia sericea, Taraxacum officinale, Trifolium nanum* and *T. pratense*. More workers than queens forage in late mid-season on *Aconitum columbianum, Astragalus flexuosus, Linaria dalmatica, Monarda fistulosa, Pedicularis grayi* and *P. groenlandica*. Queens are entirely absent on *Allium geyeri, Pedicularis racemosa*, and *Penstemon whippleanus*, which bloom in late

mid-season. Late-blooming species attract all three *Bombus* castes and include *Besseya alpina*, *Delphinium barbeyi*, *Linaria vulgaris*, *Mertensia ciliata*, *Monarda fistulosa*, *Onosmodium molle*, *Oxytropis lambertii*, *Pedicularis sudetica*, *Polygonum bistortoides*, *Primula parryi*, *Sedum rhodanthum*, *S. stenopetalum*, *Trifolium dasyphyllum*, and *T. parryi*. Since some queens are carrying pollen at this time, they must forage far into the season despite the abundance of foraging workers in their colonies. Queens without pollen may be either old foragers or new queens, which gather no pollen until the next season. *Penstemon procerus* and *Trifolium hybridum* bloom late and attract workers and males only. No species was pollinated exclusively by males.

COACTIONS BETWEEN FLOWERS AND INSECTS

Reproductive dependence of flowers upon foraging insects for their pollination is demonstrated in Table 8 with *Penstemon virens*, *P. whippleanus*, and *Phacelia sericea* as exceptions. Self-pollination potentials were studied by enclosing plants prior to bloom with cages of galvanized window screen (18 x 14 mesh). Upon completion of flowering, comparable numbers of enclosed and open-pollinated flowers in the immediate vicinity were examined for fruit production. Absence of fruiting under the cages indicated lack of self-pollination in the absence of pollinators too large to enter through the openings in the enclosure. Regular fruiting under the enclosures indicated either self-pollination in the absence of insects or pollination by insects small enough to penetrate the enclosures. Small numbers of fruits produced within the insect exclosures by *Erysimum nivale*, *Lupinus argenteus*, *Mertensia ciliata*, *M. viridis*, *Polemonium viscosum* (at 3440m), and *Primula parryi* (pin) may be the result of incidental success by thysanopteran flower inhabitants or exceptional self-pollination. All other plant species exhibited obligate dependence upon insect pollen vectors experimentally excluded from the flowers. Fruiting below the 25% level in open-pollinated *Lupinus argenteus* may result from lesser attractiveness of the nectarless flower to potential pollinators (Table 7). However, great abundance of pollinators on *Trifolium dasyphyllum* and *T. parryi*, both of which contain nectar, excludes this explanation for their very low fruiting. Fruit production below the 50% level in the open-pollinated flowers of *Pedicularis parryi* (at 3540m) and *Trifolium nanum* (at 3630m) is probably due to a dearth of pollinators. Very few insects were observed on *Pedicularis parryi* at the Waldorf site. Peak of pollinator activity at the Mt. Goliath site of *Trifolium nanum* occurs earlier in the season when attractive *Primula angustifolia* is in bloom.

To correlate corolla tube or spur length with tongue length of nectar-foraging insects attracted by nectar retained in the bottom tubes and spurs, 25 tubes or spurs were measured in the field for each plant species (Table 9). Labial (prementum + glossa) length of nectar-foraging insects was measured using methods developed by Medler (1962). Fifty individuals of each female caste were measured except where fewer insects were available (Table 10).

Queens have longer tongues than workers within each *Bombus* species. Long tongues (mean above 11mm) are found on queens of *Bombus appositus*, *B. californicus*, *B. kirbyellus*, *B. fervidus*, *B. nevadensis auricomus*, *B. nevadensis nevadensis*, and *B. morrisoni*; while queens of *B. melanopygus*, *B. mixtus*, and *B. frigidus* have short tongues (mean less than 8mm) in order of decreasing tongue length, respectively. By the same criteria no workers have long tongues, but those of *B. flavifrons*, *B. centralis*, *B. melanopygus*, *B. sylvicola*, *B. bifarius*, *B. frigidus*, *B. occidentalis*, and *B. mixtus* have short tongues of decreasing length, respectively.

Corolla tube and spur lengths were measured from the base to the outer end in uniform corollas or to the base of a cleft or constriction in corollas having these modifications. All corollas measured were bilaterally symmetrical except those of *Erysimum*, *Mertensia*, and *Polemonium* species. By the criteria used for insect tongues, most corolla tubes and spurs are long. Only the native *Mertensia viridis* and *Astragalus flexuosus* and the introduced *Trifolium hybridum* and *Melilotus officinalis* have short tubes with nectar. Remaining flowers with short tubes, namely *Pedicularis racemosa*, *Lupinus argenteus*, and *P. groenlandica*, lack nectar.

There is no exclusive correspondence of lengths of tongues and corollas such that the species with longest tongue forages only on flowers with the longest corolla tube or spur. *Bombus appositus*, for example, has a longer tongue than any other species, yet it forages for nectar on native plants with corolla tubes or spurs ranging in mean length from 10.2 to 21.8mm, on introduced *Linaria dalmatica* with spurs 32.2mm long, and on introduced *Melilotus officinalis* with a mean tube length of only 2.8mm. That this and other *Bombus* species may forage for nectar in tubes or spurs apparently exceeding the mean length of their tongues may be the result of a varying depth of nectar in the corolla or insertion of all or part of the insect's head into the constricted or intact basal portion of the corolla. Short-tongued bumble bees forage actively for nectar in short corollas, but some also forage on long-tubed flowers. *Bombus mixtus* workers, with a mean tongue length of 7.36mm, for example, forage for nectar on *Pedicularis bracteosa*, with a mean tube length of 17.1mm.

Reciprocal functional adaptations between pollination mechanisms and pollinator behavior were investigated by high-speed cinematography and close-range

stereophotography. These have been reported in detail by Macior (1970c) for the seven species of *Pedicularis* included in the present study. In the rostrate, nectarless flowers of *Pedicularis groenlandica* and *P. racemosa* foragers remove totally concealed pollen by wing vibrations while pollinating nototribically in *P. groenlandica* and sternotribically in *P. racemosa*. Nectar-secreting flowers of *P. bracteosa*, *P. crenulata*, *P. grayi*, *P. parryi*, and *P. sudetica* are pollinated nototribically by foragers gathering nectar in an upright position, and sternotribically in *P. bracteosa*, *P. grayi*, and *P. sudetica* by insects scraping pollen with their legs in an inverted position at the tip of the galea of the flower. The latter are usually smaller individuals than the nototribic pollinators.

All thirteen species in the Leguminosae studied were uniformly pollinated sternotribically by insects foraging in an upright position. In *Lupinus argenteus* pollinators removed pollen extruded through the tip of the keel by exsertion of the style when the keel was depressed by the insect's body weight. In all other species the body weight depressed the keel allowing the essential parts to rise through a dorsal cleft in the keel brushing pollen on the ventral thorax and abdomen.

In the Scrophulariaceae, except for *Pedicularis*, bilaterally symmetrical flowers were nototribically pollinated by insects foraging for nectar and pollen or nectar only. The flowers of *Besseya alpina*, with exserted stamens, were pollinated exclusively by nectar-foragers among the bumble bees. Other similar flowers open to most pollinators by reason of their generalized flower structure included *Allium geyeri* (Liliaceae), *Onosmodium molle* (Boraginaceae), *Phacelia sericea* (Hydrophyllaceae), *Polygonum bistortoides* (Polygonaceae), *Sedum rhodanthum* and *S. stenopetalum* (Crassulaceae), and the heads of *Taraxacum officinale* (Compositae). These species attracted a wide variety of pollinators other than bumble bees and exhibited no particular morphological adaptations to *Bombus* species. In the Cruciferae, three species of *Erysimum* were restrictive in their corollas by reason of the long tube formed by the four unfused claws of their petals. *Delphinium* and *Aconitum* in the Ranunculaceae were highly restrictive and sternotribically pollinated. While *Dodecatheon* is sternotribically pollinated by pollen-vibrating insects inverted at the tip of the anther cone; *Primula*, also in the Primulaceae, is pollinated like *Erysimum* by direct nectar probing in a radially symmetrical tube. *Metensia* (Boraginaceae) has a constricted corolla and connate anthers filled with very fine pollen that sifts onto the ventral side of inverted pollinators hanging from the corolla. Some of these insects vibrate pollen from the anthers. The long, radially symmetrical tube of *Polemonium* (Polemoniaceae) is open to long-tongued nectar-foragers. *Iris* (Iridaceae) is nototribically pollinated by bumble bees and occasional hummingbirds. *Monarda* (Labiatae) is also nototribically pollinated by bumble bees.

Although the highly modified flowers of *Corydalis aurea* (Fumariaceae) are pollinated by nectar-foraging bumble bees, they are perfectly fertile under insect exclosures indicating regular self-pollination. Due to collapse of plants under cages, precise numbers of fruits could not be determined.

Several species of bumble bees were observed gleaning nectar through corolla perforations. Only *Bombus occidentalis* perforated corollas and removed nectar through the perforations on *Aconitum columbianum* (galea), *Linaria dalmatica*, *L. vulgaris*, *Mertensia ciliata*, *Oxytropis lambertii*, and *Penstemon secundiflorus*.

Hummingbirds were observed regularly pollinating *Pedicularis grayi* along with bumble bees. On the other flowers, the birds were infrequent in their visits and could not be considered regular pollinators.

