POLLINATION ECOLOGY WITHIN THE SIERRA NEVADA

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Little published information is available on the intricacies of the pollination ecology of the Sierra Nevada. My own synecological studies of the basic descriptive features and driving variables of pollination ecology (Moldenke 1975, 1976) throughout western North America can be supplemented with few specific studies actually carried out within the Sierra Nevada. In this paper I will very briefly describe some overall descriptive features and present an approach for testing the selective mechanisms responsible for producing the observable patterns.

Two of the research methodologies that I, and my associates John Neff, Pat Lincoln and Ray Heithaus, have employed over the past 10 years or so, have been the following:
A) In order to establish what actually does happen pollination-wise within a community of plants, we have employed as thoroughly as possible what we call "the perfect observant vacuum cleaner approach". We establish a 0.5 km² research site in as undisturbed a natural community as possible. Within each site: we census all the plant species present; we transplant to the greenhouse or bag each species to determine whether it is genetically compatible or genetically incompatible and incapable of setting selfed seed; we collect every insect we observe visiting every flower in the community, determining whether it actually serves as a pollinator or merely acts as an herbivore exploiting the community floral resource without any substantial indirect pollination benefit; and we determine finally which species of pollinators visit which plants in what relative abundances.

We sample each site two to three times a week for two consecutive years for: 1) completeness; 2) to answer the inevitable questions remaining from the first year; and most importantly, 3) to try to average out (to some extent) variability in abundance patterns from year to year. We have done this now in 18 different communities in California and about 18 more in tropical Costa Rica, the Mediterranean climates of Chile, the deserts of Arizona and Argentina and the subalpine and alpine Rocky Mountains of Colorado. The data I will draw upon for this address is based on work done in the years 1969-1973 at Mather 1500-1800 meters in Tuolumne and Mariposa Counties, Tioga Pass Hall Natural Area 3300-3500 meters in Mono County, Dore Crest 4000-4200 meters in Mono County, and as representative

of the low-elevation Sierra Nevada grasslands data are also
cited from the Stanford University Campus at sea level.

What, then, is the basic idea behind working at the
community level, rather than studying the autecology of a par-
ticular plant species? The answer involves the issue of
repeatibility and generalization, particularly to distinguish
the basic features of the interaction patterns and hence the
primary driving variables of the system, from the secondary
variables involving only several constituent species. All too
often pollination studies are based on one particular species
(usually only a single population!) during only a single
blooming season.

If there is one predominant feature of all pollination
ecology, it is that most phenomena are extremely localized
and that there is great variability in the abundance, specific
identity and flight patterns of pollinators within as little
a distance as 100 meters or between the same geographical
location during subsequent years. This is the case, of course,
because each species of plant and each pollinator is responding
to its own set of environmental variables and predation, and
because pollinator flight patterns are determined competitively
by the conditions existing within extremely circumscribed areas.
A plant species at a particular density growing with three other
blooming plants is treated differently when growing at a differ-
ent density with the same plants or at the same density with
three other species of plants.

	pollinator species	total pollinator abundance	habitual + obligately selfing species
Dore Crest 4100m	78	1,132	47
Timberline 3400m	350	29,045	30
Mather 1700m	630	340,837	22

TABLE 1. Pollinator species richness and abundance along
transect. Habitually selfing species indicates that class
of species so infrequently visited by pollinators that
cross-pollination cannot be considered the usual method of
reproduction in the sites studied.

TABLE 2: FLOWER VISITORS

		Stanford–		Mather			Tioga Pass		– Dore Crest
		Grass-land	Grass-land	Forest	Chaparral	Meadow	Forest	Talus	Alpine
Bees	species	163	146	165	141	36	72	91	36
	individuals	19,602	38,716	33,122	26,400	1,060	1,241	4,176	716
Beetles	species	47	37	36	63	10	16	27	2
	individuals	57,161	57,039	27,063	89,116	74	4,131	1,634	26
Butterflies	species	35	24	26	13	19	15	60	19
	individuals	3,801	2,767	1,837	3,710	37	68	664	200
Muscoids	species	24	19	9	16	45	44	53	5
	individuals	2,345	525	86	321	1,416	1,588	3,785	94
Syrphids	species	22	18	21	23	7	16	21	4
	individuals	925	682	69	927	17	83	132	15
Beeflies	species	31	24	26	10	1	5	9	4
	individuals	6,699	4,842	4,493	26,438	2	12	48	48
Wasps	species	26	30	23	22	0	4	21	6
	individuals	448	1,100	811	874	0	11	191	7
Hummingbirds + Sphingid Moths	species	1	1	3	2	2	4	4	2
	individuals	31	20	14	87	6	52	196	22
total species		386	326	327	316	158	202	337	77
total individuals		98,452	100,827	68,670	170,375	5,101	10,263	13,681	1,182

However, with these caveats in mind, there are indeed certain useful, predictable and generalizable features about pollination systems that can be distinguished by studying the sum total of species under a rather variable set of environmental conditions (such as those met with in 0.5 km^2).

  1. Some types of plants are always preferred to others (under widely different density conditions) by the majority of pollinator species.

  2. Some types of plants are faithfully visited by a specific pollinator, which visits only that single species regardless of its density or what other plants are blooming contemporaneously.

  3. Certain environments favor insect activity in terms of temperature and illumination, others are favorable in providing unlimited nesting sites, others favor the activity of a certain type of pollinator while hindering other types.

  4. Pollinators are generally limiting in certain environments, floral resources are limiting in others.

Having observed nearly 1½ million insects in our experimental sites, we are able to make the following sorts of general statements about the pollination ecology of the Sierra Nevada.

  1. With increasing altitude (or more appropriately, increasing severity of the environment for poikilotherms) the species richness of potential pollinator species drops dramatically from 737 at Stanford, to 1/10 that at alpine altitudes (Table 1). Along with species richness, total pollinator abundance drops even more dramatically to 0.3% that at mid-elevation. Correlated to decreasing pollinator abundance and diversity at higher altitudes, the number of habitual and obligately selfing species increases (Table 1).

  2. A closer look at the types of flower-visitors at each site shows that these trends hold for all of the different pollinator types individually except for the muscoid flies, which are extremely abundant flower visitors at subalpine altitudes (Table 2).

  3. If one examines only the efficiency of different types of breeding systems and the importance of only those flower visitors which function as significant pollinators, one sees the complex pattern presented in Table 3. Disproportionately important modes are: solitary bees (including specialist-feeding species) at low and mid-elevation grassland and chaparral; bumblebees in mid- and high-elevation scrub; muscoids at subalpine sites; wind-pollination in high-elevation sites; and selfing in grassland communities and high elevations.

TABLE 2. Species richness and abundance of different classes of flower-visiting animals. See Moldenke (1975) for methods of obtaining data.

POLLINATOR	range in California	Stanford Grassland	Mather Grassland	Forest	Chaparral	Tioga Pass Meadow	Forest	Talus	Dore Crest Alpine
Solitary Bee	9-62	41↑	40↑	30	62↑	9↓	1?	20	27
(Specialists)	(2-37)	(20)⇑	(28)⇑	(13)	(37)⇑	(6)↓	(10)⇓	(15)	(15)
Bumblebee	0-47	10	12	21	47↑	15	19	22↑	24⇑
Beefly	0-23	20	16	17	23	0↓	2↓	5↓	0↓
Beetle	0-20	16	13	5	15	0	5	6	0
Wasp	0-7	1	2	3	7	0	0	0	1
Butterfly	1-20	7	13↑	4	20⇑	2	4	8	8
Moth	0-3	1	2	0	0	1	0	1	2
Muscoid fly	1-16	3	3	2	1	16↑	16↑	8⇑	5
Syrphid fly	0-18	4	4	3	1	2	0	2	1
hummingbird & sphingid moth	0-14	3	1	3	12⇑	2	5	6	4
wind	9-35	16	31⇑	12	12	35⇑	29⇑	20	25↑
± habitual selfer	7-42(m)	41⇑	42⇑	25	7↓	19	22	35⇑	39⇑
(obligate selfer)	[1-11(m)]	(18)⇑	(4)	(4)	(1)	(5)	(2)	(3)	(2)
vegetative reprod.	0-8	1	0	1	0	8⇑	6⇑	7⇑	3⇑

TABLE 3. Breeding systems and actual agents of pollination. Specialist-feeding bees are a subclass of solitary bees; obligate selfer is a subclass of habitual selfer. Vegetative reproduction includes only the most extensive and successful forms of apomixis.

What causes the complex pattern revealed in Table 3? The majority of community pollination phenomena are caused by the interplay of two variables, which do not always result in the expected manner. The two variables are: 1) decreasing pollinator abundance with increasing severity of climate; and 2) the fact that a particular community type is often more similar between differing altitudinal replicates, than any two physiognomically different sites at the same geographical and altitudinal location are to one another.

Three examples of this very significant variable are plant diversity, genetic self-compatibility and pollinator food-utilization patterns (Moldenke 1975). Table 4 quantifies measures of plant diversity along the altitudinal transect. "Diversity" measures both the total number of species and their respective relative abundances. As such, diversity is an excellent indicator of the resource base available to the potential pollinators of a community, rather than measures such as total species count. Notice in Table 4 how similar community types cluster around similar diversity values.

H Diversity	Community Type	Total Species
3.90	Mather Forest	182
3.74	Subalpine Forest	126
3.58	Stanford Oak-Madrone Forest	104
3.30	Dora Crest Alpine Tundra	79
3.07	Stanford Chaparral Scrub	90
3.02	Subalpine Talus Scrub	181
2.77	Coastal Sage Scrub	191
2.70	Mather Grassland	103
2.76	Subalpine Marsh-Meadow	137
2.20	Stanford Serpentine Grassland	150
1.81	Mather Chaparral Scrub	62

TABLE 4. Species richness and diversity of the flora at the experimental sites.

Table 5 analyses the emphasis on genetic self-compatibility as a breeding strategy in the different experimental sites. The most significant measure in this context is the percentage of the total floral biomass of the community.

Figure 1 may be used to illustrate the importance of both variables. The extremes (both specialization and super-generalization of food selection patterns increase in importance with increasing altitude and climatic severity. However, regardless of altitude, specialist feeding patterns are important in grasslands and super-generalists are important in forests. Since the ranges of the values (not shown on the figure) averaged for each statistic on the left-hand column are in all cases much greater than for the right-hand column, this signifies that the primary variable determining pollinator feeding strategies is community physiognomy, rather than pollinator diversity or abundance!

	% species	% individuals	% biomass (floral)
Tioga Pass Meadow	74	97	55
Mather Grassland	87	97	90
Stanford Serpentine Grassland	79	85	70
Tioga Pass Forest	61	90	<0.01
Mather Forest	49	75	<0.01
Stanford Oak-Madrone Forest	44	48	<0.01
Tioga Pass Scrub	65	85	49
Mather Chaparral Scrub	31	81	<1
Stanford Chaparral Scrub	46	60	<1

TABLE 5. Measures of genetic self-compatibility in different community types. Compatibility is especiallly important in grasslands by all measures, but least so in terms of biomass. In forest communities all the large or common plants are heavily outcrossed and incompatible; pollinators are very infrequent, but nearly all species are perennial. The lack of potential pollen vectors at the high altitudes is reflected by a noticeable increase of compatible plants in all community types.

RELATIVE EMPHASIS ON NICHE FEEDING STRATEGIES

FIGURE 1

Timberline
Mather
Stanford
Point Reyes + Weeds

Grasslands
Scrub
Forest

$$\% \text{ emphasis} = \frac{\% \text{ species} + \% \text{ individuals} + \% \text{ biomass}}{3}$$
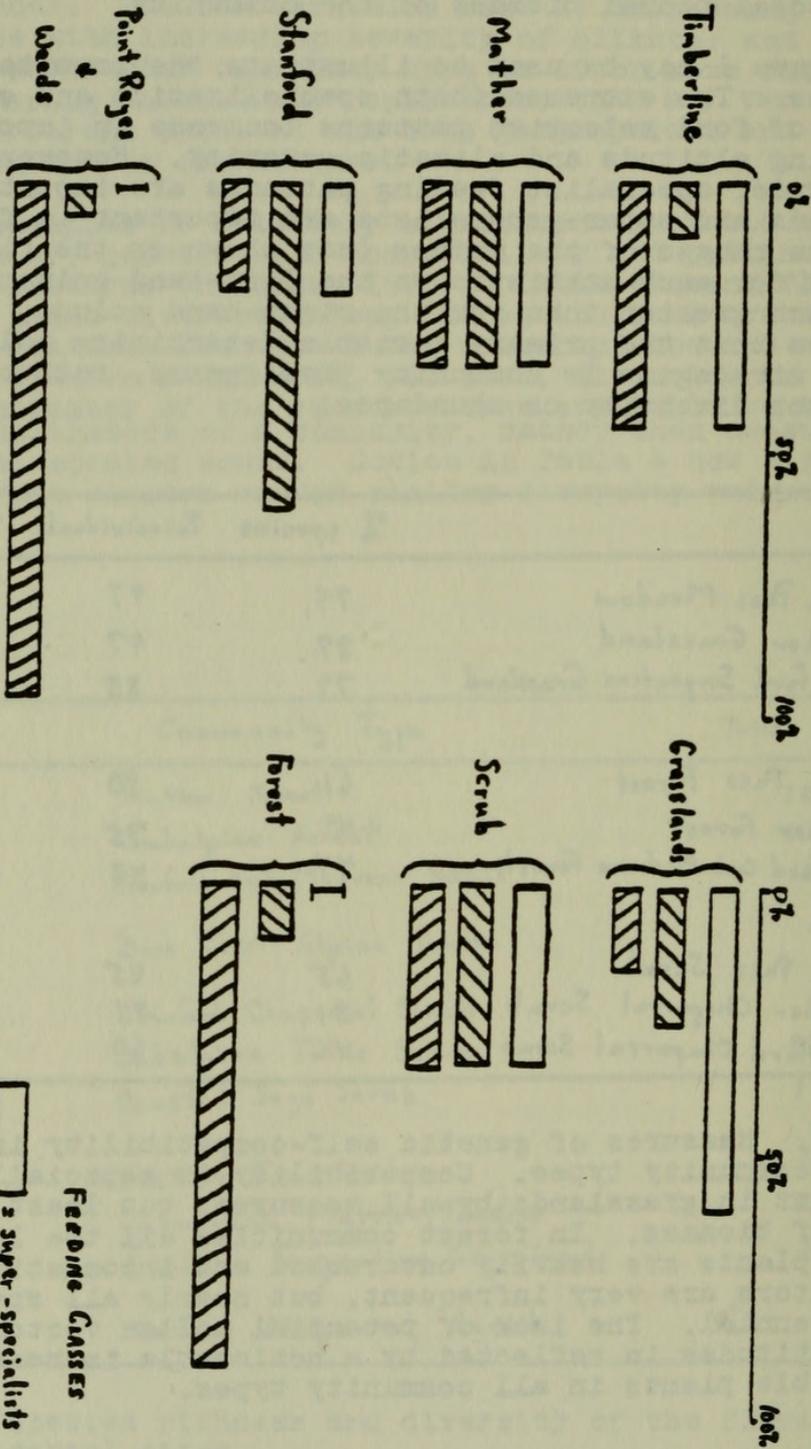
FEEDING CLASSES

= super-specialists
= allophage
= super-generalists

In a very generalized fashion, the preeminent features of the pollination ecology of the Sierra Nevada are summarized in Table 6. These statements represent the general trends evidenced at specific point sites; they should not be taken to imply that they will hold for much more than a majority of the plant species in any as yet unstudied particular location.