Small bees, flies, and lepidopterans were also observed foraging, or attempting to forage on the flowers in this study. Flowers with exserted essential parts and radial symmetry are probably pollinated regularly by these insects. Bilaterally symmetrical but open flowers of *Penstemon* species were regularly pollinated by other bees in addition to *Bombus* species, but flowers with constricted or closed mouths were pollinated almost exclusively by bumble bees.

DISCUSSION

PHENOLOGY OF ANTHESIS AND POLLINATOR ACTIVITY

Coincidence of anthesis and inception of pollinator colonies in a given area is a functional necessity of colony development since nectar and pollen form the sole nourishment of bumble bees. In the short season of the alpine tundra, where thermal variations are smaller than at lower elevations, both colony establishment and anthesis may be regulated by photoperiodic factors more than by thermal ones as suggested for some alpine plant species by Holway and Ward (1965). However, thermal factors are important in plant communities inundated by temporary snowfields where blooming is dependent upon the rate of snow ablation (Holway and Ward, 1963).

Vertical distributions of *Bombus* species in this study are comparable to those summarized for similar arctic-alpine regions by Mani (1968). Duration of an annual colony depends on the duration of forage availability. At any given elevation colonies may be terminated before temperatures drop below minimal requirements for foraging activity, as reported by Downes (1964).

Sequence of development within a bumble bee colony

involves the production of one or more broods of workers followed by terminal production of reproductive castes. Since all natural colonies excavated in this study contained workers, it is not likely that seasonal stress or competition with other species has forced any *Bombus* species in the study area to curtail production of workers or to become a social parasite like the workerless *Bombus hyperboreus* in the high arctic. However, *Psithyrus* species are all obligate inquilines. Females collect no pollen, and there is no worker caste as in *Bombus* species. The 1600-4000m vertical range of *P. insularis* in the Front Range (Table 5) reflects the effective adaptation of this inquiline to bumble bees of the area. Found foraging for nectar on 16 species of bilaterally as well as radially symmetrical flowers, *P. insularis* exhibits no strong preference for any particular flower form.

FORAGING BEHAVIOR OF INSECT POLLINATORS

That *Bombus* foragers in this study tend to be monolectic for proper pollen probably reflects habituation of individuals to a particular pollen source. This, in turn, depends on the degree of heterogeneity of the plant community and the relative abundance of any one plant species attractive to *Bombus* pollinators. Clements and Long (1923) and Grant (1950) have summarized earlier studies showing floral fidelity of *Bombus* pollinators to vary widely not only in degree, but also between different *Bombus* species. The phenomenon is most likely related to environmental circumstances more than to any innate behavioral characteristic of the foraging insects. It is possible that such fidelity may involve two plant species where one affords nectar while a nectarless species such as *Pedicularis groenlandica* or *Dodecatheon pulchellum* can provide pollen only.

Ability of foraging individuals to transfer a complex behavior pattern to a floral mechanism not adapted to such behavior was seen at Site 19. *B. sylvicola* pollinators of *Pedicularis groenlandica* occasionally attempted to vibrate pollen from the sympatric and synchronously blooming *P. sudetica* flowers normally pollinated by *B. frigidus* and *B. kirbyellus* without vibration. Although such behavior on *P. sudetica* is extraordinary, it may provide a selective pressure on its corolla in the direction of the rostrate *P. groenlandica* form. It may also reflect a constancy of behavior pattern that is not restricted to a single plant species.

Floral cues directing pollinators to pollen and nectar forage include odor, color, and form. Flowers in this study did not have particularly strong fragrances. With the exception of *Pedicularis groenlandica* and *Mertensia* species, corollas did not reflect significant amounts of ultraviolet light, for which bumble bees have high visual sensitivity (Kugler 1943, 1947, 1963, 1966, 1971). Flowers attractive to bumble bees were white, yellow, blue, magenta or pink, or some combination of these colors. Only *Pedicularis grayi*, which these insects shared with hummingbirds, combined red in its color pattern. Although bumble bees have the ability to discriminate between colors, individuals foraged indiscriminately on white and maroon variants in a population of *Penstemon whippleanus*. It is certain that such variants are not maintained distinct in the population through selective foraging of pollinators on specific color forms. However, ability of pollinators to distinguish colors is not necessarily followed by selective behavior in relation to color differences.

Perforation behavior of *Bombus* foragers, described on alpine flowers by Muller (1879), cannot be a necessary consequence of a tongue length too short to reach nectar through the mouth of a corolla. In this study *Bombus mixtus*, which does not perforate corollas, has a shorter mean tongue length than *B. occidentalis*, which does perforate. However, perforation behavior appears to be invariably associated with shortness of tongue in pollinators whenever it does occur. Inverted collection of pollen by smaller bees at the tips of long, nectar-containing corolla tubes also appears directly related to shortness of tongue in these foragers. Lack of close dimensional correspondence of insect tongues and corolla tubes and spurs does not preclude a functional adaptation of foragers, but the adaptation seems to be one of *Bombus* castes rather than of species. This, in turn, is related to: (1) blooming phenology of plant species at different altitudes, (2) vertical distribution of pollinator species, and (3) phenology of insect colony development at different elevations.

COADAPTIVE EVOLUTION OF POLLINATORS AND POLLINATION MECHANISMS

In those plant species where sexual reproduction is dependent upon particular insect castes, blooming coincides with caste emergence and availability. Queen-adapted plants bloom when fewer pollinators are available and may share pollinators if they are sympatric and synchronous in anthesis. On Niwot Ridge (Site 15) *Erysimum nivale* and *Polemonium viscosum*, for example, share nectar-foraging queens of *Bombus kirbyellus* and *B. sylvicola*. The plants are similar in habit and inflorescence form. Although their radially symmetrical flowers differ in color, both the blue reflectance of *Polemonium* and the yellow of *Erysimum* are highly visible to these pollinators. Yellow-centered pink *Erysimum amoenum* and *Primula angustifolia* on Mt. Goliath (site 17) also share nectar-foraging queens of the same two pollinator species. Since individual insects have been observed actually moving repeatedly between partners of these plant pairs, the phenomenon of pollinator sharing

appears to be a phenologically induced phenotypic convergence.

Later in the season workers are more abundant than queens. At sites 5, 10, and 11 the nectarless, pink flowers of *Dodecatheon pulchellum* and *Pedicularis groenlandica* bloom synchronously in marshy meadows and are pollinated by the same worker individuals collecting pollen by vibration. This pollinator sharing is one of functional convergence since the flowers are morphologically distinct.

In disclimax habitats competition for pollinators is significant. Extremely large populations of *Astragalus bisulcatus* in a salt flat near the Boulder reservoir in the Plains (Site 1) and of *Oxytropis sericea* in overgrazed Subalpine parklands at Jefferson (Site 10) formed concentration points for *Bombus* queens. At Hilltop Terrace (Site 4), on the other hand, disturbed ground supported an abundant, heterogeneous disclimax community with much competition for insect pollinators. Therefore, strong competition for pollinators may be considered a temporary situation that will be eliminated as the heterotypic climax community is attained. In the climax community, pollinators are shared phenologically and/or ethologically until a new reproductive imbalance occurs. This phenomenon may be of considerable importance in agricultural areas where a local disclimax concentration of pollinators seriously detracts from the availability of native pollinators for cultivated crops.

Absence of precise morphological correspondence between pollinators and pollination mechanisms of flowers in the present study suggests that, in a recently-evolved biotic community, duration of natural selection is insufficient to produce direct correlations of this kind. Furthermore, in the constantly-changing geologic environment of the Front Range, it is unlikely that any community is so stable and perfectly adapted that within it such correlations would be found. Considered functionally adapted but evolutionarily labile entities, contemporary pollination mechanisms of this region are still in process of change. The degree to which they are adapted to bumble bees or to any other pollinators reflects the relative influence of these pollen vectors on the functional morphology of pollination mechanisms. The degree to which such flowers are successfully pollinated by various other vectors would then be a measure of the preadaptive potential for further coevolution with the same or different pollinators.

Categorization of pollination mechanisms according to particular kinds of pollinators by Delpino (1868-1869) has long served to direct attention to the morphological correspondence between pollinators and flowers. Recent studies like those of Crosswhite and Crosswhite (1966) on *Penstemon* and of Pelton (1961) on *Mertensia ciliata* join the present study in redirecting attention to the diversity of pollinators on flowers that may be primarily adapted to one kind of pollen vector at present. Such studies also emphasize the necessity of understanding the total ecological context in which coadaptive evolution of pollinators and floral mechanisms occurs.

ACKNOWLEDGEMENTS

Acknowledged with sincere gratitude is grant support from the National Science Foundation (GB-5184, GB-7779); field assistance of Mr. Stephen Adamowicz, Mr. David Brzoska, and Mr. Dennis Franke; technical assistance of Miss Susan Leach, Miss Janice Moore, Miss Chrystyna Strileckyj, and Miss Cheryl Schmardebeck; and logistic support in the field from Dr. John Marr and the staff of The University of Colorado Institute of Arctic and Alpine Research. The author is grateful to Dr. H. E. Milliron for suggestions regarding insect indentification especially concerning *Bombus kirbyellus*, previously identified as *B. balteatus* in The University of Colorado collection.

BIBLIOGRAPHY

Clements, F. E., and F. L. Long. 1923. Experimental pollination—an outline of the ecology of flowers and insects. Carnegie Inst. Wash. Publ. 336. Washington, D. C. 274p.

Cockerell, T. D. A. 1907. The bees of Boulder Co., Colorado. Univ. Colo. Stud. 4: 239-59.

. 1919. The bees of Gold Hill, Colorado. Canad. Ent. 51: 271-3.

. 1928. Supplementary notes on Colorado bees, with a list of all the genera. Univ. Colo. Stud. 16: 99-126.

., and W. W. Robbins. 1910. An introduction to the study of Rocky Mountain bees. Univ. Colo. Stud. 7: 179-95.

Crosswhite, F. S., and C. D. Crosswhite. 1966. Insect pollinators of *Penstemon* Series Graciles (Scrophulariaceae) with notes on *Osmia* and other Megachilidae. Amer. Midl. Nat. 76: 450-67.

Delpino, F. 1868-1869. Ulteriori osservazioni e considerazioni sulla dicogamia nel regno vegetale. Atti Soc. Ital. Sci. Nat. 11: 265-332; 12: 21-141.

Downes, J. A. 1964. Arctic insects and their environment. Canad. Entomol. 96: 279-307.

Frisch, K. von. 1914. Der Farbensinn und Formensinn der Biene. Zool. Jahrb., Abt. allg. Zool. Physiol. 35: 1-182.

. 1919. Uber den Geruchsinn der Bienen und seine blutenbiologische Bedeutung. Zool. Jahrb., Abt. allg. Zool. Physiol. 37: 1-238.

Grant, V. 1950. The flower constancy of bees. Bot. Rev. 16: 379-98.

Harrington, H. D. 1964. Manual of the plants of Colorado. 2nd ed. Sage, Denver, 666p.

Hicks, C. H. 1925. Nesting habits and parasites of certain bees of Boulder Co., Colorado. Univ. Colorado Stud. 15: 217-52.

Holway, J. G., and R. T. Ward. 1963. Snow and meltwater effects in an area of Colorado alpine. Amer. Midl. Nat. 69: 189-97.

. 1965. Phenology of alpine plants in northern Colorado. Ecology 46: 73-83.

Kenoyer, L. A. 1916a. Insect pollination of timberline flowers in Colorado. Proc. Iowa Acad. Sci. 23: 483-6.

. 1916b. Insect pollination of *Frasera stenosepala*. Proc. Iowa Acad. Sci. 23: 487-8.

Kugler, H. 1943. Hummeln als Blutenbesucher. Ergebn. Biol. 19: 143-323.

. 1947. Hummeln und die UV-Reflexion an Kronblattern. Naturwiss. 34: 315-6.

. 1963. UV–Musterung auf Bluten und ihr Zustandekommen. Planta 59: 296-329.

. 1966. UV-Male auf Bluten. Ber. deutsch. bot. Ges. 79: 57-70.

. 1971. UV-Musterung bei Alpenblumen. Jahrb. Ver. Schutze Alpenfl. u. Tiere 36: 61-5.

Macior, L. W. 1964. An experimental study of the floral ecology of *Dodecatheon meadia*. Amer. Jour. Bot. 51: 96-108.

. 1965. Insect adaptation and behavior in *Asclepias* pollination. Bull. Torrey Bot. Club 92: 114-26.

. 1966. Foraging behavior of *Bombus* (Hymenoptera: Apidae) in relation to *Aquilegia* pollination. Amer. Jour. Bot. 53: 302-9.

. 1967. Pollen-foraging behavior of *Bombus* in relation to pollination of nototribic flowers. Amer. Jour. Bot. 54: 359-64.

. 1968a. Pollination adaptation in *Pedicularis groenlandica*. Amer. Jour. Bot. 55: 927-32.

. 1968b. Pollination adaptation in *Pedicularis canadensis*. Amer. Jour. Bot. 55: 1031-5.

. 1968c. *Bombus* (Hymenoptera, Apidae) queen foraging in relation to vernal pollination in Wisconsin. Ecology 49: 20-5.

. 1969. Pollination adaptation in *Pedicularis lanceolata*. Amer. Jour. Bot. 56: 853-9.

. 1970a. The pollination ecology of *Dicentra cucullaria*. Amer. Jour. Bot. 57: 6-11.

. 1970b. Pollination of ecology of *Dodecatheon amethystinum* (Primulaceae). Bull. Torrey Bot. Club 97: 150-3.

. 1970c. Pollination ecology of *Pedicularis* in Colorado. Amer. Jour. Bot. 57: 716-28.

. 1973. The pollination ecology of *Pedicularis* on Mount Rainier. Amer. Jour. Bot. 60: 863-71.

Mani, M. S. 1968. Ecology and biogeography of high altitude insects. Junk, The Hague. 527p.

Marr, J. W. 1961. Ecosystems of the East Slope of the Front Range in Colorado. Contrib. No. 4 Univ. Colorado Inst. Arctic and Alpine Res., Boulder. 134p.

Medler, J. T. 1962. Morphometric analyses of bumble bee mouthparts. Verhandl. XI. Internat. Kongr. Entomol. Wien 1960. 2: 517-21.

Milliron, H. E., and D. R. Oliver. 1966. Bumble bees from northern Ellesmere Island, with observations on usurpation by *Megabombus hyperboreus* (Schonh.) (Hymenoptera: Apidae). Canad. Entomol. 98: 207-13.

Mitchell, T. B. 1962. Bees of the eastern United States. Vol. 2. N. Carolina Agric. Expt. Sta. Tech. Bull. No. 152. 557p.

Muller, H. 1879. *Bombus mastrucatus*, ein Dysteleolog unter den alpinen Blumenbesuchern. Kosmos 5: 422-31.

Pelton, J. 1961. An investigation of the ecology of *Mertensia ciliata* in Colorado. Ecology 42: 38-52.

Stephen, W. P. 1957. Bumble bees of western America. Oregon State Coll. Agric. Expt. Sta. Bull. No. 40, Corvallis. 163p.

Weber, W. A. 1967. Rocky Mountain flora. Univ. Colorado Press, Boulder. 437p.

Table 1. Air Temperatures (°C) at Four Elevations in the Front Range (1966-1967).*

	Elevation (m) and Month											
	2288			2654			3111			3721		
	June	July	August	June	July	August	June	July	August	June	July	August
Mean (1966)	15.8	22.1	18.1	13.5	20.1	16.1	8.3	12.9	10.9	4.9	10.5	7.6
Range (1966)	2.8-32.5	9.5-33.6	3.7-33.0	0.0-30.8	7.8-31.4	2.8-30.8	-2.8-22.4	2.2-25.2	-1.1-22.4	-5.6-14.6	3.4-18.5	-1.7-17.4
Mean Diurnal Difference (1966)	14.2	16.0	26.5	13.9	15.2	13.7	12.7	15.7	15.7	8.7	8.2	8.7
Mean (1967)	12.9	18.7	18.1	16.8	16.6	15.6	6.8	11.2	9.6	3.12	8.8	6.7
Range (1967)	3.4-26.9	8.4-31.9	6.2-33.0	1.1-29.7	3.9-27.4	3.9-27.4	-2.8-20.1	-0.6-21.3	-0.6-21.8	-4.5-14.6	0.0-16.8	-1.1-14.6
Mean Diurnal Difference (1967)	11.2	13.1	14.2	11.6	12.6	12.7	11.8	13.4	13.7	7.9	7.8	7.8

*Data supplied by The University of Colorado Institute of Arctic and Alpine Research.

Table 2. Air Temperatures (°C) at Five Elevations on Mt. Evans (5 July - 9 August 1968, 1 July - 18 August 1969)

	Elevation (m) and Month									
	3691		3965		4087		4201		4319	
	July	August	July	August	July	August	July	August	July	August
Mean (1968	6.6	6.2	8.5	7.2	4.3	3.8	5.1	4.3	4.0	4.3
Range (1968)	-2.8- 11.8	2.8- 12.3	-3.9- 21.3	-2.2- 19.0	-1.7- 9.0	0.0- 7.8	-0.6- 16.8	1.1- 10.1	-0.6- 10.1	0.6- 11.2
Mean Diurnal Difference (1968)	7.2	5.3	17.6	16.3	5.8	4.7	5.7	4.4	4.9	4.4
Mean (1969)	11.0	12.3	10.4	10.9	7.5	9.1	7.4	8.7	5.9	8.1
Range (1969)	9.0- 13.7	9.5- 14.6	7.3- 13.4	8.4- 12.3	3.9- 10.1	7.0- 11.2	3.9- 12.6	5.9- 10.6	3.1- 9.8	4.8- 10.6
Mean Diurnal Difference (1969)	2.8	2.9	6.4	4.0	3.0	3.1	5.7	4.3	4.0	5.3

Table 3. Research Sites and Their Plant Associations

Site No.	Site Location & Habitat	Zone	Elevation (m)	Blooming Period	Plant Species
1	Boulder-Golden, disturbed roadsides & grazed grasslands	Plains	1580-1680	late May-mid-June	Astragalus bisulcatus, A. flexuosus, A. striatus, Cryptantha **virgata.** Erysimum asperum, Onosmodium molle, Oxytropis lambertii, Penstemon secundiflorus.
2	Table Mesa, moist grassland	Plains	1880	late May-early June	Iris missouriensis, Thermopsis divaricarpa.
3	Sunrise Canyon Road, fallow fields	Foothills	2367	late June-early July	Astragalus flexuosus, A. striatus, Melilotus officinalis, Oxytropis lambertii, Trifolium hybridum, T. pratense.
4	Hilltop Terrace north of Nederland, disturbed roadside of new development	Montane	2560	mid-June-mid-July	Astragalus flexuosus, A. stratus, Calochortus gunnisoni, Cryptantha virgata, Delphinium nelsonii, Erysimum asperum, Gaillardia aristata, Geranium fremontii, Mertensia lanceolata, Onosmodium molle, Oxytropis lambertii, Penstemon secundiflorus, P. virens, Potentilla fissa, Rosa woodsii, Scutellaria brittonii, Sedum stenopetalum, Senecio wootoni, Swertia radiata, Thermopsis divaricarpa, Trifolium pratense.
5	North Beaver Creek at Nederland, marshy meadow	Montane	2530	mid-June-mid-July	Dodecatheon pulchellum, Iris missouriensis, Pedicularis groenlandica, Prunus virginiana, Thermopsis divaricarpa.
6	Tolland (Boulder Park) mesic meadow	Montane	2711	late July	Penstemon procerus
7	Rainbow Lakes-Left Hand Canyon area, roadsides and fallow fields	Subalpine	2770-3015	late June-early August	Allium cernuum, Astragalus tenellus, Erysimum asperum, Gaillardia aristata. Geranium fremontii, Gilia calcarea, Grindelia subalpina, Linaria dalmatica, L. vulgaris, Lupinus argenteus, Mertensia lanceolata, Onosmodium molle, Oxytropis lambertii, Pedicularis parryi, Penstemon secundiflorus, P. virens, P. whippleanus, Phacelia sericea, Rosa woodsii, Thermopsis divaricarpa, Trifolium pratense.