B) The second major emphasis of our laboratory has centered on bees. Since bees are the most important pollinator type (Moldenke 1976) in California, we have made a special effort to understand their distributions, relative abundances and floral visitation patterns. Several years ago we catalogued all of the published information available as well as all the information on all the specimen labels of all the bees in the major collections in California, together with our own data as well. There are about 2,500 species of bees in the arid southwestern United States and the catalogued information (incomplete and sketchy as it is) was rather voluminous (Moldenke & Neff 1974). This information was not published, since four of the largest bee genera are still in the process of taxonomic revision, but it is available to interested researchers from me personally.

This project was remarkably fruitful to my mind, for it allowed for the first time:
1) relatively accurate estimates of the total bee species richness in the different regions of California (Table 7). Note particularly the intermediate values pertinent to the different regions of the Sierra Nevada.
2) relatively sound decisions on the flower-visiting behaviors of about 80% of the species of bees in the western United States, for instance: generalist feeders on anything; specialist feeders on one particular plant family; or specialist feeders on one particular genus over a very broad geographic expanse. In making these general statements about bee feeding habits, I fully realize that there is no such thing as a true theoretical generalist feeder or theoretical specialist. No generalist feeder visits all the resources in the exact proportions of their density; and only, probably, at most 99% of the females of any specialist-feeding bee, in nearly all of its populations exploit the appointed flower -- and of course they may visit a wide variety of flowers for nectar, sometimes effectively pollinating them too.
3) an idea of which plant genera are associated consistently with specialist pollinators only; which ones are serviced by generalist pollinators; and which ones by both.

	Mature Chaparral	Grassland	Forest
wind pollination	nearly absent	prominent, but never more than X% of most abundant species	nearly all dominants
pollinator abundance	very high	high	low
pollinator diversity	very high	high	very low
abundant pollinator groups	all high	all high except hummingbirds	bumblebees out, important butterflies & absent
nocturnal pollination	yes	occasionally	rarely
limiting resource (in general)	Insects - compete for plants	dominants: insects compete for plants; non-dominants: plants compete for pollinators	plants compete for pollinators
specialist pollinators	assoc. w all dominants	many dominants assoc. w specialists	very rare
breeding system	all dominants ad rare animals heavily outcrossed	many dominants are facultual inbreeders	dominants monoecious and heavily outcrossed; herb layer mostly perennial and genetically self-incompatible
special features	recolonization problems after burns	extreme annual weather-correlated variability	Sundappling

TABLE 6. General features of the pollination dynamics of plant communities within the Sierra Nevada.

TABLE 7. Distribution of bee groups in Biotic Regions of California (Moldenke, 1976)

	Colletidae	Andreninae	Panurginae	Melittidae	Halictidae	Megachilidae	Anthophoridae	Apidae	Total bee species	Plant Genera with specialist pollinators	Total specialist bee pollinators
TRANSMONTANE											
No. Great Basin	13	30	12	0	21	72	50	15	213	17	118
Great Basin	12	18	12	0	19	66	47	5	179	14	98
Owens Valley	21	22	86	6	48	120	84	7	394	33	253
DESERT											
Mojave Desert	29	29	101	9	80	105	103	1	456	33	271
Colorado Desert	27	22	137	14	86	92	104	0	482	35	299
MONTANE											
Trinities + Siskiyous	17	43	0	0	21	80	46	13	220	11	86
Alpine Sierras	15	18	4	0	25	87	20	14	183	13	89
Northern Sierras	23	70	15	0	62	137	81	10	398	28	170
Southern Sierras	20	80	25	2	96	170	116	7	516	38	219
Montane + Alpine so. Calif.	12	53	20	3	95	146	85	8	422	30	186
COASTAL											
Dunes and Sage	10	30	3	1	43	24	41	10	172	12	52
MEDITERRANEAN											
No. Coast Ranges	16	60	9	0	61	114	106	11	377	33	152
So. Coast Ranges	21	96	40	2	89	132	132	8	520	44	262
Cismontane so. Calif.	22	98	43	7	122	119	138	7	555	47	253
No. Central Grassland	13	48	9	0	41	45	72	10	238	29	108
So. Central Grassland	19	84	30	1	57	54	80	7	282	36	161

4) by applying subsequent studies on bee phylogeny and
biogeography, it allows us for the first time to estimate the
number of independent events during the coevolution of bees
and plants in which specialist-bees have become tied to a
particular group of plants.

5) the realization that nearly three-quarters of the
non-anemophilous California plant genera are actually pollin-
ated by at least two very different types of pollinators, and
that nearly one-half of the genera are serviced by at least
three distinct types. This means that the often-cited
generalizations about 1:1, pollinator:plant, tightly coupled
systems is scarcely relevant to California (Table 8).

We will utilize the results of this research later on in
this presentation in specific ways pertinent to an analysis
of the pollination ecology of the Sierra Nevada. I would like
to pass on now to an analysis of the mechanisms responsible
for producing many of the patterns heretofore described in
my previous papers. Wind-pollinated plants will be excluded
from this discussion.

. . . . .

From the botanical point of view, one of the basic pieces
of data emerging from our community pollination studies is a
chart of when each species blooms and the relative contribu-
tion of each species to the total floral biomass resource of
the community (Figure 2). The entry representing each species
is determined by the behavior of the sum of all populations in
the study site. In the field, anthesis was judged on a scale
of+1 to +5 to -1, with +1 signifying that a few flowers have
appeared on a very small fraction of the population, +5
signifying full-bloom of nearly all individuals, -1 signifying
only a few scattered flowers remaining on a few scattered.
individuals; the charts and analyses include only the period
+3, +4, +5, -4, -3 for each species of non-anemophilous plants.

TABLE 8. Pollination Syndromes of the California Flora.
Vector categories represent the most efficient modes of pollin-
ation for a particular plant genus rather than simply the total
flower visitors. A: Only categories with listings more than 5
included in the table; B: Indicates pollination by indicated
mode and at least two others; C: Indicates pollination by indi-
cated mode and at least one other; D: Obligate selfing is a
subset of habitual selfing; E: Difficult to delineate between
modes without further investigation (57 taxa cited jointly).
From Moldenke (1976).

Table 8.

				POLLINATION MODE												
Water Pollination	Wind Pollination	Obligate Selfer Ⓘ	Habitual Selfer Ⓘ	Generalist Bees Ⓘ	Specialist Bees	Hummingbird	Sphinx Moth	Moths (nocturnal)	Butterflies	Wasps	Beetles	Muscoid Flies	Beeflies	Syrphids	Primitive Flies	
X																5
	X															136
		X														76
			X	(x)												246 Ⓐ
		(x)		X												56
				X	X											27
					X											9
						X										10
				X		X										22
							X									3
								X								4
									X							2
										X						0
				X						X						5
											X					1
				X							X					9
												X				5
				X								X				4
													X			5
				X									X			15
				X	X								X			7
														X		0
				X										X	X	18
															X	6
		X		X	(←⎯⎯ 2 x ⎯⎯→)											49 Ⓑ
		X	X	X (←⎯⎯ 1 x ⎯⎯→)												20 Ⓒ
		X	X	X (←⎯⎯ 2 x ⎯⎯→)												70 ⒷⒸⒷ
				(←⎯⎯ 2 x ⎯⎯→)												5 Ⓑ
X				(←⎯⎯ 2-5 x ⎯⎯→)												27

Ⓐ = California Genera Possessing Stated Mode of Pollination
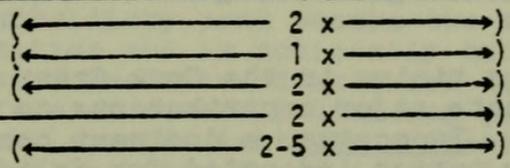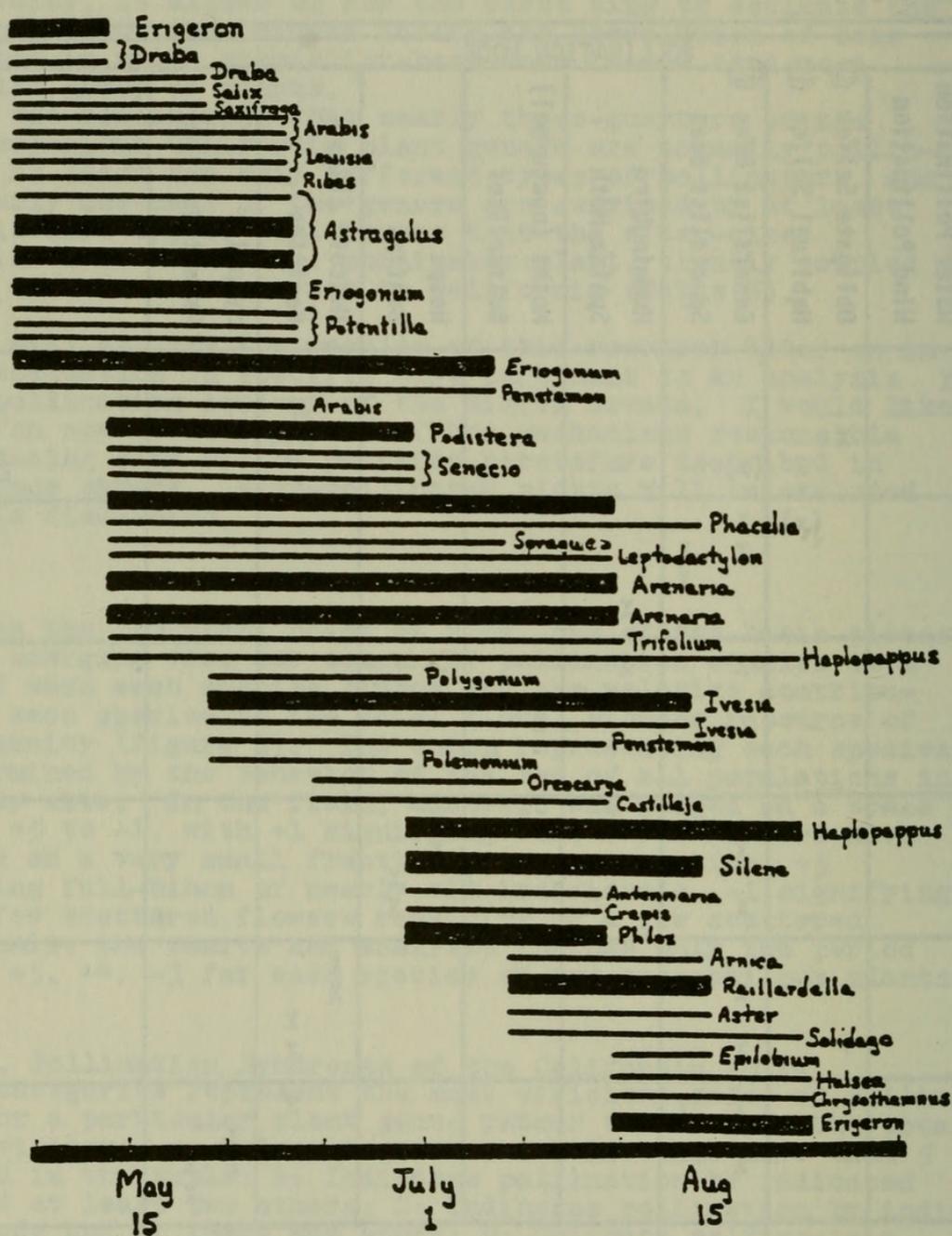
FIGURE 2. Anthesis timing in the Dore Crest alpine community.
Thick lines indicate major contributants to the community floral
biomass resource. Tanacetum, a dominant community feature, which
blooms during the period indicated for Solidago was accidently
omitted from the figure during preparation.

ANTHESIS INITIATION

Since the anthesis period of each plant species is subject
to a large number of independent variables, we might expect to
find (examining floral initiation time alone) that the distri-
bution of all species within a community would follow a
bell-shaped or normal distribution as a result of the Central
Limit Theorem. The Central Limit Theorem states that the
total distribution of a population of independent random
events is normally distributed, or "bell-shaped". In a
temperate climate, we would expect the peak to be slightly to
the left of the middle of the total growing season, in order
for seed maturation to ensue, and we might additionally expect
the left tail to be somewhat truncated by the spring frosts.
However, if the initiation of flowering by each species was
not a randomized event relative to the other species in the
community, then the time at which irregular pulses occurred
should reveal the nature of the driving variable(s).

The pattern of floral initiation of the mid-elevation
communities is basically normally distributed, as expected (Fig.3).
This data was not compared directly to any particular simulated
curve because of the reasons presented in the Discussion. The
approximation to a normal curve is best in the Mather grassland
and forest communities, which have the largest total number of
species and therefore would be expected to show the least
irregular bias due to small sample size. The center of the
main peak is at May 15th in all three Mather communities, even
though the flowering season in the snow-covered grassland
starts a full month after that in the neighboring chaparral
and forest communities. As the total blooming season increases
at Mather from 6 to 7 months in the three communities, the peak
of the floral initiation curve broadens from two weeks in the
grassland to seven weeks in the chaparral.