Table 3. Research Sites and Their Plant Associations (Continued)

Site No.	Site Location & Habitat	Zone	Elevation (m)	Blooming Period	Plant Species
8	Grazed, mesic meadow above Central City	Subalpine	2925	late June-mid-July	Astragalus alpinus, Corydalis aurea, Dodecatheon pulchellum, Erysimum asperum, Mertensia ciliata, M. lanceolata, Onosmodium molle, Oxytropis lambertii, Penstemon secundiflorus, P. virens, Polygonum bistortoides, Potentilla fruticosa, Swertia radiata, Taraxacum officinale, Thermopsis divaricarpa.
9	INSTAAR base station & Clear Lake (Georgetown), aspen woodlands	Subalpine	2380; 3080	mid-June-mid-July; mid-July-mid-August	Aconitum columbianum, Astragalus alpinus, Castilleja septentrionalis, Dodecatheon pulchellum, Mertensia ciliata, Pedicularis grayi.
10	Jefferson (South Park), mesic to wet meadow; dry overgrazed rangeland	Subalpine	2900	late June-early August	Dodecatheon pulchellum, Pedicularis crenulata, P. groenlandica, Thermopsis divaricarpa, Oxytropis sericea.
11	INSTARR "C-1" and "Kiwi" stations, marshy meadows and adjacent roadsides	Subalpine	3110, 3235	early June-mid-July	Caltha leptosepala, Dodecatheon pulchellum, Pedicularis groenlandica, Trollius laxus; Lupinus argenteus, Penstemon secundiflorus, P. whippleanus, Phacelia sericea, Thermopsis divaricarpa.
12	Floral Park (US rte. 40 east of Berthoud Pass), stream margin in spruce-fir forest	Subalpine	3265-3295	early June-mid-August	Aconitum columbianum, Castilleja septentrionalis, Delphinium barberyi, Mertensia ciliata, Pedicularis bracteosa, P. groenlandica.
13	Arapahoe Pass Trail, south-facing mesic meadow slope	Subalpine	3355	mid-July-mid-August	Aconitum columbianum, Delphinium barbeyi, Gentiana calycosa, Helianthus nuttallii, Mertensia ciliata.
14	Berthoud Pass, dry forest floor with seepages	Subalpine	3475	mid-July-mid-August	Pedicularis bracteosa, P. groenlandica, P. racemosa.

Table 3. Research Sites and Their Plant Associations (Continued)

Site No.	Site Location & Habitat	Zone	Elevation (m)	Blooming Period	Plant Species
15	Niwot Ridge (timberline to highest meadows)	Alpine	3505-3905	early June-late July	Allium geyeri, Arctostaphylos uva-ursi, Besseya alpina, Caltha leptosepala, Campanula parryi, C. uniflora, Castilleja occidentalis, Chionophila jamesii, Dodecatheon pulchellum, Dryas octopetala, Erigeron melanocephalus, E. simplex, Erysimum nivale, Geum rossii, Hymenoxys acaule, H. grandiflora, Kalmia polifolia, Lloydia serotina, Mertensia viridis, Pedicularis groenlandica, P. parryi, P. sudetica, Phacelia sericea, Polemonium viscosum, Polygonum bistortoides, Primula angustifolia, P. parryi, Trifolium parryi.
16	Waldorf (above Georgetown), mesic-dry east-facing slope	Alpine	3515-3550	early-late July	Castilleja occidentalis, Erysimum nivale, Hymenoxys grandiflora, Mertensia ciliata, Pedicularis parryi, Penstemon secundiflorus, Polemonium viscosum, Trifolium dasyphyllum, T. parryi.
17	Mt. Goliath, west (dry) slope	Alpine	3690	mid-June-early August	Erysimum amoenum, Geum rossii, Hymenoxys grandiflora, Lloydia serotina, Mertensia viridis, Polemonium viscosum, Primula angustifolia, Silene acaulis, Trifolium dasyphyllum, T. nanum.
18	Lincoln Lake; steep east-facing mesic slope	Alpine	3780	late June-early August	Castilleja occidentalis, Hymenoxys grandiflora, Mertensia viridis, Pedicularis parryi, Polemonium viscosum, Primula angustifolia, Trifolium dasyphyllum, T. nanum.
19	Summit Lake Flats (Mt. Evans), marshy seepage meadow	Alpine	3900	late July-late August	Castilleja occidentalis, Geum rossii, Pedicularis groenlandica, P. sudetica, Polygonum bistortoides, Silene acaulis, Sedum rhodanthum, S. rosea, Trifolium parryi.
20	Dry-mesic slope north of Summit Lake Flats	Alpine	3965	mid-June-mid-August	Besseya alpina, Caltha leptosepala, Castilleis occidentalis, Erysimum amoenum, Geum rossii, Lloydia serotina,

Table 3. Research Sites and Their Plant Associations (Continued)

Site No.	Site Locations & Habitat	Zone	Elevation (m)	Blooming Period	Plant Species
					Mertensia viridis, Polemonium viscosum, Polygonum bistortoides, Primula angustifolia, Sedum rhodanthum, Silene acaulis, Trifolium dasyphyllum, T. nanum, T. parryi.
21	Mt. Evans peak, tundra meadow	High Alpine	4087	late June-mid August	Besseya alpina, Chionophila jamesii, Gentiana romanzovii (late August), Mertensia viridis, Primula angustifolia, Trifolium nanum, T. parryi.
22	Mt. Evans peak, tundra meadow	High Alpine	4200	variable; mid-June-early August or mid-July-late August	Besseya alpina, Castilleja occidentalis, Chionophila jamesii, Erigeron simplex, Gentiana romanzovii, Geum rossii, Primula angustifolia, Trifolium nanum.
23	Mt. Evans peak, tundra meadow	High Alpine	4315	variable; mid-June-mid-August or mid-July-late August	Besseya alpina, Chionophila jamesii, Primula angustifolia, Trifolium nanum.

Table 4. Peak Blooming Period of Plant Species (1966 and 1969 seasons)

Plant Species	Elevation (to nearest 50-meter interval)
	2350 2400 2450 2500 2550 2600 2650 2700 2750 2800 2850 2900 2950 3000 3050 3100 3150 3200 3250 3300 3350 3400 3450 3500 3550 3600 3650 3700 3750 3800 3850 3900 3950 4000 4050 4100 4150 4200 4250 4300
Aconitum columbianum	6 — 7 — 6*
Astragalus flexuosus	3 — 5 — 1
Astragalus striatus	4 — 1
Castilleja occidentalis	4 — 5 — 7 — 7 7 — 6 — 6 — 5 — 9
Castilleja sulphurea	6
Chionophila jamesii	5
Delphinium barbeyi	7 — 8
Dodecatheon pulchellum	1 — 3 — 3 — 3 — 3 — 3 — 3 4
Mertensia ciliata	4 — 5 — 6 — 5
Mertensia viridis	3 — 4 — 3 — 6 — 5 — 7
Oxytropis lambertii	3 — 4 — 5 — 5
Oxytropis	5
Pedicularis bracteosa	6 — 6
Pedicularis crenulata	4
Pedicularis grayi	7

Table 4. Peak Blooming Period of Plant Species (1966 and 1969 seasons) (continued)

| Plant Species | Elevation (to nearest 50-meter interval) | | |

Table 5. Vertical Distribution (to Nearest 100-Meter Interval) and Frequency of Bombus and Psithyrus Individuals Collected

Species	Elevation (meters)													
	1600	1700	1800	1900/2400	2500	2600	2700	2800	2900	3000	3100	3200	3300
appositus	157	0	3	16	157	15	17	3	76	57	0	1	8	0
bifarius	7	0	0	7	187	110	346	28	583	138	24	19	21	0
californicus	-------	-------	-------	1	3	5	1	0	0	4	-------	-------	-------	-------
centralis	-------	-------	-------	10	18	16	67	0	69	9	0	0	0	0
fervidus	173	5	12	23	4	-------	-------	-------	-------	-------	-------	-------	-------	-------
flavifrons	-------	-------	-------	-------	9	12	2	48	466	71	3	223	8	0
fraternus	9	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------
frigidus	-------	-------	-------	-------	-------	-------	-------	-------	2	1	0	6	0	0
griseocollis	156	0	4	26	1	0	0	0	0	0	0	0	0	0
huntii	161	6	17	8	2	0	3	0	0	0	0	0	0	0
kirbyellus	-------	-------	-------	-------	-------	-------	-------	-------	-------	1	0	1	4	0
melanopygus	-------	-------	-------	-------	3	4	31	12	158	23	3	8	48	0
mixtus	-------	-------	-------	-------	-------	3	0	5	128	3	29	79	70	0
morrisoni	153	0	3	43	4	2	0	1	0	0	0	0	0	0
nevadensis auricomus	220	6	13	22	------	------	------	------	------	-------	------	------	------	------
nevadensis nevadensis	1283	3	36	77	14	2	4	0	0	61	0	0	0	0

Table 5 (Continued)

Species	Elevation (meters) 3400	3500	3600	3700	3800	3900	4000	4100	4200	4300
appositus	0	0	0	1	0	0	1	-------	-------	-------
bifarius	2	0	2	46	0	2	11	3	24	-------
californicus	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------
centralis	16	-------	-------	-------	-------	-------	-------	-------	-------	-------
fervidus	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------
flavifrons	23	6	7	39	3	15	6	10	10	-------
fraternus	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------
frigidus	0	0	1	6	6	22	10	4	15	-------
griseocollis	0	0	0	1	0	0	1	-------	-------	-------
huntii	0	0	0	0	0	0	0	1	-------	-------
kirbyellus	98	9	27	893	77	999	301	597	1010	55
melanopygus	0	50	6	73	0	1	0	15	15	15
mixtus	22	113	0	2	-------	-------	-------	-------	-------	-------
morrisoni	0	0	0	3	-------	-------	-------	-------	-------	-------
nevadensis auricomus	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------
nevadensis nevadensis	0	0	0	47	0	0	0	1	19	-------

Table 5. Vertical Distribution (to Nearest 100-Meter Interval) and Frequency of Bombus and Psithyrus Individuals Collected (Continued)

Species	Elevation (meters)													
	1600	1700	1800	1900/2400		2500	2600	2700	2800	2900	3000	3100	3200	3300
occidentalis	21	1	0	7	48	18	24	11	131	53	0	3	2	0
rufocinctus	93	0	3	5	28	10	46	1	1	44	1	1	0	0
sylvicola	-------	-------	-------	-------	2	2	1	0	0	17	5	4	31	0
Psithyrus insularis	8	0	2	4	17	7	62	1	7	36	16	3	0	0
P. suckleyi	-------	-------	-------	-------	------	2	1	0	1	2	-------	-------	-------	-------

Table 5 (Continued)

Species	Elevation (meters) 3400	3500	3600	3700	3800	3900	4000	4100	4200	4300
occidentalis	0	1	3	28	0	7	2	4	11	3
rufocinctus	0	0	0	0	0	0	3	-------	-------	-------
sylvicola	20	14	81	681	144	618	510	354	1152	53
Psithyrus insularis	0	1	0	8	0	0	1	-------	-------	-------
P. suckleyi	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------

Table 6. Vertical Distribution of Excavated Bombus Nests and of Bombus Queens and Psithyrus Females Collected While Hunting Nesting Sites

Species	Individuals	Nests	Vertical Range (m)
appositus	1	2	2620-2928
bifarius	17	0	2560-4200
californicus	3	3	2530-2930
fervidus	4	0	1880
flavifrons	12	2	2830-3970
fraternus	1	0	1880
frigidus	0	2	3600-3630
griseocollis	2	0	1880
kirbyellus	27	2	3600-4090
mixtus	1	0	2840
morrisoni	1	0	1880
nevadensis auricomus	3	0	1580-1880
nevadensis nevadensis	7	0	1880-2900
occidentalis	1	1	1880-2370
rufocinctus	13	0	1830-3970
sylvicola	56	3	3620-4310
Psithyrus insularis	43	-	1580-3690
Psithyrus suckleyi	1	-	2840

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
Aconitum columbianum	appositus	Q	1	1	0	0
		W	15	12	0	0
	centralis	M	1	-	-	-
	flavifrons	Q	5	1	0	0
		W	330	93	19	1
		M	1	-	-	-
	occidentalis	W	2	0	0	1
Allium geyeri	bifarius	W	38	0	11	4
	flavifrons	W	3	0	1	0
	melanopygus	W	2	0	0	1
	occidentalis	W	4	0	2	1
Astragalus bisulcatus	appositus	Q	157	84	7	1
	bifarius	W	7	0	0	0
	fervidus	Q	167	88	7	0
		W	6	5	0	0
	fraternus	Q	9	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	griseocollis	Q	156	56	5	0
	huntii	Q	161	33	5	0
	morrisoni	Q	153	55	13	0
	n. auricomus	Q	219	75	11	0
	n. nevadensis	Q	1100	505	19	0
		W	183	106	7	0
	occidentalis	Q	21	0	0	4
	rufocinctus	Q	93	18	2	0
	Psithyrus insularis	F	7	-	-	-
Astragalus flexuosus	bifarius	W	15	9	5	0
	centralis	W	4	1	3	0
	flavifrons	W	1	1	0	0
	huntii	W	1	1	0	0
	occidentalis	W	1	1	0	0
	rufocinctus	Q	7	4	2	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
Astragalus striatus	appositus	Q	9	0	1	0
	bifarius	Q	7	1	0	0
		W	2	1	1	0
	rufocinctus	Q	7	1	0	o
Besseya alpina	frigidus	M	1	-	-	-
	sylvicola	W	14	0	0	0
		M	6	-	-	-
	Psithyrus insularis	F	4	-	-	-
Castilleja occidentalis	bifarius	W	1	0	0	1
	kirbyellus	Q	89	14	7	2
		W	125	28	28	3
	melanopygus	W	1	0	1	0
	occidentalis	Q	1	1	0	0
	sylvicola	Q	1	1	0	0
		W	2	0	0	1

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
Castilleja sulphurea	appositus	Q	2	0	1	0
	flavifrons	Q	15	9	4	3
		W	28	12	6	1
	occidentalis	W	1	0	1	0
Chionophila jamesii	bifarius	Q	4	3	1	0
		W	10	3	7	0
	flavifrons	Q	1	0	0	0
		W	1	0	15	0
	kirbyellus	Q	4	0	1	3
		W	84	11	22	2
	melanopygus	W	42	15	15	1
	occidentalis	W	7	1	4	0
	sylvicola	Q	16	4	5	0
		W	11	2	5	1
Corydalis aurea	bifarius	Q	6	0	0	1
		W	7	0	2	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	californicus	Q	1	0	0	0
	occidentalis	Q	2	0	0	0
		W	2	0	0	0
	Psithyrus insularis	F	6	-	-	-
Delphinium barbeyi	appositus	W	2	2	0	0
	flavifrons	Q	4	1	0	0
		W	3	1	2	0
	kirbyellus	Q	3	0	0	0
		W	42	0	0	0
		M	24	-	-	-
Delphinium ramosum	appositus	W	2	0	0	0
	flavifrons	Q	2	2	0	0
		W	4	1	0	0
Dodecatheon pulchellum	bifarius	Q	11	2	9	0
		W	67	24	4	2
	centralis	Q	1	1	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	flavifrons	Q	11	1	7	0
		W	1	1	0	0
	melanopygus	Q	3	0	0	0
		W	53	21	31	1
	mixtus	Q	35	5	29	1
		W	1	0	1	0
	occidentalis	Q	4	0	2	1
		W	37	20	14	0
	rufocinctus	Q	6	1	4	0
	sylvicola	Q	4	1	2	0
		W	2	1	1	0
Erysimum amoenum	kirbyellus	Q	9	0	0	0
	sylvicola	Q	20	0	0	1
	Psithyrus insularis	F	1	-	-	-
Erysimum asperum	appositus	Q	3	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	bifarius	Q	22	0	1	0
		W	3	0	0	1
	centralis	Q	1	0	0	0
	morrisoni	Q	2	0	0	0
	occidentalis	Q	1	0	0	0
	rufocinctus	Q	4	0	0	0
	sylvicola	Q	2	0	0	0
	Psithyrus insularis	F	41	-	-	-
	P. suckleyi	F	2	-	-	-
Erysimum nivale	kirbyellus	Q	7	0	0	0
	sylvicola	Q	3	0	0	0
Iris missouriensis	appositus	Q	6	0	0	0
	bifarius	Q	11	0	1	0
		W	7	0	3	0
	centralis	Q	2	0	0	0
	fervidus	Q	4	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
Iris missouriensis (continued)	flavifrons	Q	1	0	0	0
	fraternus	Q	1	0	0	0
	griscocollis	Q	11	0	0	0
	huntii	Q	5	0	0	0
	melanopygus	Q	1	0	0	1
	morrisoni	Q	21	0	0	1
	n. auricomus	Q	5	0	0	0
	n. nevadensis	Q	25	0	0	3
		W	1	0	0	0
	occidentalis	Q	6	0	0	0
		W	2	0	0	0
	rufocinctus	Q	1	0	0	0
	Psithyrus insularis	F	5	-	-	-
	P. suckleyi	F	1	-	-	-
Linaria dalmatica	appositus	Q	2	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
		W	40	9	0	0
	bifarius	W	12	2	0	0
	centralis	W	18	3	2	0
	flavifrons	Q	1	0	0	0
		W	14	7	1	0
	occidentalis	W	8	0	0	1
Linaria vulgaris	appositus	Q	1	0	0	0
		W	5	0	0	5
	bifarius	W	48	0	0	2
		M	1	-	-	-
	centralis	W	12	1	1	4
	flavifrons	W	8	2	0	1
	melanopygus	W	1	0	0	0
	mixtus	W	1	0	0	0
	occidentalis	W	16	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
Lupinus argenteus	bifarius	Q	2	0	1	0
		W	4	0	2	2
	centralis	W	1	0	0	1
	mixtus	W	1	0	1	0
Melilotus officinalis	appositus	Q	20	2	15	3
		W	2	0	1	1
	bifarius	Q	1	0	0	0
		W	8	1	6	1
	fervidus	Q	1	0	1	0
	huntii	W	1	0	0	0
	n. nevadensis	W	4	0	4	0
	occidentalis	W	2	2	0	0
	rufocinctus	Q	5	0	3	2
	Psithyrus insularis	F	1	-	-	-
Mertensia ciliata	bifarius	W	3	0	0	1