At the Tioga Pass and Dore Crest sites the pattern of
floral initiation is distinctly bimodal throughout (Figure 3).
The major peak occurs about May 15th, which is the beginning
of the total growing season, regardless of the length of each
of the growing seasons in the four respective communities. In
the subalpine forest, subalpine meadow and Dore Crest alpine
communities there is a subsidiary peak at July 15th during
basically a total 2½ month blooming season. In the subalpine
talus-fell community, the total blooming season extends for
3½ months and the subsidiary peak occurs two weeks later than
in the other communities and is noticeably broader. The entire
growing season is so foreshortened at these high-elevation
sites that in the face of severely limiting pollinators 43-60%
of the resident plant species initiate anthesis as soon as
physiologically possible; this trend is facilitated by the
presence of perennials as 96% of the flora (Moldenke 1975).
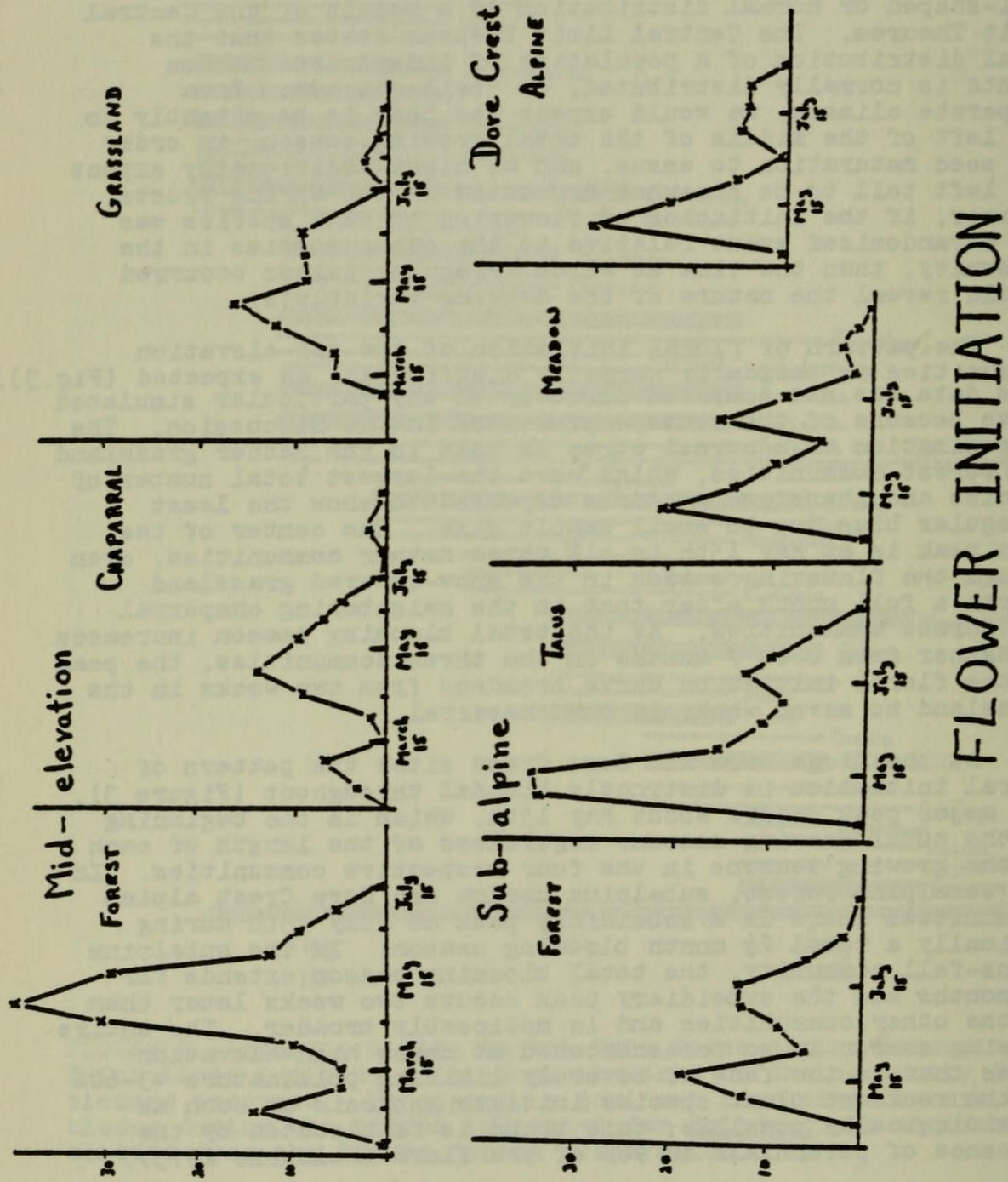
FIGURE 3. Number of species of resident plants initiating anthesis during the weeks indicated at the experimental sites.

Not all species initiate bloom abnormally early, the second
peak clearly indicates that about 30-40% of the species still
initiate blooming at what would be considered the normal time
based on the results at mid-elevation.

SYNCHRONOUS BLOOM

    Since the total length of time each species spends blooming
is presumably under independent control as well for each of
the species, we should expect a normal distribution through
time for the total plant species in bloom during each week.
Since this distribution is a cumulative result of the initia-
tion times, it should and does peak at or shortly after the
initiation curves. The distributions for all seven communities
are indeed apparently normal; Mather communities have narrow
peaks at May 1 - June 15 with distinct tails, while Timberline
communities are very broad and without distinct tails (Figure 4).
The peak in the total number of simultaneously blooming plants
in the Mather chaparral is delayed about two weeks compared
to forest and grassland communities; this delay is correlated
to a 2-4 week longer total blooming season.

    The total number of simultaneously blooming species in
all of the subalpine and alpine communities yeilds too broad a
curve for meaningful distinctions. The precise peak occurs
on July 1 for alpine and talus-fell communities, whereas in
the meadow and forest communities it does not occur until a
full month later. I presume that this correlates with the
considerably more stressful evapotranspiratory difficulties
in the former as the season progresses and snow melt is
concluded. Undoubtedly there is significant variability from
year to year in the precise length and initiation of blooming
seasons depending upon amount of snow pack. When summing the
behavior of all populations within 0.5 km^2, as was done
throughout these studies, significant microenvironmental
gradients are not distinguished (see Discussion).

TOTAL FLORAL BIOMASS

    Though total community floral biomass might be expected
to follow a simple and repeatable pattern, the extreme
disparity in the relative abundances of the dominant plants
in most communities seem to preclude anything approaching
smooth curves. Floral biomass is estimated not in nutritional
terms but is calculated by the product of the two largest
linear dimensions of the flower (inflorescence), times the
number of flowers (inflorescences) per plant, times the number
of individuals in the census (see Methods: Moldenke 1975).
As such, this is not a direct measure of floral reward though
it probably does approximate it in relative terms.
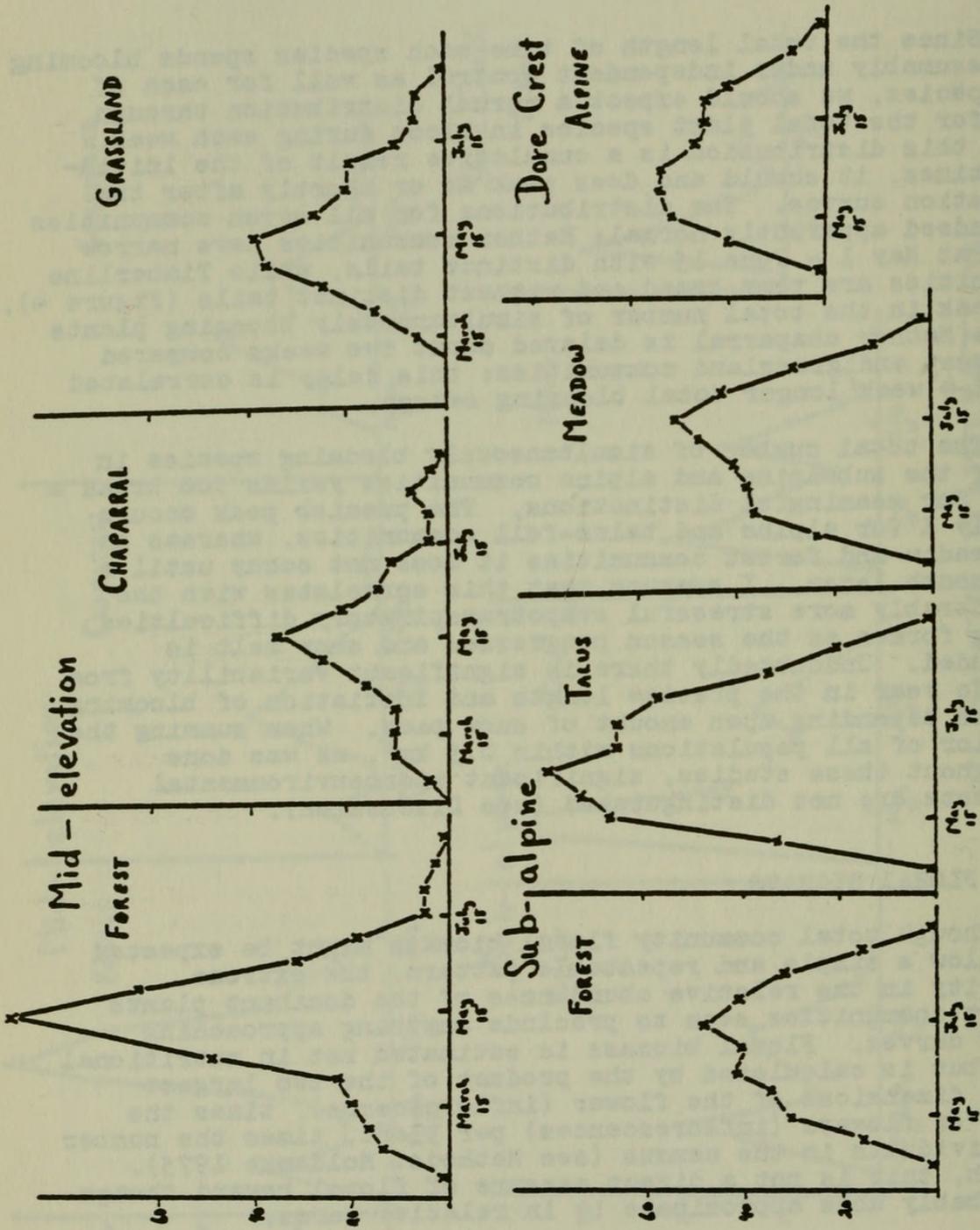
FIGURE 4. Number of plant species in bloom during the weeks indicated within the experimental sites.

Several conclusions are apparent from an analysis of the biomass data (Figure 5):

1) The peak biomass is not necessarily correlated with the peak number of flowering species. In Dore Crest and Mather chaparral communities the biomass peak occurs respectively several weeks after and before the peak of simultaneously blooming species (Figure 5).

2) The Mather grassland and Tioga Pass meadow communities demonstrate clear bimodal biomass availability patterns (Figure 5).

3) Many of the most heavily visited plant species seem to produce very minor amounts of floral biomass (e.g., Haplopappus spp., Achillea lanulosa, Ranunculus californicus, Ceanothus integerrimus, Eriogonum latifolium ssp. nudum, Rhamnus crocea, Lotus scoparius, Grindelia camporum, Phacelia spp., Gilia capitata, Eriodictyon californicum, Potentilla glandulosa, Hackelia sp., Horkelia fusca, Ligusticum sp., Sphenosciadium capitellatum). In my experience most of these species are aggressive early colonists of disturbed areas and would normally be widely scattered and unpredictable in distribution. It is interesting that many generations of selection under such conditions has indeed somehow produced plant species with especially attractive flowers to a wide spectrum of possible pollinators.

4) Many of the most heavy contributants to community floral biomass resource are very poorly visited by potential pollinators (e.g., Adenostoma fasciculatum, Nemophila spatulata, Boisduvallia densiflora, Trichostema rubisepalum, Amelanchier spp., Phlox spp., Mimulus primuloides, Ledum glandulosum, Ranunculus alismellus, Holodiscus spp.).

5) In all communities except the chaparral, anemophilous flower types usually account for 10-1000 times the floral biomass produced by entomophilous and ornithophilous plants (data not presented here; Moldenke 1975, 1976). This is generally true throughout the temperate and arctic regions of the world.

I think that it is unwise to draw more specific conclusions from this type of data. The biomass curve is determined in general outline by only 3-10% of the resident species; slight changes in their blooming seasons or amount of bloom from year to year could and probably does alter the shape of the curve significantly.

ANNUAL VERSUS PERENNIAL

Intuitively, one might expect that annual plant species would differ significantly from perennials in terms of their flowering phenology, since many of the options available to perennials are not open for annuals. However, such is not the
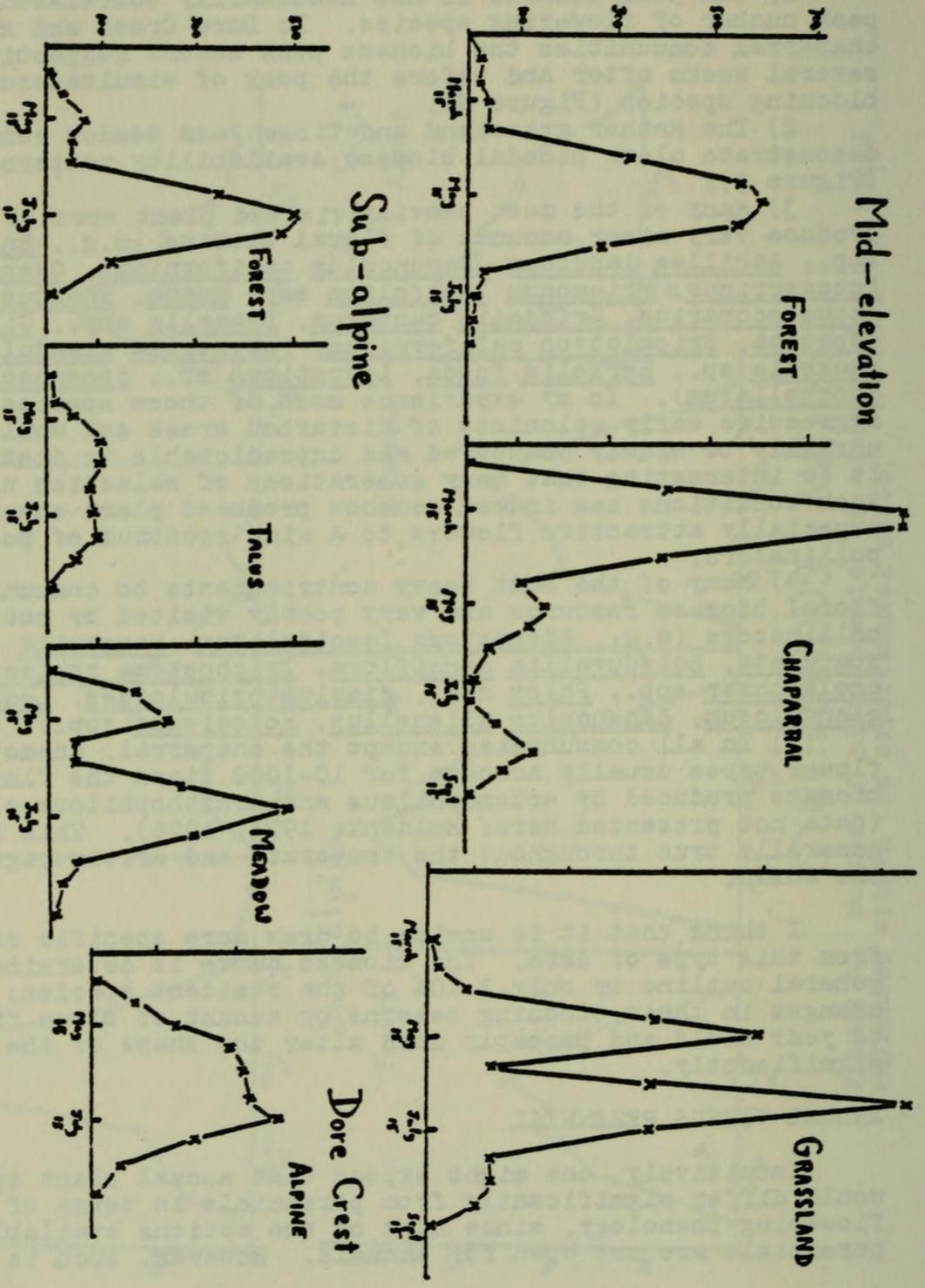
COMMUNITY FLORAL BIOMASS

FIGURE 5. Total community floral biomass during the weeks indicated. Biomass units in cm².

case. The respective phenological behavior of annuals and
perennials in the four communities with a significant number
of species of annuals, is basically the same whether one plots
floral initiation (Figure 6), synchronously blooming species
or floral biomass.