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	centralis	Q	9	0	1	1
		W	50	32	10	0
	melanopygus	W	21	8	1	1
		M	1	-	-	-
	mixtus	Q	16	1	1	1
		W	78	21	11	1
	occidentalis	Q	2	0	0	0
		W	6	1	1	0
	rufocinctus	Q	1	0	0	0
	Psithyrus insularis	F	2	-	-	-
Mertensia viridis	bifarius	Q	3	0	2	0
		W	1	0	1	0
	flavifrons	Q	5	0	3	0
		W	1	0	0	0
	frigidus	Q	14	3	3	0
		W	1	0	1	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	kirbyellus	Q	93	0	19	2
		W	17	0	7	5
	melanopygus	Q	1	0	0	0
		W	9	1	7	1
	mixtus	Q	1	0	0	0
	sylvicola	Q	190	2	20	2
		W	4	0	2	0
Monarda fistulosa	appositus	Q	2	0	0	0
		W	11	0	0	0
		M	1	-	-	-
	bifarius	W	8	0	0	1
	centralis	W	14	0	0	2
	flavifrons	W	6	0	0	1
	n. nevadensis	W	2	0	0	0
	occidentalis	W	10	1	0	0
	rufocinctus	Q	1	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
Onosmodium molle	bifarius	Q	4	0	0	0
		W	61	2	4	6
		M	1	-	-	-
	centralis	W	15	1	2	2
		M	2	-	-	-
	flavifrons	W	1	0	0	1
	mixtus	W	1	0	0	0
	occidentalis	Q	1	0	0	0
	rufocinctus	Q	10	0	1	0
	sylvicola	W	12	3	2	0
	Psithyrus insularis	F	4	-	-	-
Oxytropis lambertii	appositus	Q	35	14	6	0
		W	33	14	5	0
	bifarius	Q	6	0	0	0
		W	9	3	1	0
		M	1	-	-	-

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	californicus	Q	1	1	0	0
		W	1	0	0	0
	centralis	Q	4	4	0	0
		W	7	0	1	0
	fervidus	Q	9	4	0	0
	flavifrons	Q	1	0	0	0
		W	6	2	0	0
	griseocollis	Q	4	1	0	0
	huntii	Q	17	4	0	0
	melanopygus	W	1	0	0	0
	morrisoni	Q	3	1	1	0
	n. nevadensis	Q	43	10	0	0
		W	7	3	2	0
	occidentalis	W	47	0	1	3
	rufocinctus	Q	21	3	1	1
	Psithyrus insularis	F	3	-	-	-

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
Oxytropis sericea	appositus	Q	10	8	1	0
	kirbyellus	Q	1	1	0	0
	bifarius	Q	4	0	0	2
	flavifrons	Q	3	0	0	2
	n. nevadensis	Q	41	28	1	0
		W	7	6	0	0
	occidentalis	Q	2	0	0	0
	rufocinctus	Q	4	0	2	0
	Psithyrus insularis	F	1	-	-	-
Pedicularis bracteosa	flavifrons	Q	9	3	2	0
		W	9	3	5	0
	kirbyellus	Q	4	2	2	0
	melanopygus	W	26	11	11	0
	mixtus	Q	9	3	4	0
		W	44	7	19	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Forages	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	occidentalis	W	1	1	0	0
	sylvicola	W	6	3	1	0
Pedicularis crenulata	appositus	Q	21	11	1	0
		W	1	0	0	0
	californicus	Q	4	2	0	0
	flavifrons	Q	4	2	0	1
	frigidus	Q	1	1	0	0
	rufocinctus	Q	4	2	1	0
Pedicularis grayi	bifarius	W	1	1	0	0
	flavifrons	W	53	20	19	0
	frigidus	W	5	3	0	0
	kirbyellus	W	1	0	0	0
	melanopygus	Q	1	0	0	0
		W	3	3	0	0
	mixtus	W	11	5	0	0
	occidentalis	W	3	2	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	sylvicola	W	2	2	0	0
Pedicularis groenlandica	appositus	Q	3	0	0	0
	bifarius	Q	9	1	2	2
		W	236	100	126	1
	centralis	W	9	2	7	0
	flavifrons	Q	2	0	2	0
		W	32	7	20	2
	melanopygus	Q	3	2	1	0
		W	112	59	52	1
	mixtus	Q	3	1	0	0
		W	9	3	4	0
	occidentalis	Q	2	0	1	0
		W	85	44	35	3
	sylvicola	W	151	58	81	2
Pedicularis parryi	bifarius	W	1	0	1	0
	flavifrons	Q	3	0	3	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	melanopygus	Q	2	1	1	0
		W	3	1	2	0
	mixtus	Q	2	1	1	0
	sylvicola	Q	2	0	1	0
Pedicularis racemosa	flavifrons	W	2	1	1	0
	melanopygus	W	46	30	11	0
	mixtus	W	112	81	26	0
	occidentalis	W	1	0	1	0
	sylvicola	W	42	42	0	0
Pedicularis sudetica	frigidus	W	16	4	8	1
	kirbyellus	Q	1	0	0	0
		W	30	4	3	0
		M	16	-	-	-
	melanopygus	W	1	1	0	0
	mixtus	W	1	0	0	0
	sylvicola	W	5	3	2	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
Penstemon procerus	bifarius	W	12	5	0	0
		M	2	-	-	-
	flavifrons	W	31	14	2	0
		M	1	-	-	-
	melanopygus	W	6	2	1	0
		M	4	-	-	-
	mixtus	W	4	0	1	0
		M	1	-	-	-
Penstemon secundiflorus	appositus	Q	1	0	1	0
	bifarius	W	3	1	1	0
	centralis	W	3	1	1	1
	fervidus	Q	3	0	0	0
		W	1	0	0	0
	flavifrons	Q	1	0	0	1
		W	1	0	0	1
	huntii	Q	6	0	0	1

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	n. auricomus	Q	4	0	0	1
		W	1	0	0	1
	n. nevadensis	Q	1	0	0	0
	occidentalis	Q	1	0	0	0
		W	2	0	0	2
	sylvicola	W	3	1	0	0
Penstemon virens	appositus	Q	7	0	0	0
		W	4	3	0	1
	bifarius	Q	75	3	2	0
	bifarius	W	203	68	25	3
	centralis	Q	4	0	0	1
		W	60	23	17	0
	flavifrons	Q	1	0	0	0
		W	6	1	2	1
	huntii	W	2	1	0	0
	melanopygus	Q	2	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
		W	29	10	3	1
	n. auricomus	Q	1	0	0	0
	occidentalis	Q	2	0	0	0
		W	20	1	0	0
	rufocinctus	Q	33	1	0	1
	Psithyrus insularis	F	4	-	-	-
Penstemon whippleanus	appositus	W	1	1	0	0
	bifarius	W	3	3	0	0
	flavifrons	W	58	50	7	1
	melanopygus	W	2	0	0	0
	mixtus	W	40	16	1	3
	sylvicola	W	2	1	0	1
Phacelia sericea	bifarius	Q	9	0	0	0
		W	20	4	1	1
	flavifrons	Q	1	0	0	1
		W	1	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	frigidus	Q	1	0	0	0
	mixtus	W	2	0	1	0
	rufocinctus	Q	1	0	0	0
	sylvicola	Q	5	0	0	1
		W	1	0	0	0
	Psithyrus insularis	F	18	-	-	-
Polemonium viscosum	flavifrons	Q	2	0	0	0
	kirbyellus	Q	40	0	2	6
	sylvicola	Q	1	0	0	1
Polygonum bistortoides	balteatus	W	2	0	0	0
	bifarius	W	10	0	4	2
	flavifrons	W	1	0	0	1
	frigidus	W	2	0	0	1
	melanopygus	W	5	0	1	0
	occidentalis	W	17	0	11	0
	sylvicola	Q	3	0	0	1

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
		W	179	0	41	17
		M	8	-	-	-
	Psithyrus insularis	F	2	-	-	-
Primula angustifolia	bifarius	Q	2	0	1	0
	kirbyellus	Q	5	0	0	0
	sylvicola	Q	80	0	0	3
	Psithyrus insularis	F	3	-	-	-
Primula parryi	flavifrons	Q	1	0	1	0
		W	9	3	2	2
	kirbyellus	W	30	1	1	1
		M	62	-	-	-
	n. nevadensis	W	1	0	0	0
	sylvicola	Q	1	0	0	0
		W	1	0	0	0
Sedum rhodanthum	bifarius	W	1	0	0	1