COMPETITION FOR POLLINATORS: BETWEEN COMMUNITY COMPARISONS
a) Overlap of anthesis periods

     If pollinators are a resource that is ever competed for
by plants within a community, then there should be a tendency
for plants to bloom asynchronously. In particular, there
should be a limit on the largest total number of plants
blooming at the peak of the season. As the growing season
increases in length, the ease of blooming asynchronously
should increase and a smaller percentage of the flora should
be blooming at the peak. In the Mather communities (total
blooming season = ca. 26 weeks), 52-58% of the flora is blooming
at the peak, whereas at Tioga Pass (total blooming season =

COMMUNITY	Total Species in bloom at peak week	Total Species in community	% Total Species in bloom at peak week
Dove Crest alpine	35	59	65%
Subalpine talus	79	127	62%
forest	51	78	65%
meadow	52	86	60%
Midelevation chaparral	31	57	55%
forest	91	152	58%
meadow	37	71	52%

TABLE 9. Characteristics of the non-anemophilous flora at
the peak week of bloom during the year.
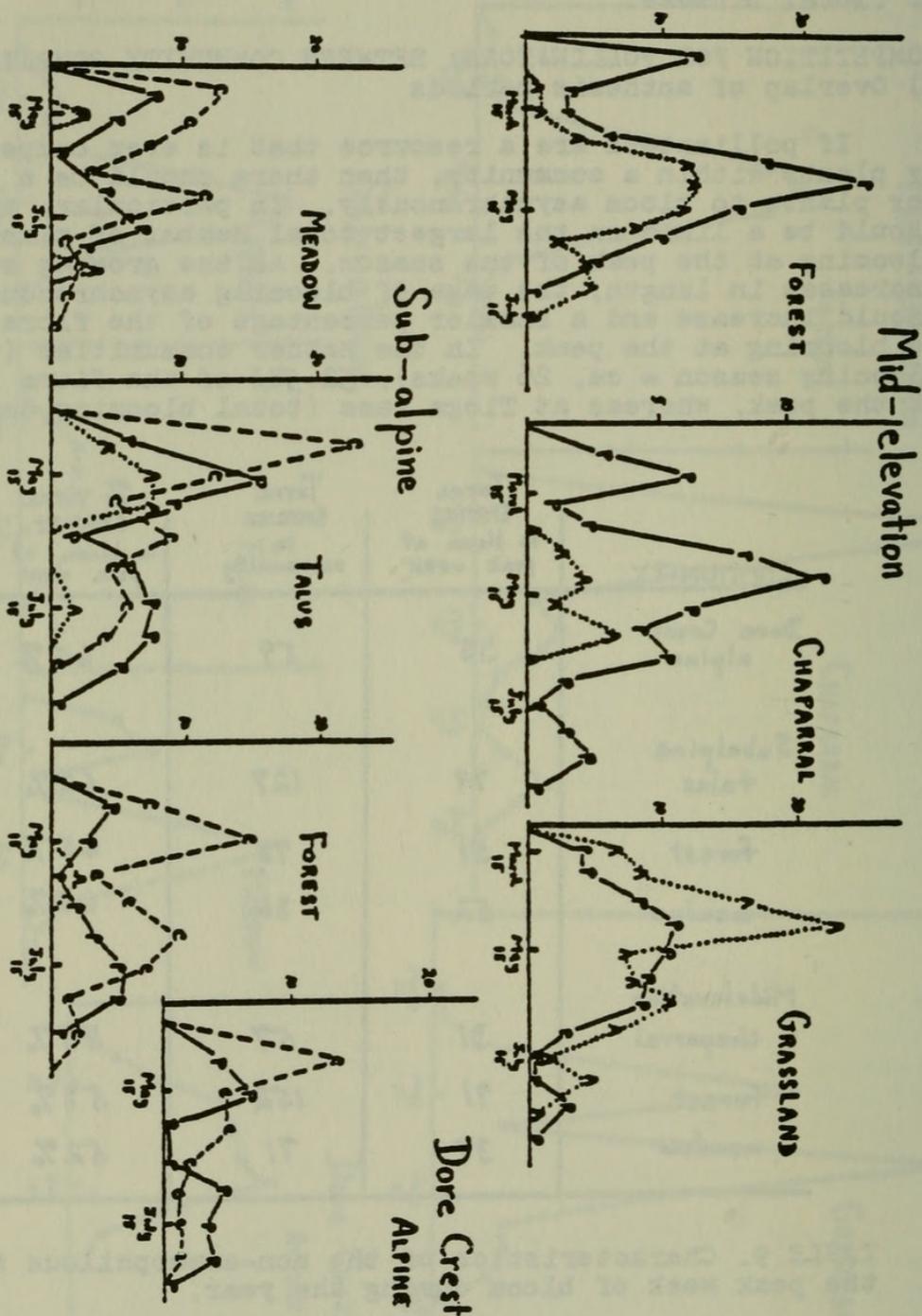
FIGURE 6. Timing of floral initiation by annual plants (A), incompatible perennial plants (P) and genetically compatible perennial plants (C) during the weeks indicated at the subalpine sites; all perennials are lumped (P) at the mid-elevation sites.

ca. 19 weeks) 60-65% of the flora is blooming at the peak
(Table 9).

   In the most species-rich community studied (Mather forest
= 152 spp./0.5 km^2) the total number of synchronously
blooming species is 91, whereas in nearly the least species-rich
community (Mather chaparral = 57 spp./0.5 km^2) the number is
only 31 (Table 9). Now, if plants must compete for pollinators
(as we assume), we would expect that in the Mather forest there
would be a larger percentage of the flora forced to rely upon
genetic self-compatibility at the peak of the bloom and we
would also expect that at the peak there would be more floral
morphologies adapted to a particular type of pollinator class.
Such species, by excluding all classes of pollinators save one,
greatly increase the relative worth of the floral reward and
in so doing facilitate the specificity of intraspecific pollen
transfer.

COMMUNITY	total length of blooming season (weeks)	number self-compatible species in bloom at peak week	% self-compatible species in bloom at peak week
Dore Crest alpine	18	25	70%
Subalpine talus	22	60	76%
forest	18	37	72%
meadow	18	37	71%
Midelevation chaparral	28	11	36%
forest	26	45	50%
meadow	24	22	60%

TABLE 10. Abundance of genetically self-compatible species
during the week of peak bloom as related to the length of the
blooming season.

b) Escape through Self-Compatibility

In the Mather Forest at the peak of the bloom 50% (45
species) are genetically capable of selfing in the event
pollinators are not attracted to the flowers, while 36%
(11 species) are self-compatible in the chaparral (Table 10).
This conforms to prediction, as does the rank order of all
seven communities except for the exceptionally low figure
of the Mather forest in comparison with the high altitude
communities. In this one exception, the low percentage of
self-compatible plants in the Mather forest is especially
peculiar though, since the total species in bloom and the
floral biomass peaks coincide in the forest.

c) Exclusionary Syndrome Insurance

The morphology of certain flowers when compared to the
span of morphological types represented by the pollinators
within an entire community, often clearly excludes certain
types of pollinators. Other features of flowers, such as
nocturnal anthesis, differentially poisonous nectar and
particularly aberrant scents and nectar compositions, also
function to attract pollinators of certain types exclusively.
Generally only one pollinator type visits flowers of these
species, one distinctly morphologically and behaviorly
adapted to a particular syndrome. However, many other plant
species (not specialized in any noticeable manner) are
visited by only one pollinator type. Usually these are
species which happen to be low on the general rank preference
order of the community; the pollinator type which visits
them in any one locality is not particularly adapted to that
particular plant species, and in fact the pollinator type of
these infrequent visitors would be expected to vary between
locations as conditions of local competition change. Hence
"exclusionary flower" is defined primarily on the basis of
morphology, rather than localized results of flower visitation
observations, although such a deliniation must in fact be
somewhat circular.

In the Mather forest there are six distinct exclusionary
syndromes (flowers adapted for pollination by: bumblebee (12),
small bee (8), beefly (7), mosquito/gnat (4), moth (2),
hummingbird (2)) at the blooming peak, whereas in the
chaparral there are only four (adapted for: hummingbird (4),
small bee (4), bumblebee (2), moth (1)). Throughout the
year, there are a total of 48 species with ± exclusionary
flowers in the forest, 16 in the chaparral (Table 11).
However, since there are three times the number of entomo-
philous and ornithophilous species resident in the forest as
the chaparral (Table 9), the percentages of exclusionary
flower types are not significantly different (Mather chaparral
28%; forest 31%). The community with the largest percentage
of exclusionary-flowered species (42%) is the Mather grassland,

COMMUNITY	Total Species with Exclusionary Morphologies at peak week	Total Species with Exclusionary Morphologies through year	% species with Exclusionary Morphologies through year	Different Syndromes at peak week (c polyphilic)	most important exclusionary morphologies through year	most important exclusionary morphologies at peak week
Dove Crest alpine	8	10	18%	1	SB >> BB, BT	BB
Subalpine talus	25	37	30%	3	SB >> BT, BB	BB > SB > MT
Subalpine forest	23	27	34%	1	SB > BB, HB	BB
Subalpine meadow	18	22	25%	1	BB > SB > M	BB
Midelevation chaparral	11	16	28%	4	SB > BB > BM	SB > BB, HB
Midelevation forest	25	48	31%	6	BM >> SB > BB	SB > BB, BM
Midelevation meadow	15	30	42%	5	SB >> BB, BM	SB > BB > BM

TABLE 11. Plant species with exclusionary floral morphologies at the different experimental sites. Classes of morphological syndromes: BB=bumblebee, SB=small bee, BT=butterfly, MT=moth, HB=hummingbird, M=muscoid fly.

which possesses an intermediate number of total species in
the community and an intermediate number of total species in
bloom at the flowering peak.

Therefore, in a cross-community comparison these measures
are either inappropriate or they imply that plants in these
California communities are not responding phenologically to
competition for pollinators. However, it should be noted at
this point that Moldenke (1975) has pointed out that the
percentage of self-compatible species within the total flora
is a relatively constant characteristic of community physiog-
nomy and is independent of total number of species and length
of blooming season.

COMMUNITY	GENETICALLY INCOMPATIBLE SPECIES that bloom off peak	GENETICALLY SELF-COMPATIBLE SPECIES		% GENETICALLY SELF-COMPATIBLE SPECIES		% COMPATIBLE SPECIES which HABITUALLY SELF	
		blooming off peak	blooming at peak	blooming off peak	blooming at peak	blooming off peak	blooming at peak
Dore Crest alpine	13	25	25	62%	70%	80%	72%
Subalpine talus	20	34	60	63%	76%	64%	64%
forest	13	20	37	61%	72%	50%	53%
meadow	12	20	37	64%	71%	55%	48%
Midelevation chaparral	9	2	11	22%	36%	0%	28%
forest	10	26	45	72%	50%	20%	27%
meadow	5	15	22	75%	60%	33%	80%

TABLE 12.   Breeding system of plants which are in bloom during
the peak week of bloom relative to the systems employed by all
species in bloom at least two weeks earlier or later throughout
the year.

COMPETITION FOR POLLINATORS: WITHIN COMMUNITY COMPARISONS
a) Selfing

     Within any community, the predicted effects of competition
for pollinators can be tested for by observing the relative
frequency of genetic self-compatibility, frequency of selfing
and bee feeding habits as the season progresses. Table 12
demonstrates that the species richness of genetically self-
compatible plants is greatest at the peak in all communities.
At Mather the percentage of plants that are self-compatible
is usually greatest flanking the peak, but even more signifi-
cantly however, the percentage of those plants that are both
self-compatible and that habitually or obligately self is much
greater at the peak (Table 12). At subalpine and alpine
localities there is no significant difference in the habitual
selfers on- and off-peak; an artifact due to the extremely
long individual blooming seasons and the broad community
peak, even though the proportions of self-compatibility are
about 10% greater at the peak. At the mid-elevation sites,
then, 27-80% of the self-compatible plants at the peak of
the bloom are forced to self habitually. These species are
the losers in the face of superior competition for pollinators.

b) Overlap of Anthesis Periods

     If plants are indeed generally competing for pollinators,
then in a community characterized by generalist pollinators
the peak number of synchronously blooming plants should be
lessened. All plant communities at subalpine and alpine
regions in California are severely pollinator-limited (Moldenke
1975, 1976), mid-elevation grassland and chaparral being
pollinator-rich. However, the Mather grassland and chaparral
support respectively 37 and 31 synchronously flowering species
whereas the average for Tioga Pass and Dore Crest is 51,
even though total plant species richness is much lower (Table 4).
Within the Mather communities, the forest relies heaviest on
generalist-feeding bumblebees and beefly pollinators. It
is the forest which demonstrates the highest number of
synchronously blooming plant species, two to three times the
number in adjacent communities characterized by many specialist-
feeding pollinators within the total resident fauna.

c) Specialist-Feeding Pollinators & Exclusionary Syndromes

     Discrepancies from our predictions, however, could be
permissable if species of plants at the peak of the bloom are
efficiently serviced by specialists. In the Mather forest
community, during the peak of the bloom 4-8 times as many
plant species are visited by specialist-feeding bees than
during the periods March 1 - April 30 and July 1 - September 1.
In addition, during the peak from May 1 - June 30 there are
5-6 (+ polyphilic) different specialized exclusion floral
morphologies in use, a number which decreases precipitously
towards either tail (Table 13). If we assume that the selec-
tive advantage which produces specialized floral morphologies

is the efficient exclusion of many potentially inefficient
pollinators, with the net result of protecting a large reward
for the selected pollinator, then the selective advantage of
such exclusion-flowers should have been greatest precisely
when there was the highest level of synchrony from competitor
flower species. The lower values of synchronous species
blooming in the Mather grassland and chaparral are correlated,
of course, with a much smaller total entomophilous and
ornithophilous flora; however, the same trends in exclusionary-
flowered species and specialist bee pollinators are present
(Table 13).

In all the Sierra Nevada communities studied, flowers
which bloom at the beginning or end of the season very seldom

COMMUNITY	Peak weeks of specialist-feeding bee activity	Percentage of blooming species serviced
Dore Crest alpine	—	—
Subalpine talus	6/7 - 6/30	22-25%
forest	6/23 - 7/15	25%
meadow	5/21-5/23+4/15-6/23	18-20%
Midelevation chaparral	{3/7 - 4/7 + 5/30} {+ 7/15 - 7/23}	50-100%
forest	5/15 - 6/15	20-25%
meadow	4/7 + 5/28-6/15	25-33%

TABLE 13. Dates (month/day) encompassing periods of highest
specialist-feeding bee activity relative to the percentages
of the non-anemophilous flora actually serviced during that
specific period.