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	frigidus	W	10	3	1	4
	kirbyellus	W	10	0	1	0
		M	4	-	-	-
	melanopygus	Q	1	0	0	0
		W	5	0	3	0
	occidentalis	W	1	0	1	0
	sylvicola	Q	2	0	0	0
		W	142	20	46	14
		M	25	-	-	-
Sedum stenopetalum	kirbyellus	W	1	1	0	0
	melanopygus	W	2	1	0	0
	occidentalis	W	3	1	1	0
	sylvicola	Q	1	0	0	1
		W	64	17	7	0
		M	29	-	-	-
Taraxacum officinale	bifarius	Q	32	0	0	1

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
		W	13	0	7	6
	flavifrons	Q	2	0	0	0
	melanopygus	Q	1	0	0	0
		W	2	0	0	2
	mixtus	Q	9	0	0	2
	occidentalis	Q	2	0	0	0
		W	1	0	1	0
	rufocinctus	Q	1	0	0	0
	Psithyrus insularis	F	9	-	-	-
	P. suckleyi	F	2	-	-	-
Thermopsis divaricarpa	appositus	Q	19	5	3	2
	bifarius	Q	14	2	1	1
	californicus	Q	6	0	0	0
	centralis	Q	9	3	0	0
	fervidus	Q	15	5	4	0
	flavifrons	Q	17	9	1	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	griseocollis	Q	13	2	1	0
	huntii	Q	3	0	0	0
	morrisoni	Q	22	4	0	0
	n. auricomus	Q	15	1	1	0
	n. nevadensis	Q	52	7	0	1
		W	1	0	0	0
	occidentalis	Q	2	0	0	0
	rufocinctus	Q	21	1	3	1
Trifolium dasyphyllum	bifarius	W	6	2	2	0
	flavifrons	Q	2	0	1	1
	kirbyellus	Q	6	1	2	0
		W	59	29	2	1
		M	4	-	-	-
	sylvicola	Q	30	9	2	2
		M	105	63	7	2
Trifolium hybridum	bifarius	W	30	14	3	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	flavifrons	W	3	0	0	0
	melanopygus	W	4	1	2	0
		M	1	-	-	-
	occidentalis	W	1	1	0	0
	sylvicola	W	2	0	2	0
	Psithyrus insularis	F	1	-	-	-
Trifolium nanum	appositus	Q	1	0	0	0
	bifarius	Q	18	2	0	0
		W	16	11	4	0
	flavifrons	Q	41	3	2	0
		W	2	0	2	0
	frigidus	Q	17	3	1	0
		W	4	3	0	0
	griseocollis	Q	1	0	0	0
	huntii	Q	1	0	-0	0
	kirbyellus	Q	879	235	11	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
		W	1085	447	96	0
	melanopygus	W	45	18	15	1
	n. nevadensis	Q	20	16	3	1
		W	6	0	0	0
	occidentalis	Q	4	0	0	0
		W	19	12	2	1
	rufocinctus	Q	2	0	0	0
	sylvicola	Q	1091	240	19	0
		W	937	586	128	1
Trifolium parryi	appositus	Q	1	0	0	0
	bifarius	Q	2	0	1	-
		W	13	4	5	1
	flavifrons	Q	1	0	0	0
		W	12	5	6	1
	kirbyellus	Q	44	17	7	4
		W	1228	502	205	7

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
		M	45	-	-	-
	melanopygus	W	14	3	4	3
		M	1	-	-	-
	morrisoni	Q	2	0	0	0
		W	1	0	0	0
	n. nevadensis	Q	28	8	3	0
		W	29	10	6	0
	occidentalis	W	5	0	1	3
	sylvicola	Q	68	17	3	0
		W	273	76	127	6
		M	6	-	-	-
Trifolium pratense	appositus	Q	94	2	29	1
		W	20	6	3	0
	bifarius	Q	9	0	1	1
		W	10	2	4	0
	californicus	W	1	0	0	0

Table 7. Total Bombus and Psithyrus Foragers on Plant Species and Analysis of Pollen Types in Corbicular Loads

Plant Species	Insect Species	Caste	Total Foragers	Total Pollen Foragers		
				Proper Pollen	Mixed Pollen	Foreign Pollen
	centralis	W	1	0	1	0
	fervidus	Q	4	1	0	0
	flavifrons	Q	2	0	1	0
		W	3	0	3	0
	griseocollis	Q	1	0	1	0
	kirbyellus	W	1	0	1	0
	morrisoni	Q	1	0	0	0
		W	2	0	2	0
	n. nevadensis	Q	1	0	0	0
		W	8	1	0	0
	rufocinctus	Q	13	0	1	0
	Psithyrus insularis	F	12	-	-	-

Table 8. Fruit Production of Flowers under Insect Exclosures and of Open-pollinated Flowers

Plant Species	Elevation (m)	Under Exclosures			Open-pollinated		
		Total Flowers	Total Fruits	Percent Fruiting	Total Flowers	Total Fruits	Percent Fruiting
Aconitum columbianum	2860	70	0	0	80	68	85
Castilleja occidentalis	3690	223	0	0	224	156	70
Chionophila jamesii	3660	82	0	0	114	73	64
Delphinium barbeyi	3350	120	0	0	115	106	92
Dodecatheon pulchellum	2860	107	0	0	95	78	82
Dodecatheon pulchellum	3110	28	0	0	28	23	82
Dodecatheon pulchellum	3350	25	0	0	22	22	100
Dodecatheon pulchellum	3440	49	0	0	44	39	89
Erysimum amoenum	3960	205	0	0	205	198	97
Erysimum nivale	3440	459	2	<1	592	563	95
Iris missouriensis	2720	43	0	0	30	16	53
Lupinus argenteus	3080	444	3	<1	289	70	24
Mertensia ciliata	3290	116	2	2	127	75	59
Mertensia viridis	3440	527	33	6	648	492	76
Mertensia viridis	3690	525	16	3	525	371	71
Pedicularis bracteosa	3230	273	0	0	291	255	88
Pedicularis crenulata	2900	432	0	0	519	264	51

Table 8. Fruit Production of Flowers under Insect Exclosures and of Open-pollinated Flowers

Plant Species	Elevation (m)	Under Exclosures			Open-pollinated		
		Total Flowers	Total Fruits	Percent Fruiting	Total Flowers	Total Fruits	Percent Fruiting
Pedicularis grayi	3080	216	0	0	216	113	52
Pedicularis groenlandica	3230	384	0	0	205	199	97
Pedicularis groenlandica	3290	343	0	0	386	343	89
Pedicularis groenlandica	3920	74	0	0	84	76	90
Pedicularis parryi	3440	252	0	0	229	194	85
Pedicularis parryi	3540	154	0	0	182	70	38
Pedicularis racemosa	3260	310	0	0	194	184	95
Pedicularis racemosa	3260	324	0	0	341	318	93
Pedicularis sudetica	3290	202	0	0	211	171	81
Pedicularis sudetica	3900	272	0	0	305	241	79
Penstemon secundiflorus	2960	224	0	0	122	93	76
Penstemon virens	2960	655	114	17	407	364	89
Penstemon whippleanus	3110	662	286	43	369	236	64
Phacelia sericea	3080	247	42	17	237	220	93
Polemonium viscosum	3440	150	2	1	180	108	60
Polemonium viscosum	3960	159	0	0	159	111	70
Primula angustifolia	3690	48	0	0	48	33	69

Table 8. Fruit Production of Flowers under Insect Exclosures and of Open-pollinated Flowers

Plant Species	Elevation (m)	Under Exclosures			Open-pollinated		
		Total Flowers	Total Fruits	Percent Fruiting	Total Flowers	Total Fruit	Percent Fruiting
Primula parryi (pin)	3660	264	2	<1	310	212	68
Primula parryi (thrum)	3660	89	0	0	70	56	80
Thermopsis divaricarpa	2900	69	0	0	74	49	66
Trifolium dasyphyllum	3630	206	0	0	244	3	1
Trifolium nanum	3630	60	0	0	60	25	42
Trifolium nanum	3690	291	0	0	291	243	84
Trifolium nanum	3960	160	0	0	160	102	64
Trifolium nanum	4080	114	0	0	114	87	76
Trifolium nanum	4310	144	0	0	144	110	76
Trifolium parryi	3630	289	0	0	248	18	7

Table 9. Corolla Tube and Spur Lengths (mm)

Plant Species	Tube or Spur Length			coefficient of variation
	Range	Mean*	S. D.	
Astragalus flexuosus	5-7	5.8	0.7	12.07
Astragalus striatus	12-14	12.6	0.6	4.76
Castilleja occidentalis	15-19	16.2 .638	1.5	9.26
Castilleja sulphurea	15-17	16.1 .634	0.8	4.97
Chionophila jamesii	16-18	16.6	0.6	3.61
Corydalis aurea	12-13	12.3	0.4	3.25
Delphinium barbeyi	20-23	21.8 .858	0.8	3.67
Delphinium ramosum	16-18	17.2	0.5	2.91
Erysimum amoenum	10-11	10.3	0.4	3.88
Erysimum asperum	13-16	14.0	1.0	7.14
Erysimum nivale	12-14	13.5	0.6	4.44
Linaria dalmatica	29-38	32.2	2.2	6.83
Linaria vulgaris	24-27	25.9 1.020	0.9	3.47
Lupinus argenteus	5-6	5.6	0.5	8.93
Melilotus officinalis	2-3	2.8	0.4	14.29
Mertensia ciliata	12-14	12.9 .508	0.4	3.10
Mertensia viridis	7-8	7.8	0.4	5.13
Monarda fistulosa	18-20	19.4	1.2	6.19
Oxytropis lambertii	13-15	13.7	0.6	4.38
Oxytropis sericea	11-13	12.1	0.5	4.13
Pedicularis bracteosa	16-18	17.1 .673	0.7	4.09
Pedicularis crenulata	12-15	13.5	0.8	5.93
Pedicularis grayi	18-23	19.8	1.2	6.06
Pedicularis groenlandica	5	5.0	0.0	0
Pedicularis parryi	9-11	10.1	0.7	6.93
Pedicularis racemosa	6-7	6.6	0.5	7.58