TABLE 14: Exclusionary Flowers

	Mar 1	Apr 1	May 1	June 1	July 1	Aug 1	Sep 1

DORE CREST
- #specialist-visited species: 5 7 11 11 7 4 5 4 2
- #exclusionary syndromes: 1 2 2 2 2 2 2 1
- #exclusionary species: 4 7 7 7 7 7 6 1
- exclusionary species/total spp.: + + +

TIMBERLINE TALUS
- #specialist-visited species: 4 14 19 14 15 14 12 10 3 2
- #exclusionary syndromes: 3 5 5 5 5 5 4 3 2
- #exclusionary species: 9 24 24 24 25 26 24 10 7 2
- exclusionary species/total spp.: + + + + + + .

TIMBERLINE FOREST
- #specialist-visited species: 4 5 6 7 10 11 8
- #exclusionary syndromes: 2 3 4 5 5 5 4 3 2
- #exclusionary species: 2 9 12 15 17 23 22 14 6
- exclusionary species/total spp.: + + +

TIMBERLINE MEADOW
- #specialist-visited species: 3 5 7 8 6 8 7 4 2
- #exclusionary syndromes: 2 3 3 3 4 4 4 2 3 1
- #exclusionary species: 3 9 9 13 15 13 16 6 5 1
- exclusionary species/total spp.: + +

MATHER CHAPARRAL
- #specialist-visited species: 3 6 6 8 6 8 11 9 3 2 11 3 2 1
- #exclusionary syndromes: 2 2 3 4 4 4 4 1 1 1
- #exclusionary species: 3 3 6 11 6 7 5 1 1 1
- exclusionary species/total spp.: . * * * * * * * . . .

MATHER FOREST
- #specialist-visited species: 1 2 2 2 9 11 17 14 7 3 2 2
- #exclusionary syndromes: 1 3 4 5 6 6 5 5 4 1 1 1
- #exclusionary species: 1 3 5 12 25 35 31 11 6 1 1 1
- exclusionary species/total spp.: * * * * . .

MATHER MEADOW
- #specialist-visited species: 1 3 5 6 6 6 5 5 2 2 1
- #exclusionary syndromes: 2 4 5 5 4 3 3 2 1 1 1
- #exclusionary species: 2 9 11 15 14 9 11 2 1 1 1
- exclusionary species/total spp.: * + + + * + *

possess exclusionary morphologies (Table 14). The ratio of
exclusionary species to total entomophilous and ornithophilous
species at the week of peak bloom is approximately 26% in all
communities (range = 19-41%; Table 14). In four of these
communities this ratio is nearly equal to the ratio of total
exclusionary species to total species for the entire year;
in the subalpine forest, Mather forest and Mather grassland
the ratio at the peak week is considerably less. In all
communities, however, the total number of different exclusionary
syndrome types is disproportionately highest at the peak weeks
of synchronous bloom.

d) Modification of Compatibility Strategies

    Perennial plants throughout most regions of California
are generally genetically incapable of setting selfed seed.
If it is true that competition for pollinators is important
in determining the reproductive strategies of plants, then
at the peak of the bloom there should be a selective advantage
accruing to perennial species which can evolve the ability to
set selfed seed if competitors induce all of the available
pollinators away. (There are, of course, long-term costs
involving reduced population polymorphism or individual
heterozygosity which will usually counter such a shift on
the part of the entire community.)

    In all three Mather communities the incidence of
genetically self-compatible perennials coincides with the
blooming peak (Figure 7). At the Tioga Pass and Dore Crest
sites, most perennials are genetically self-compatible or
apomictic (Moldenke 1975) and hence determine the shape of
the anthesis curve. In the subalpine meadow and talus-scree
the incidence of genetically incompatible perennials is
highest in the time periods immediately flanking the blooming
peak; in the subalpine forest the incidence curve of
incompatible perennials is broad and flat, overlapping the
peak but also disproportionately prominent after the peak
(Figure 7). In the alpine community, the incidence of
incompatible perennials is evidently equivalent to the
periodicity of self-compatible perennials, but the very low
total species richness and long average blooming season
per species obscure resolution.

TABLE 14. Relative abundances of exclusionary-flowered species
during the week of peak bloom and percentage of the total
non-anemophilous flora of the experimental sites. Total number
of plant species visited by specialist-feeding bees during the
week in question. *= greater than 33%; += greater than 20%;
•= greater than 33%, but total number of species less than 2.
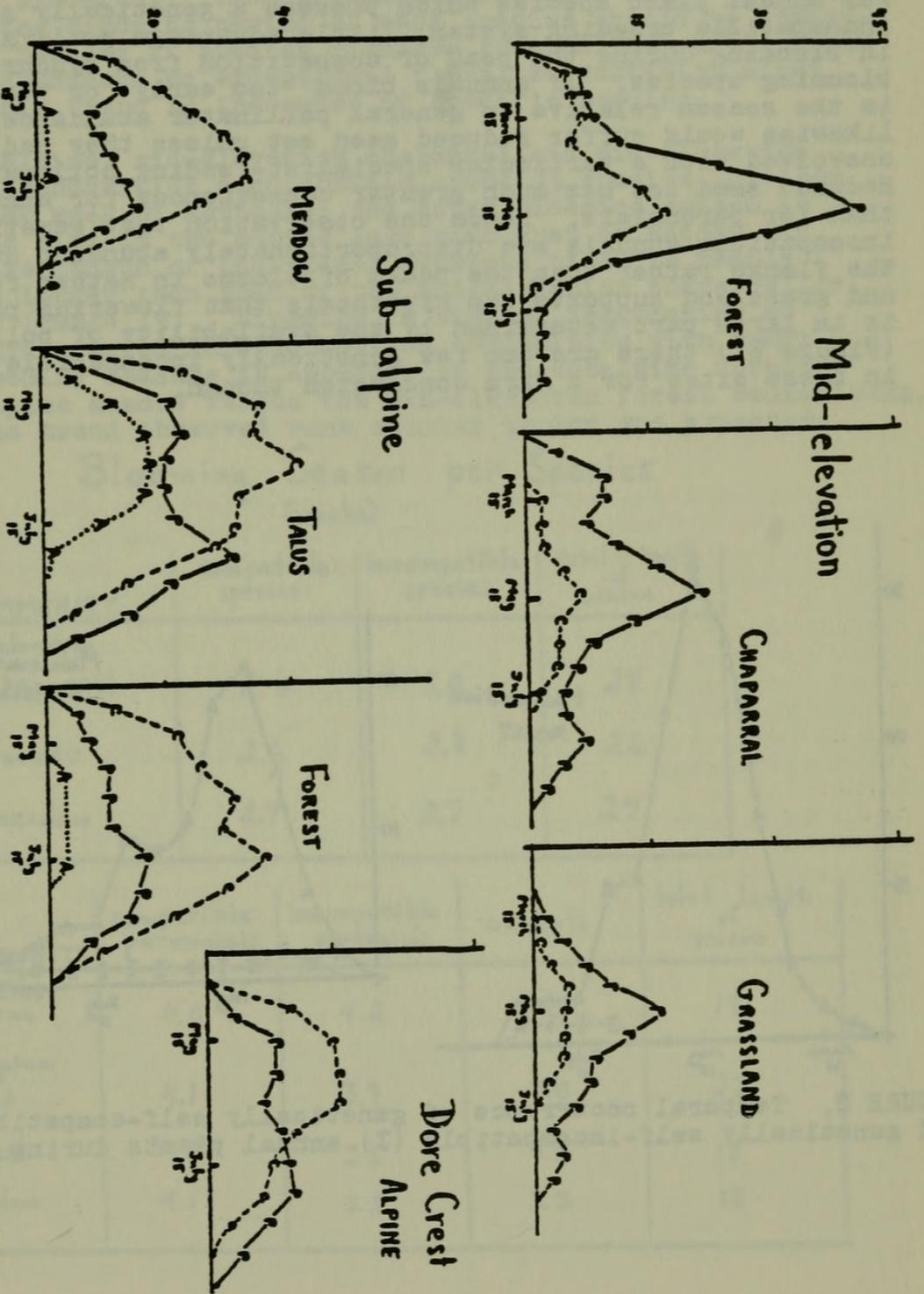
FIGURE 7. Total species of genetically self-compatible perennials (C), self-incompatible perennials (P) and annuals (A) in bloom throughout the weeks of the blooming season in subalpine and alpine localities; at mid-elevation only all genetically incompatible (P) and all genetically self-compatible (C) plant species are indicated.

On the other hand, annual plants are usually genetically
self-compatible in California. Though there are too few
annual plants at subalpine and alpine localities for analysis,
annual plants are abundant in the Mather forest and grassland.
For annual plant species which possess a genetically self-
incompatible breeding system, little advantage would accrue
in blooming during the peak of competition from synchronously
blooming species. If annuals bloom "too early" or "too late"
in the season relative to general pollinator abundance, they
likewise would suffer reduced seed set unless they had
coevolved with a particular specialist-feeding pollinator.
Reduced seed set has much greater consequences for annuals
than for perennials. Hence the observation that genetically
incompatible annuals are disproportionately abundant during
the flanks rather than the peaks of blooms in Mather forest
and grassland supports the hypothesis that flowering phenology
is in large part determined by the availability of pollinators
(Figure 8); there are too few genetically incompatible plants
in these sites for a firm conclusion though.
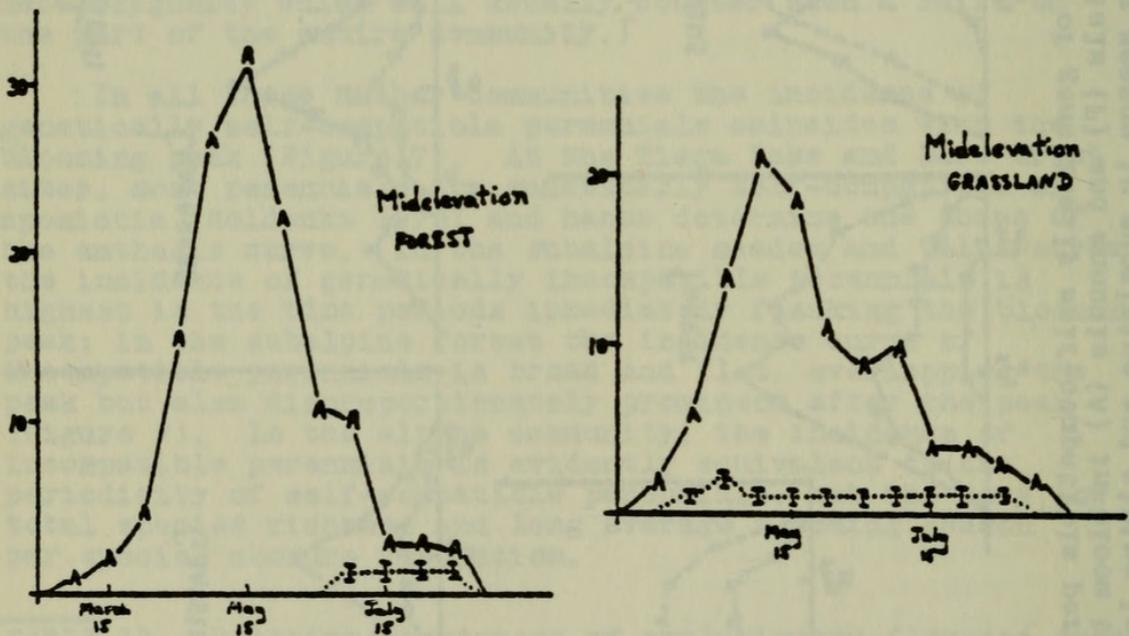
FIGURE 8. Temporal occurrence of genetically self-compatible (A)
and genetically self-incompatible (I) annual plants during the year.

e) Length of Blooming Period

If there is a maximum theoretical value of niche overlap
(anthesis synchrony), then in communities with short blooming
seasons, the blooming period of each species should be corres-
pondingly reduced if species richness remains the same. High
relative abundance or exceptional floral attractivity might
counter this trend in instances of specific species.

The alpine, mid-elevation chaparral and mid-elevation
grassland communities each contain about 35 species in bloom
at the peak week of anthesis; the total blooming season at
the alpine site is two months less than that at Mather but
the average length of individual anthesis times is nearly
two weeks longer than that of the mid-elevation chaparral or
grassland (Table 15). Likewise, a similar lengthening of
the blooming period in species-rich communities with short
total blooming seasons is apparent in the subalpine forest
and subalpine meadow versus the mid-elevation forest comparisons.
Hence, the trend observed runs counter to the one expected.

Blooming Season per Species (weeks)

COMMUNITY	compatible species	incompatible species	total length of season
Midelevation chaparral	2.6	3.0	28
forest	2.6	2.8	26
meadow	2.7	2.7	24

COMMUNITY	compatible perennials	incompatible perennials	annuals	total length of season
Dore Crest alpine	4.0	4.2	—	18
Subalpine talus	4.1	3.9	4.0	22
forest	4.1	3.5	4.5	18
meadow	4.1	3.5	3.3	18

TABLE 15. Average length of blooming season for an individual
plant species in each of the experimental regions.

However, another contrasting possibility conforming to predictions would be for selective advantage to accrue to genetically compatible plants under the conditions of the shorter blooming season. This alternative apparently is the more usual happening, since the shortening of the blooming season is indeed correlated at all seven sites with an increasing total percentage of self-compatible species.

In carrying this line of reasoning one step further, we would hypothesize that in pollinator-poor communities the length of blooming period for each pollinator-limited (genetically incompatible) species should increase relative to species capable of selfing. We observe, in fact, the opposite tendency in all the alpine and subalpine communities. The mean length of anthesis period for incompatible plants in all high-elevation communities is 3.8 (range = 3.5-4.2) weeks, whereas it is 4.1 (range = 4.0-4.1) for the compatible perennials (Table 15).

POLLINATOR BEE DISTRIBUTION & COEVOLUTION OF SPECIALIST
FEEDING HABITS

Bees are the effective pollinators of an average of 52% of the Timberline and 66% of the Mather plant species (including anemophilous species). Not only do they account for the pollination of more species of plants than any other group, they are also, by far, the most species-rich assemblage of floral visitors (Moldenke 1976). In addition, since many species will consistently visit the flowers of only one species or genus of plants, regardless of density or the abundance of competing flowers, many bee species assume a unique pollinator role, far out of proportion to their often small sizes and limited numbers.