Table 9. Corolla Tube and Spur Lengths (mm)

Plant Species	Tube or Spur Length			
	Range	Mean*	S. D.	
Pedicularis sudetica	11-12	11.5	0.5	4.35
Penstemon procerus	8-9	8.6	0.5	5.81
Penstemon secundiflorus	13-15	14.4	0.8	5.56
Penstemon virens	9-11	10.2	0.5	4.90
Penstemon whippleanus	15-17	15.7	0.7	4.46
Polemonium viscosum	21-23	21.8	0.8	3.67
Thermopsis divaricarpa	13-16	14.4	0.9	6.25
Trifolium dasyphyllum	11-13	11.5	0.6	5.22
Trifolium hybridum	6-7	6.9	0.3	4.35
Trifolium nanum	13-16	14.5	0.8	5.52
Trifolium parryi	13-15	13.9	0.6	4.32
Trifolium pratense	12-14	13.0	0.6	4.62

*sample size = 25 individual flowers

Table 10. Labium (Prementum + Glossa) Length for Bombus and Psithyrus

Species	Caste*	Labium Length (mm)			Sample Size
		Range	Mean	S. D.	
appositus	Q	12.18-14.01	12.81	0.38	50
	W	9.14-13.31	10.48	0.95	50
bifarius	Q	7.40-9.05	8.38	0.40	50
	W	4.96-6.53	5.75	0.37	50
californicus	Q	11.05-13.39	12.26	0.38	19
	W	7.23-11.65	10.01	0.75	32
centralis	Q	8.53-10.44	9.35	0.46	15
	W	5.83-8.27	7.07	0.58	45
fervidus	Q	10.78-13.05	12.03	0.46	50
flavifrons	Q	7.74-11.58	10.23	0.71	50
	W	5.39-9.84	7.81	0.80	50
fraternus	Q	8.26-10.70	9.67	0.68	9
frigidus	Q	7.05-8.26	7.27	0.37	31
	W	4.22-6.27	5.73	0.40	49
griseocollis	Q	8.61-11.23	10.12	0.46	50
huntii	Q	9.40-10.28	9.82	0.20	50
kirbyellus	Q	11.39-13.13	12.11	0.40	50
	W	8.18-10.96	9.36	0.62	50
melanopygus	Q	6.79-8.87	7.53	0.64	8
	W	5.31-7.23	6.49	0.36	49
mixtus	Q	5.83-8.18	7.36	0.36	50
	W	4.27-5.74	5.09	0.38	50
morrisoni	Q	10.35-11.66	11.01	0.29	50
nevadensis auricomus	Q	11.05-12.96	11.83	0.46	50
nevadensis nevadensis	Q	10.26-13.22	11.81	0.68	49
	W	8.17-11.57	10.13	0.68	50
occidentalis	Q	7.57-9.05	8.29	0.27	49
	W	5.22-6.27	5.71	0.25	50
rufocinctus	Q	6.96-8.79	8.08	0.37	49
sylvicola	Q	6.79-9.40	8.50	0.48	49
	W	4.88-7.14	5.79	0.58	50

Table 10. Labium (Prementum + Glossa) Length for Bombus and Psithyrus

Species	Caste*	Labium Length (mm)			Sample Size
		Range	Mean	S. D.	
Psithyrus insularis	F	7.14-9.22	8.18	0.43	50

* Q = queen W = worker F = female

$$t_s = \frac{\bar{y}_1 - \bar{y}_2}{\sqrt{\frac{1}{n}(s_1^2 + s_2^2)}}$$ (variance = (s.d.)²)

or if $n_1 \neq n_2$ $\sqrt{\frac{s_1^2}{n_2} + \frac{s_2^2}{n_1}}$

bifarine t $\frac{8.38 - 7.94}{\sqrt{\frac{1}{50}(.16 + .183)}}$ $t_s = 5.31$ df = 98

britains t $\frac{5.75 - 5.68}{\sqrt{\frac{1}{50}(.14 + .072)}}$ $t_s = 1.074$ df = 98

Chartons t $\frac{10.23 - 9.43}{\sqrt{\frac{1}{50}(.50 + .70)}}$ $t_s = 5.15$ df = 98

Slav. t $\frac{7.81 - 7.63}{\sqrt{\frac{.64}{26} + \frac{.93}{50}}}$ $t_s = .87$ df = 76

ovsld. t $\frac{8.50 - 8.09}{\sqrt{\frac{.23}{30} + \frac{}{49}}}$ $t_s = 4.39$ df = 77

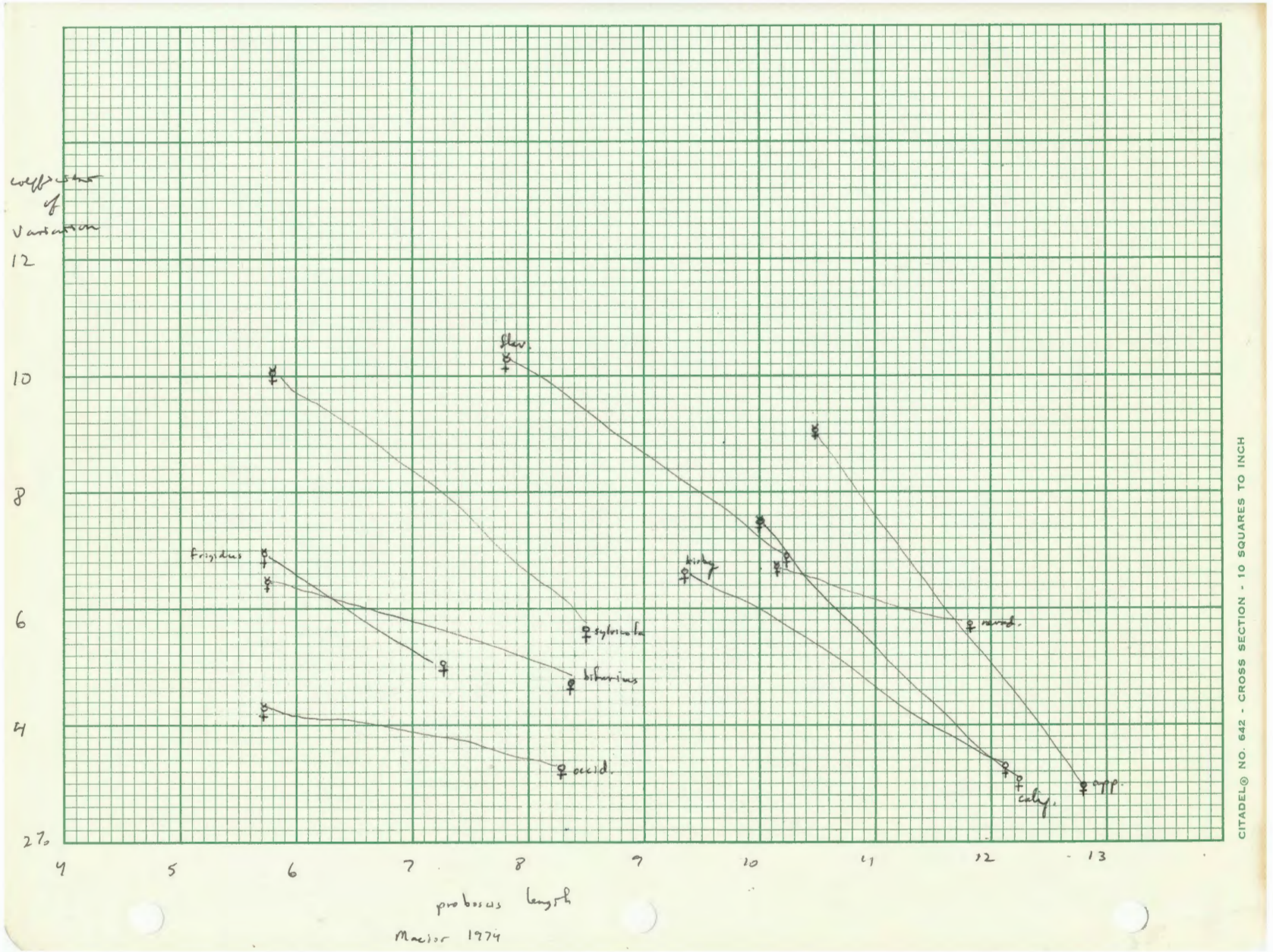
ovsld t $\frac{6.29 - 5.71}{\sqrt{\frac{1}{50}(.06 + .22)}}$ $t_s = 7.77$ df = 98

mixmus t $\frac{7.82 - 7.36}{\sqrt{\frac{.332^2}{50} + \frac{.36^2}{8}}}$ $t_s = .04$ df = 56

mixmus t $\frac{5.53 - 5.09}{\sqrt{\frac{.402}{50} + \frac{.38}{22}}}$ $t_s = 2.92$ df = 70

malmo phyms t $\frac{8.07 - 7.53}{\sqrt{\frac{.325}{8} + \frac{.64}{50}}}$ $t_s = 3.08$ df = 56

malmo phyms t $\frac{6.49 - 6.15}{\sqrt{\frac{.36}{50} + \frac{.58}{49}}}$ $t_s = 3.79$ d.f. = 97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fraxinus
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