There are approximately 520 species of pollen-collecting bees resident in the Sierra Nevada. The southern half of the mountain chain is the most species rich, supporting 1.25x the number of species in the northern region (ca. 350), while the alpine regions support only about 0.5x the number of the northern forested and scrub regions (Moldenke 1976). The bee fauna of the Sierra Nevada demonstrates a very low degree of endemicity (ca. 6%; Table 16). Within the Sierra Nevada the range of most species includes the entire length of the mountain chain, with 5% distributed additionally throughout only the coastal mountains of California as well. Thirteen percent have ranges including all the mountainous regions along the Pacific Coast north into Canada; 29% are distributed throughout all the mountains of western USA and Canada; and 8% are distributed transcontinentally through Canada and the northern United States to the Appalachians and the East Coast. Nearly all of the Sierran bees with ranges that basically

DISTRIBUTION OF SIERRAN BEES

	transcontinental n.NAm.	montane US&Canada n.Am.	high alpine US & Canada n.Am.	Great Basin southern California n.Am.	arid southwest USA	Pacific Coast wde. only	all California endemic	dcit.	endemic alpine Sierran
COLLETIDAE									
Colletinae (12)	5	4	4	0	2	1	0	0	0
Hylaeinae (15)	4	5	5	2	3	0	1	0	1
MELITTIDAE (2)	0	0	0	0	0	0	0	1	1
ANDRENIDAE									
Andreninae (100)	12	12	34	6	12	2	4	16	0
Panurginae (53)	0	0	1	0	0	13	2	4	0
HALICTIDAE									
Halictinae (26)	2	2	8	0	8	22	7	4	13
Dufoureinae (2)	0	0	2	0	1	1	0	0	0
MEGACHILIDAE									
Anthidiini (24)	1	1	11	1	12	0	7	0	6
Megachilini (154)	13	13	59	7	33	21	7	28	10
ANTHOPHORIDAE									
Anthophorinae (65)	4	4	18	0	21	19	9	12	1
Xylocopinae (4)	4	4	0	0	0	0	1	3	2
APIDAE									
Bombini (2)	8	9	7	1	2	0	0	5	0
519	47	153	18	71	100	35	91	50	39

TABLE 16. Distributional ranges (inclusive) of bee species inhabiting the Sierra Nevada. Cleptoparasitic bees excluded from analysis.

which patterns of floral dependencies have evolved within the
Sierra Nevada. The floral choice preferences of many bees are
reasonably well-known within California, but since there has
been relatively less work done in other regions of the
American West, one cannot determine with assurance whether
the flowers utilized in regions outside of California are the
same or not. Bees with apparent generalized feeding habits
over broad geographic expanses may be specific to single
species locally; and vice-versa. When it is well-established
that certain widespread bees are indeed specialized feeders
on the same plant genus throughout all of western United
States, for instance, I know of no way to distinguish the area
where the floral dependence first evolved and the areas to
which it subsequently spread. Presumably such species may
belong to alliances that originated in the montane Rocky
Mountains and subsequently spread westward to occupy the
Sierra Nevada.

However, the segment of the bee fauna of the Sierra
Nevada which is either strictly endemic or confined to California
and immediately adjacent regions and has phylogenetic origins
traceable either within California itself or to the south-
western deserts, provides a partial explanation of the
pattern of coevolutionary inter-relationships and how they
evolved. Approximately 33% of the total bee fauna of the
Sierra appears to be generalized feeders; only 5% of the
locally evolved and endemic species seem to be generalized
feeders. Most of the Sierran bee species with generalized
feeding tendencies are apparently part of transcontinentally
or Holarctically distributed genera (e.g., _Bombus_, _Evylaeus_,
Dialictus, _Hylaeus_, _Ceratina_); since they demonstrate
generalized feeding traits one might expect that their
distributions would be less constrained and that their
ancestries would be less easily traceable to a particular
include the entire Great Basin vegetation, are restricted
in large part to the alpine and high-elevation east-facing
slopes. Seventeen percent are distributed primarily in the
montane chaparral and grasslands of southern California;
within the Sierra Nevada these species are largely confined
to the chaparral regions of Kern and Tulare Counties. Very
few resident species are primarily distributed throughout
the arid southwestern United States, though a large percentage
of the Sierran bees have evolutionary ancestries clearly
traceable to these southern arid regions of the United States
and northern Mexico (about 40 resident genera and subgenera:
Moldenke 1976b).

The wide distributions of most bees inhabiting the Sierra
Nevada, renders difficult the task of determining precisely

TABLE 17

SIERRAN POLLEN-COLLECTING BEES

feeding specialization	#species	#independently evolved groups
— polyleges —	170(6?)	47
— unknown —	55	—
Summer/fall composite	75	21
Lasthenia	1(1?)	2
Stephanomeria	2	2
Spring dandelions	4	1
Sunflowers	4	4
Lupinus/Lotus/Astragalus	25(2?)	8
Trifolium	7	4
Psoralea	1	—
Clarkia	9(6samples)	3
Cayophytum	5(1?)	2
Camissonia	3(1?)	3
Phacelia	19	9
Eriodictyon	2	2
Cryptantha	10	3
Salix	12(1?)	8
Ceanothus	7(?)	7
Lomatium/Sanicula	3	2
Cruciferae	2	2
Mimulus	2(1?)	2
Salvia/Lepechinia/Trichostema	1	1
Penstemon	9	3
Campanula	2	2
Limnanthes	2	2
Gilia/Linanthus	6(1?)	5
Navarretia	—	—
Arenaria	—	—
Ribes	—	—
Symphoricarpos	—	1
Zygadenus	—	—
Eschscholzia	9	3
Monardella	2	2
Eriogonum	—	1
Peridridia	(1?)	2
Potentilla	—	1
Adenostoma	—	2
Calystegia	—	1
Malacothamnus	6	5
Sidalcea	1	—
Mertensia	2	2
Arctostaphylos	2	2
Ranunculus	5	3

source area. The widespread genus <u>Dianthidium</u>, is comprised
in large part of specialized feeders; however, <u>D</u>. <u>dubium</u> of
the Sierra Nevada belongs to a complex of closely related.
(and probably primitive) group of species which are all
generalized feeders.

As Table 17 reveals, there are specialist-feeding bees
associated with at least 48 plant genera throughout the Sierra
Nevada (57% specialists, 10% feeding preference unknown -- of
total bee fauna). Of the bees whose origins we can trace
with some degree of accuracy, there are four basic patterns
to their coevolutionary lineages of host associations. One
large group of species (28) represents Sierran-endemic
specialists which feed on the same group of plants as their
closest relatives do elsewhere; the effected plant genera are
widespread (e.g., <u>Calochortus</u>, <u>Camissonia</u>, spring dandelions.
<u>Eriogonum</u>, <u>Eschscholzia</u>, fall & summer composites, <u>Lupinus</u>/
<u>Astragalus</u>, <u>Penstemon</u>, <u>Phacelia</u>). Another group (at least 9)
of these specialist bees are quite probably derived directly
from ancestors with broadly generalized feeding tendencies;
with the exception of <u>Centris</u> <u>rhodomelas</u> on <u>Psoralea</u> and
<u>Ashmeadiella</u> <u>salviae</u> on <u>Salvia</u>/<u>Lepechinia</u>/<u>Trichostema</u>, the
plant genera concerned have been the realized objective of
coevolutionary feeding switches on many occasions (e.g..
<u>Clarkia</u>, <u>Eriogonum</u>, <u>Eschscholzia</u>, <u>Gilia</u>, <u>Lasthenia</u>). The
third group (27 species) embraces host switches between
genera within the same family (Compositae, Hydrophyllaceae/
Boraginaceae, Malvaceae, Onagraceae, Polemoniaceae). With
the exception of the shifts from <u>Eriastrum</u> and <u>Sphaeralcea</u>,
most involve radical changes in the timing or emergence dates
to be synchronous with the new host (Table 18). Another
clearly defined class (15 species) of host-plant switches
involves radical taxonomic changes but little if any temporal
displacement (Table 19). In only two cases (<u>Camissonia</u> to
<u>Ranunculus</u>; <u>Sidalcea</u> to <u>Clarkia</u>) do the old and the new hosts
look strikingly similar to the human eye. There are 18 other
instances of circumstantial host-switches involving a new host
very dissimilar from whatever the ancestor is likely to have
specialized upon (host ancestry unknown, presumably a
specialist but no relatives feeding on anything at all related)
and additionally within the genera <u>Andrena</u> (9 species).
<u>Panurginus</u> (1 species) and <u>Micralictoides</u> (2 species) there
are specialized feeders whose ancestry is obscure (the ancestors
may have been generalized feeders or perhaps specialists on
very unrelated plant groups).

TABLE 17. Total number of species and total number of different
   phyletic lineages of specialist-feeding bees associated with
   indicated plant genera within the Sierra Nevada. Grasslands
   within the Central Valley proper excluded from analysis.

Though such studies on a wider geographic scale have not been undertaken, presumably these same four classes of coevolutionary relations with host plants are encountered in all regions that support specialist-feeding bees. A full listing of the pollen-collecting bees resident in the Sierran region is given in the Appendix; plant host data are supplied wherever known. The large genera Dialictus, Andrena, Panurginus, and Osmia are currently under taxonomic revision; Evylaeus and Emphoropsis are in need of revision still.

OCCURRENCE OF CORNUCOPIA SPECIES

As pointed out in previous publications (Moldenke 1975, 1976), in all communities the distribution of pollinator species per plant is log-normal, that is there are very large numbers of plants serviced by 0-2 pollinator species, much fewer by several pollinator species and extremely few species of plants serviced by disproportionately large numbers of pollinator species. "Cornucopia species", defined as species supporting 5x the average number of pollinators per species for the entire community (Moldenke & Lincoln 1979), are basically the result of the differential success of the different species in competing for pollinators.

Coevolutionary Host-Plant Switches

I   range extension associated with same/similar plant
    genus in ancestral area   (28)

II polylectic generalized-feeding ancestor gives rise to
    specialized-feeding descendent   (9)

III range extension associated with a switch to a
    different (but confamiliar) genus
         —usually involving a shift in seasonal emergence
         time

IV a shift of hosts to a taxonomically unrelated genus
         —usually not involving a temporal switch
         —often between visually very distinct groups

TABLE 18. The four types of coevolutionary host association demonstrated by bees within the Sierra Nevada.

GROUP III HOST-SWITCHES:

Camissonia → Clarkia	Andrena (Onagandrena)
Camissonia → Gayophytum	Dufourea (4)
Camissonia → Clarkia	Andrena (Diandrena)
Camissonia → Gayophytum	Andrena (Onagandrena)
Oenothera → Clarkia	Megachile (Derotropis) (3)
Sphaeralcea → Malacothamnus	Diadasia
Sphaeralcea → Sidalcea	Diadasia (2)
Eriastrum → Gilia	Perdita (Glossoperdita)
Eriastrum → Navarretia	Perdita (Glossoperdita)
summer composites → Stephanomeria	Melissodes (Callimelissodes)
summer composites → Lasthenia	Andrena (Stenandrena)
Phacelia ←?→ Nemophila	Dufourea (1)
Phacelia → Cryptantha	Proteriades (7)
Eriodictyon ←?→ Phacelia	Nomadopsis (Micronomadopsis) (1)

GROUP IV HOST-SWITCHES:

Larrea ?→ Adenostoma	Hesperapis (Amblyapis)
Camissonia ?→ Arenaria	Andrena (Diandrena)
Camissonia → Ranunculus	Andrena (Diandrena)
Lasthenia → Limnanthes	Andrena (Callandrena)
Ranunculus → Limnanthes	Panurginus
Ranunculus → Nemophila	Panurginus (?)
Calochortus ?→ Potentilla	Nomadopsis (Nomadopsis) (2)
Potentilla → Monardella	Nomadopsis (Nomadopsis)
Calochortus ?→ Eriodictyon	Nomadopsis (Nomadopsis)
Campanula ←?→ Calochortus	Dufourea (2)
Sphaeralcea → Clarkia	Diadasia
summer composites → Clarkia	Melissodes (Callimelissodes)
Lasthenia → Limnanthes	Andrena (Hesperandrena)

TABLE 19. Examples of coevolutionary host association switches
hypothesized, corresponding to the latter two categories in
Table 18. Numbers in parenthesis indicate the total number of
species within the group endemic to the Sierra Nevada. Many
of these examples must be regarded as tentative in the light of
present knowledge of the recent phylogeny of bees within California.

Since all of the species (Table 20) have generally open polyphilic flowers that can be utilized by any available flower-feeder, their temporal occurrence during the season is a clear clue to the strength of competition for pollinators. Polyphilic flowers could not be cornucopias if they bloomed at the peak of synchronous bloom unless they were the overwhelming contributant to the floral biomass as long as pollinators were abundant and diverse and utilizing most of the plant species present. Cornucopias are very seldom the dominant plants in the communities studied, hence the fact that all cornucopia species (14) at Mather occur primarily during the late summer and not during the peak follows expectation (Table 20). At

CORNUCOPIA SPECIES

	minimum number of species defining a cornucopia	# Cornucopia species	temporal occurrence of cornucopia anthesis periods
Dore Crest	16	1	peak
Subalpine Talus	37	7	peak
Forest	32	2	peak
Meadow	14	4	peak
Mid-Elevation Chaparral	55	3	2 at peak 1 later than peak
Forest	20	8	late skew
Grassland	43	.3	bimodal around peak

TABLE 20. Abundance and temporal occurrence of cornucopia species at the experimental sites. Cornucopia species are defined as species visited by five times the average number of flower-visiting species characteristic of that community. Species are: Erigeron sp.; Eriogonum spp. (2), Sphenosciadium, Ligusticum, Potentilla, Senecio, Solidago; Ligusticum, Potentilla glandulosa; Veratrum, Polygonum bistortoides, Potentilla, Salix, Ranunculus californicus, Perideridia, Solidago; Clarkia spp. (2), Chamaebatia, Monardella, Gilia capitata, Eriogonum nudum, Thysanocarpus, Horkelia; Eriodictyon, Ceanothus integerrimus, Haplopappus. (in order indicated on Table)

Tioga Pass and Dore Crest the cornucopia species occur temporally during the peak of synchronous bloom. These high altitude localities are so pollinator-limited, 1/14 to 1/100 respectively tha number of pollinators at Mather communities (Moldenke 1975), that they represent basically the only species which have successfully attracted any pollinators at all; the average number of pollinator species per cornucopia species must be at least 40 at Mather but is only 24 at these high-altitude sites.

DISCUSSION

The data cited in this analysis were not collected specifically for the approach taken herein. I am of the firm conviction that any such studies must quantify micro-environmental and year-to-year variability in order to be sufficiently rigorous to purport to be more than introductory hypotheses. Specifically, such a study must quantify the initiation of anthesis by a species within an area, the initiation and cessation by each component population thereof, and the average length of anthesis (and variance thereof) by individual plants. Since this type of information is not available to my knowledge, I have utilized data from my own field studies to outline what I hope to be interesting approaches that subsequent researchers may test. Likewise, I have not employed statistical tests in this approach, lest they impart the impression of rigor that the data base does not warrant.

SUMMARY

Competition between plants for pollinators increases the blooming season of plant species in pollinator-limited environments, thus increasing the percentage of the flora that is blooming during any given week. Perennials, then, have a premium on blooming immediately following the dormant season. In communities that are not seriously pollinator-limited, floral initiation time is not pulsed and rather conforms to the Central Limit Theorem, implying independent control on the flowering phenology of each species. As the total length of permissible blooming season lengthens, the peak of maximum synchronous bloom is delayed. The peak in total available community floral biomass is not always correlated to maximum number of species in bloom; additionally, some of the least important contributants to community floral biomass are the most heavily visited by pollinators and vice-versa. Though annual plants as a group might be expected to differ signif-icantly from perennial plants in the timing of their blooming season, in fact they do not.

Though competition for pollinators in communities with progressively more total species would be expected to produce a larger percentage of self-compatible species (the "losers") at the peak of the bloom and a larger emphasis on exclusion floral morphologies (the winners, or the ones that can "afford an insurance policy"), this in fact does not take place. The total percentage of self-compatible species in a community is determined by community type. The percentage of species with exclusion flowers of the total species is apparently consistent in all Sierra Nevada communities.

Within all communities the proportion of genetically self-compatible species that is in fact unvisited by pollinators and therefore has to habitually self is highest at the peak of synchronously blooming species. Additionally, this competition for pollinators is revealed in the disproportionate occurrence of genetically incompatible annual species flanking the anthesis peak, while the disproportionate abundance of self-compatible perennial species occurs at the anthesis peak.

Plant communities which are pollinator-limited have much fewer total entomophilous and ornithophilous species at the peak of anthesis, since a larger percentage of the community species total is wind-pollinated; the precise number of successfully animal-vectored species in a community varies widely and does not cluster about a particular limit independent of community type. A mechanism which permits the successful synchronous outcrossing at the peak of bloom is the disproportionate number of plants serviced by specialist-feeding bees; this allows efficient pollination even when in low density or when competing species may have successfully usurped all the generalist pollinators. Specialized-feeding habits of course would not evolve in bees, if it were not competitively forced upon them by competition for their floral resources as well; more species of specialist-feeding bees are in fact active during the peak synchrony of anthesis than at any other period.

Most of the bees native to the Sierra Nevada are rather widespread throughout mountainous western United States, and endemicity is very low. Bee species endemic to montane California and with phylogenetic lineages traceable to California itself or desert southwestern U.S.A. are largely specialized in their feeding habits. They demonstrate four patterns of coevolutionary host-specialization and switching: specialist-feeding species on hosts with relatives on congeneric hosts in adjacent areas; specialist-feeders on plant genera commonly associated with many specialist-feeding groups, evolved directly from generalist feeders; specialist-feeders on different genera with different anthesis times within the same plant family; and specialists on species of plants blooming synchronously with the original hosts, but taxonomically and morphologically distinct.

BIBLIOGRAPHY

Moldenke, A. R. 1975. Niche specialization and species diversity
        along a California transect. Oecologia 21: 219-242.

                1976. California pollination ecology and
        vegetation types. Phytologia 34: 305-361.

                1976b. Evolutionary history and diversity of
        the bee faunas of Chile and Pacific North America.
        Wasmann Journal of Biology 34: 147-178.

Moldenke, A. R. & P. Lincoln. (in press) Pollination ecology
        in montane Colorado: a community analysis.

APPENDIX: Bee fauna of the Sierra Nevada, pollen-plant sources given
where known. Due to the very preliminary state of knowledge of the
biology of these many species, an indication of the relative degree
of assurance about their pollen-gathering habits is noted: F=
established fact; IV= data insufficient, needs verification but
quite probably correct; ZV= extremely little direct evidence,
definitely needs verification, conclusion based on indirect
evidence; R=indirect evidence based on the clearly established
behavior of closely related species. Cleptoparasitic bees not
included in table. *=species not clearly established as living
within the Sierra per se. VR=very rare; R=rare; IF=infrequent,
but locally abundant; FR=frequent; EA=extremely abundant.

Colletes californicus* - Phacelia,F - AB
Colletes compactus* - Compositae,IV A - R
Colletes consors pascoensis - Phacelia,
          Mertensia?,ZV - AB
Colletes fulgidus fulgidus - Compositae,F
          - VA
Colletes hyalinus* - polylectic,IV - VR
Colletes kincaidii - polylectic,IV - AB
Colletes lutzi monticola - Compositae +?,
          IV - FR
Colletes nigrifrons - Potentilla,IV - R
Colletes paniscus mertensiae - Mertensia,
          F - VR
Colletes phaceliae - polylectic?,ZV - VR
Colletes simulans simulans - Compositae,
          F - VA
Colletes slevini - polylectic.IV - VA
Hylaeus basalis - polylectic(Rosaceae),IV
          - VA
Hylaeus calvus - polylectic,F - VA
Hylaeus coloradensis - polylectic,F - FR
Hylaeus cressoni cressoni - polylectic,F
          - EA
Hylaeus ellipticus - polylectic,F - OC
Hylaeus episcopalis coquilleti - polylectic
          F - VA
Hylaeus episcopalis episcopalis -
          polylectic,F - VA
Hylaeus modestus citrinifrons - polylectic
          F - VA
Hylaeus nevadensis - polylectic,F - VA
Hylaeus nunnenmacheri - polylectic,F - VA
Hylaeus personatellus - polylectic,F - OC
Hylaeus rudbeckiae - polylectic, F - VA
Hylaeus timberlakei - polylectic,F - OC
Hylaeus verticalis - polylectic,F - VA
Hylaeus wootoni - polylectic,F - VA
Hesperapis ilicifoliae - Adenostoma,F-LA
Hesperapis regularis - Clarkia,F - LA
Andrena ablegata - Agoseris,F - R
Andrena albihirta - Salix,IV - OC
Andrena amphibola - polylectic?,IV - AB
Andrena angustitarsata - polylectic,IV-AB
Andrena arctostaphyllae - Arctostaphylos,
          IV - OC
Andrena astragali - Zigadenus,F - R
Andrena auricoma - polylectic,IV - AB
Andrena birtwelli - Potentilla,F - LF
Andrena candida - polylectic(Ceanothus),
          IV - AB

Andrena candidiformis - Ceanothus +?,IV
          - AB
Andrena carliniformis - polylectic?,IV-EA
Andrena ceanothifloris - Ceanothus,IV -FR
Andrena cercocarpi - unknown,ZV - OC⁻
Andrena chalybioides - Agoseris,F R - LA
Andrena chapmanae - unknown,ZV - AB
Andrena chlorogaster - polylectic,F - VA
Andrena chlorura - unknown,ZV - IF
Andrena cleodora melanodora - Ceanothus,
          IV - VA
Andrena cleodora cleodora - Ceanothus,IV
          -VA
Andrena chylismiae - Camissonia,F - R
Andrena citrinihirta - Compositae,F - R
Andrena coerulea - Ranunculus,F - EA
Andrena colletina* - Compositae,F - IF
Andrena columbiana - Compositae,F - AB
Andrena concinnula - Salix,F - VA
Andrena congrua - unknown,ZV - OC
Andrena costillensis - Compositae?,R-R
Andrena crataegi - polylectic (Rosaceae)
          F - AB
Andrena cressoni cressoni - unknown,ZV
          R
Andrena cressoni infasciata - Salix?,ZV
          R
Andrena cristata - Arctostaphylos,IV-R
Andrena crudeni - Nemophila,F - AB
Andrena cryptanthae - Cryptantha,F - VR
Andrena cuneilabris - Ranunculus,F - VA
Andrena cupreotincta - polylectic?,IV
          - VA
Andrena cyanophila - Potentilla,
          Ranunculus,IV - FR
Andrena duboisi - Lasthenia,Layia,F-LF
Andrena eothina - Camissonia,F - LA
Andrena erecta - unknown,IV - FR
Andrena errans - Salix,IV - AB
Andrena evoluta - Agoseris+,F - LA
Andrena flocculosa - Cornus?,ZV R - VR
Andrena forbesii - Rosaceae +?,IV - R
Andrena foxii - Camissonia,F - LA
Andrena helianthi* - Compositae,F - VR
Andrena fuscicauda - polylectic
          (Ceanothus),IV R - AB
Andrena gibberis - Salix,IV R - R
Andrena hippotes*- polylectic,IV - IF
Andrena huardi - Salix?,IV - FR
Andrena knuthiana - polylectic??,IV-FR

Andrena latifrons - unknown,IV - OC
Andrena limnanthis - Limnanthes,F - LF
Andrena lawrenci* - Compositae,IV - R
Andrena levipes - Linanthus?,IV - AB
Andrena lewisorum - Clarkia,F - LF
Andrena livida - polylectic,IV - OC
Andrena lupini - Ceanothus (+Eschsch-
        olzia?),IV - LF
Andrena lomatii - Lomatium,Sanicula F-AB
Andrena mackiae - Ceanothus??,IV - AB
Andrena macrocephala* - Nemophila,F-AB
Andrena medionitens - polylectic,IV - R
Andrena melanochroa - Potentilla,IV - IF
Andrena mesoleuca - unknown,ZV - VR
Andrena microchlora - Lomatium,Sanicula
        F - VA
Andrena miranda* - polylectic,IV - R
Andrena miserabilis - polylectic,F - FR
Andrena nemophilae* - Nemophila,
        Pholistoma,F - R
Andrena nevadensis - Salix,F - FR
Andrena nigrocaerulea - polylectic,F-VA
Andrena nudiscopa - unknown,ZV - R
Andrena nivalis* - unknown,ZV - R
Andrena nothocalaidis - dandelions,F-IF
Andrena obscuripostica - Arctostaphylos?
        IV - OC
 Andrena orthocarpi - Lasthenia,Orthocarpus
        IV R - IF
 Andrena osmioides osmioides - Cryptantha,F
        - FR
 Andrena pallidifovea - Compositae,IV R - R
 Andrena perplexa - polylectic?,IV - R
 Andrena perarmata - Salix?,IV - LF
 Andrena perimelas - polylectic?,IV - AB
 Andrena pertristis - polylectic?,IV - OC
 Andrena plana - Trifolium,F - OC
 Andrena porterae - unknown Ribes?,ZV - R
 Andrena prunorum prunorum - polylectic,F
        -EA
 Andrena puthua - Lasthenia,F - LA
 Andrena quintiliformis - polylectic
        (Ceanothus),IV - AB
 Andrena ribblei - unknown,ZV - R
 Andrena saccata - unknown,ZV - IF
 Andrena salicifloris - polylectic (Salix)
        F - VA
 Andrena sigmundi*- Salix,F - VR
 Andrena scurra scurra - Ceanothus?,IV-IF

Andrena scutellinitens - Compositae,F-FR
Andrena semipunctata - Salix,F - EA
Andrena sola - polylectic?,IV - VA
Andrena subaustralis - Salix,F - FR
Andrena striatifrons - Salix,F - EA
Andrena suavis - Ranunculus,F - EA
Andrena submoesta - Lasthenia +?,F - AB
Andrena subtilis - polylectic?,IV - AB
Andrena surda - Compositae,F - IF
Andrena torulosa - Nemophila,F - LA
Andrena timberlakei - Cryptantha,F - FR
Andrena transnigra - unknown,ZV - EA
Andrena trevoris - unknown,ZV - OC
Andrena trizonata - Salix,IV - OC
Andrena vanduzeei - Gayophytum,IV - R
Andrena vandykei - polylectic (Ceanothus),
          IV - FR
Andrena vierecki - unknown,ZV - OC
Andrena vexabilis - Lasthenia,F - R
Andrena vulpicolor* - Compositae,F - VR
Andrena w-scripta - polylectic,F - FR
Panurginus atriceps - Nemophila,Ceanothus,
          IV R - LF
Panurginus ceanothi - Ceanothus?,ZV R-VR
Panurginus nigrellus - Nemophila?,IV - LF
Panurginus nigrihirtus - Ranunculus,IV-LF
Panurginus occidentalis - Limnanthes,F-LF
Nomadopsis anthidia anthidia - Trifolium
          F - EA
Nomadopsis boharti - unknown,ZV - R
Nomadopsis cincta cincta*- Calochortus,F
          - IF
Nomadopsis comptula - Potentilla,F - LF
Nomadopsis edwardsii - Potentilla,
          (Calochortus),F - VA
Nomadopsis filiorum*- Trifolium,ZV R-VR
Nomadopsis fracta - Eriodictyon,F - LA
Nomadopsis linsleyi - Eriodictyon,F - AB
Nomadopsis micheneri - Trifolium,F - FR
Nomadopsis obscurella - Eschscholzia,
          IV - VA
Nomadopsis phaceliae* - Phacelia?,IV - R
Nomadopsis scutellaris - polylectic,IV-VA
Nomadopsis solitaria*- unknown,ZV - VR
Nomadopsis trifolii - Trifolium,Mimulus
          IV R - R
Nomadopsis xenus - Phacelia?,IV - VR
Nomadopsis zonalis sierrae - Monardella,
          F - VR

Perdita adjuncta* - Compositae,F R - R
Perdita aemula* - Compositae,ZV R - VR
Perdita bilobata*- Calochortus,IV R - OC
Perdita blaisdelli - Polemoniaceae,ZV R-R
Perdita bohartorum - unknown,ZV - VR
Perdita calochorti*- Calochortus, F R - R
Perdita ciliata - Compositae,F R - FR
Perdita claypolei limulata - Eriogonum,
          F R - VA
Perdita digna - unknown,ZV - VR
Perdita foleyi - Compositae,F R - VR
Perdita hirticeps* - Stephanomeria,F - VR
Perdita imberbis - unknown,ZV - VR
Perdita lepidosparti* - Compositae,ZV R-R
Perdita leucostoma - Calochortus,F R - AB
Perdita melanogastra - unknown,ZV - VR
Perdita navarretiae angusticeps -
          Polemoniaceae,ZV R - VR
Perdita navarretiae navarretiae -
          Polemoniaceae,F R - R
Perdita navarretiae powelli -
          Polemoniaceae,ZV R - VR
Perdita nevadensis culbertsoni -
          Perideridia,IV-LA
Perdita nevadensis nevadensis -
          unknown (Eriogonum?),IV - LA
Perdita nigrocincta*- Compositae,ZV R -VR
Perdita obtusa - Eschscholzia,Calochortus
          ?,ZV R - VR
Perdita oregonensis expleta - Compositae,
          ZV R - VR
Perdita oreophila - unknown,ZV - VR
Perdita panocheana* - unknown,ZV - VR
Perdita placida* - Compositae,ZV R - VR
Perdita pulliventris - Calochortus?,ZV R
          - VR
Perdita rivalis - Aster,Erigeron F R - FR
Perdita salicis tristis - Salix,F R - LA
Perdita scotti - Compositae,F R - IF
Perdita stottleri* - Compositae,F R - R.
Perdita subfasciata* - Compositae,F R-VR
Perdita sweezyi - Compositae(Erigeron),
          F R - IF
Perdita trisignata ornata - Lotus,F - AB
Perdita tularensis - Calochortus,F R - LF
Perdita yosemitensis - Eriogonum,F R - IF
Perdita zonalis monticola - Compositae,
          F R - VR
Halictus farinosus - polylectic,F - EA
Halictus ligatus - polylectic,F - EA

Halictus rubicundus - polylectic.F - AB
Halictus tripartitus - polylectic,F - EA
Dialictus -- unmonographed genus--
          numerous species, all polylectic
          in Sierra Nevada despite published
          reports to contrary (Eickwort,
          pers. comm.)
Lasioglossum mellipes - polylectic,F - AB
Lasioglossum olympiae - polylectic,F - AB
Lasioglossum sisymbrii - polylectic,F- VA
Lasioglossum titusi - polylectic,F - AB
Lasioglossum trizonatum - polylectic,F-AB
Evylaeus aberrans - Oenothera,IV - OC
Evylaeus allonotum - polylectic,F - FR
Evylaeus aspilurum - polylectic,F - IF
Evylaeus avalonense - polylectic,F - IF
Evylaeus cooleyi - polylectic (Clarkia),
          F - AB
Evylaeus dasiphorae - polylectic? - VR
Evylaeus glabriventre - polylectic,F -FR
Evylaeus kincaidii - polylectic,F - AB
Evylaeus miguelense - polylectic,F - FR
Evylaeus nigrescens - polylectic,F - EA
Evylaeus orthocarpi - polylectic,F - FR
Evylaeus ovaliceps - polylectic,F - AB
Evylaeus pullilabre - polylectic(Clarkia)
          IV - AB
Evylaeus sequoiae - polylectic? - IF
Evylaeus tracyi - polylectic,F - IF
Augochlorella pomoniella - polylectic,
          F - VA
Agapostemon femoratus - polylectic,F-EA
Agapostemon texanus angelicus - polylectic
          F - EA
Nomia melandri - polylectic(Medicago),
          F - EA
Micralictoides ruficaudis - Eschscholzia
          F - R
Micralictoides sp. #1 - Gilia capitata,F
          - VR
Micralictoides sp. #2 - Campanula,IV - VR
Dufourea leechi - unknown,2V - R
Dufourea afasciata - Trifolium,F R - IF
Dufourea australis* - Compositae,F - IF
Dufourea bernardina - unknown,IV - IF
Dufourea brevicornis - Gilia,Linanthus,
          F R - OC
Dufourea calientensis - unknown,IV - IF
Dufourea calochorti - Calochortus,F R-VR

Dufourea cuprea - Nemophila,F R - R
Dufourea davidsoni - Gayophytum,F R - IF
Dufourea dentipes - Calochortus,F R - IF
Dufourea femorata - Gilia capitata,F - FR
Dufourea fimbriata fimbriata - Potentilla
　　　　F - R
Dufourea fimbriata sierrae - Potentilla,
　　　　F - R
Dufourea holocyanea - Symphoricarpos,F-R
Dufourea macswainii - Clarkia,F - R
Dufourea nemophilae - Phacelia,Nemophila
　　　　F R - IF
Dufourea neocalifornica - Linanthus,F-VR
Dufourea pectinipes - Gilia,Mimulus?,IV R
　　　　- VR
Dufourea sandhouseae sandhouseae -
　　　　polylectic (Eschscholzia),F - VA
Dufourea scabricornis - Gayophytum,F R -LF
Dufourea spilura - Gayophytum,F R - LF
Dufourea spinifera - Trifolium,F R - R
Dufourea subdavidsoni - Gayophytum,F R -FR
Dufourea trochantera - Phacelia,F R - LA
Dufourea tularensis - unknown,ZV - VR
Dufourea tuolumne - Gilia,F R - R
Dufourea versatilis rubriventris -
　　　　Mimulus,F - AB
Dufourea versatilis versatilis - Gilia,
　　　　Mimulus?, IV R - IF
Dufourea virgata - unknown(polylectic?),
　　　　IV - VA
Heteranthidium timberlakei - polylectic,
　　　　IV R - FR
Anthidium atripes* - Lotus,Astragalus,
　　　　IV R - AB
Anthidium banningense - Phacelia,IV R -AB
Anthidium clypeodentatum - Lotus,Lupinus,
　　　　Astragalus,IV - OC
Anthidium collectum - Lotus,Phacelia, IV
　　　　R - EA
Anthidium edwardsii - polylectic,F - VA
Anthidium emarginatum - Phacelia,legumes,
　　　　IV R - VA
Anthidium jocosum - polylectic (Lotus),
　　　　IV R - AB
Anthidium maculosum - polylectic,IV - VA
Anthidium mormonum - Phacelia,legumes
　　　　IV R - EA
Anthidium placitum - polylectic,IV R - AB
Anthidium tenuiflorae - Phacelia,legumes
　　　　IV R - AB

Anthidium utahense - legumes,IV R - EA
Callanthidium formosum - polylectic?, IV
        - FR
Callanthidium illustre - polylectic
        (Phacelia,legumes)IV R - VA
Dianthidium dubium dubium - polylectic,
        IV R - VA
Dianthidium heterulkei heterulkei* -
        Compositae,F R - IF
Dianthidium platyurum mohavense*-
        Compositae,F R - VR
Dianthidium plenum - polylectic,IV R-OC
Dianthidium pudicum consimile -
        Compositae,F R - AB
Dianthidium pudicum pudicum -
        Compositae,F R - AB
Dianthidium singulare - Compositae,F R-OC
Dianthidium subparvum - Compositae,F R-AB
Dianthidium ulkei - Compositae,F R - EA
Anthidiellum ehrhorni - polylectic,F - FR
Anthidiellum notatum robertsonii -
        polylectic,F - EA
Chelostoma californicum - Phacelia +?,
        IV R - AB
Chelostoma incisulum - Phacelia,IV R - OC
Chelostoma marginatum incisuloides -
        Phacelia, IV R - R
Chelostoma marginatum marginatum -
        Phacelia, IV R - OC
Chelostoma minutum - Phacelia,F R - LA
Chelostoma phaceliae - Phacelia,F R - LA
Chelostoma tetramerum - unknown,ZV - VR
Chelostomopsis rubifloris - polylectic,F
        - EA

Ashmeadiella aridula astragali -
        polylectic(Lotus),IV - VA
Ashmeadiella bucconis denticulata -
        Compositae,IV - VA
Ashmeadiella cactorum basalis -
        polylectic(Lotus,Cordylanthus),IV-AB
Ashmeadiella californica californica -
        polylectic?(Compositae),IV - EA
Ashmeadiella californica sierrensis -
        Compositae?,IV - R
Ashmeadiella cubiceps cubiceps -
        Compositae?,ZV R - R
Ashmeadiella difugita emarginata -
        Compositae?,IV - R
Ashmeadiella foveata - polylectic?,IV-OC
Ashmeadiella rufitarsis*- Eriogonum,IV-R

Ashmeadiella australis - Penstemon,IV-AB
Ashmeadiella erema - Dalea +?,ZV R - VR
Ashmeadiella foxiella - unknown,ZV - VR
Ashmeadiella salviae - Salvia,Lepechinia
    Trichostemma,IV - OC
Ashmeadiella stenognatha - unknown,ZV-R
Ashmeadiella timberlakei solida - Lotus,
    Phacelia?,IV - FR
Ashmeadiella timberlakei timberlakei -
    Lotus, Phacelia, IV - AB
Heriades cressoni - Compositae,IV - VA
Heriades occidentalis - polylectic,IV-LA
Hoplitis clypeata* - unknown,ZV - VR
Hoplitis colei - Eriodictyon,IV - IF
Hoplitis grinnelli grinnelli -
    polylectic, IV - AB
Hoplitis producta gracilis -
    polylectic, IV - VA
Hoplitis sambuci - polylectic,IV - VF
Hoplitis uvulalis* - unknown,ZV - R
Hoplitis hypocrita - polylectic (Lotus,
    Astragalus),IV - AB
Hoplitis albifrons argentifrons -
    polylectic(Phacelia),F - VA
Hoplitis albifrons maura - polylectic
    (Phacelia),F - EA
Hoplitis fulgida platyura - Phacelia,
    IV R - EA
Hoplitis louisae - Phacelia,IV R - R
Hoplitis viridimicans - unknown,ZV-VR
Proteriades laevibullata - Phacelia,
    Nemophila?,IV R - R
Proteriades plagiostoma - unknown,ZV-VR
Proteriades rufina - unknown,ZV - VR
Proteriades bullifacies* - Phacelia?,
    IV R - IF
Proteriades bunocephala - Lotus?,IV - R
Proteriades howardi - Lotus,IV R - FR
Proteriades mazourka* - unknown,ZV - R
Proteriades jacintana - Cryptantha,F-FR
Proteriades boharti* - Cryptantha,ZV R-R
Proteriades evansi - Cryptantha,F R - R
Proteriades incanescens tota -
    Cryptantha,IV R - VR
Proteriades nanula sparsa - Cryptantha,
    F R - R
Proteriades seminigra yosemitensis -
    Cryptantha,F R - R

Proteriades remotula - Cryptantha,F R - IF
Anthocopa abjecta abjecta - Penstemon.
        ZV R - VR
Anthocopa abjecta alta - Penstemon,F R- IF
Anthocopa anthodyta anthodyta -
        Penstemon,Collinsia,F R - IF
Anthocopa elongata - Penstemon,F R - R
Anthocopa hebitis - Collinsia,Penstemon
        F R - VR
Anthocopa oregona - Penstemon?,ZV R - R
Anthocopa pycnognatha pycnognatha -
        Penstemon,F R - VR
Anthocopa pycnognatha solatus -
        Penstemon,F R - R
Anthocopa triodonta shastensis -
        Penstemon,F R - R
Anthocopa triodonta triodonta -
        Penstemon,F R - R
Anthocopa copelandica albomarginata -
        Phacelia, Nemophila F R - FR
Anthocopa copelandica copelandica -
        Phacelia,F R - VR
Osmia lignaria propinqua - polylectic,F-EA
Osmia ribifloris biedermannii -
        polylectic,F - VA
Osmia coloradensis - Compositae,F - EA
Osmia texana - Compositae(Cirsium),F - VA
Osmia californica - Compositae,F - EA
Osmia grinnelli* - Compositae,F - AB
Osmia montana quadriceps - Compositae,F-EA
Osmia subaustralis - Compositae,F - VA
Osmia austromaritima - unknown,ZV - VR
Osmia bakeri - unknown,ZV - R
Osmia bucephala* - unknown,ZV - VR
Osmia pikei - unknown,ZV - R
Osmia thysanica - unknown,ZV - VR
Osmia calcarata - legumes,IV R - R
Osmia giffardi - unknown,ZV - FR
Osmia hurdi - unknown,ZV - R
Osmia integra - legumes,IV - IF
Osmia kenoyeri - unknown,ZV - VR
Osmia lanei - unknown,ZV - R
Osmia longula - legumes,IV R - R
Osmia nifoata - legumes,IV R -FR
Osmia nigrifrons - legumes,IV R - IF
Osmia nigrobarbata - legumes,IV R - VA
Osmia obliqua - legumes,IV R - R

Osmia odontogaster - unknown,ZV - VR
Osmia physariae - legumes,IV R - FR
Osmia sedula - legumes,IV R - R
Osmia melanopleura - unknown,ZV - R
Osmia claremontensis - unknown,ZV - R
Osmia nemoris - polylectic (legumes),IV R,
    - AB
Osmia latisulcata - legumes,IV R - IF
Osmia aglaia - Lotus?(+Penstemon?),IV R-OC
Osmia bruneri - polylectic?,IV - AB
Osmia calla - legumes,IV R - AB
Osmia cobaltina - polylectic?,IV R - AB
Osmia cyanopoda* - legumes?,IV - VR
Osmia dolerosa - unknown,ZV - R
Osmia exigua - polylectic (Labiatae). IV-OC
Osmia gaudiosa - Lotus,IV R - FR
Osmia inermis - Ericaceae?,IV R - VR
Osmia indeprensa - unknown,ZV - IF
Osmia inurbana - unknown?,ZV - IF
Osmia kincaidii - legumes,IV R - AB
Osmia laeta - polylectic,IV R - AB
Osmia malina - legumes,IV R - IF
Osmia mertensiae - unknown,ZV - VR
Osmia nanula - unknown,ZV - R
Osmia pagosa - unknown,ZV - VR
Osmia penstemonis - Penstemon,F - IF
Osmia potentillae - unknown,ZV - R
Osmia pulsatillae - unknown,ZV - R
Osmia pusilla - unknown,ZV - IF
Osmia regulina - legumes,IV R - FR
Osmia trevoris - unknown,ZV - IF
Osmia tristella cyanosoma - unknown,ZV
    - IF
Osmia tristella tristella - unknown,ZV
    - IF
Osmia zephyros - unknown,ZV - R
Osmia albolateralis - polylectic
    (legumes),IV R - IF
Osmia atrocyanea atrocyanea -
    polylectic(legumes),IV R - AB
Osmia brevis - polylectic(Penstemon,
    Collinsia),IV - AB
Osmia bridwelli - polylectic?,IV - LF
Osmia cara - unknown,ZV - FR
Osmia cyanella - unknown,ZV - AB
Osmia densa densa - legumes?,IV R - VA
Osmia gabrielis - legumes?,IV R - FR
Osmia hendersoni - unknown,ZV - VR
Osmia hesperos - unknown,ZV - VR

Osmia iridis - unknown, ZV - VR
Osmia juxta subpurpurea - unknown, ZV-AB
Osmia paradisica - unknown, ZV - R
Osmia rostrata - unknown, ZV - LA
Osmia sculleni - Hackelia?, IV - LA
Osmia seclusa - unknown, ZV - FR
Megachile brevis brevis - polylectic, F
        - VA
Megachile brevis onobrychidis -
        polylectic, F - EA
Megachile coquilletti - polylectic, F-VA
Megachile gentilis - polylectic, F - EA
Megachile texana cleomis - polylectic, F
        - AB
Megachile texana texana - polylectic, F
        - AB
Megachile montivaga - polylectic
        (Compositae), F - EA
Megachile relativa - polylectic
        (Compositae), F - AB
Megachile rotundata - polylectic
        (Legumes), F - EA
Megachile frigida frigida - polylectic,
        F - OC
Megachile gemula - polylectic, F - OC
Megachile melanophaea calogaster -
        legumes, F - LA
Megachile melanophaea melanophaea -
        legumes, IV - AB
Megachile melanophaea submelanophaea -
        legumes, F - OC
Megachile gravita - Clarkia. F - OC
Megachile pascoensis - Clarkia. F - LA
Megachile hilata* - unknown. ZV - VR
Megachile manifesta* - unknown, ZV - R
Megachile nevadensis - Compositae, IV - EA
Megachile pseudonigra - unknown, ZV - IF
Megachile seducta - unknown, ZV - VR
Megachile subnigra angelica - Compositae
        (Chaenactis), IV - AB
Megachile subnigra subnigra - unknown, ZV
        - IF
Megachile wheeleri - Compositae, IV - AB
Megachile parallela facunda - Compositae,
        F R - R
Megachile tulariana - unknown, ZV - VR
Megachile cochisiana*- unknown, ZV - OC
Megachile comata* - unknown, ZV - VR
Megachile perihirta - Compositae (+?), IV-EA
Megachile fidelis - Compositae, F - EA

Megachile frugalis frugalis - unknown,ZV-R
Megachile frugalis pseudofrugalis -
        polylectic,F - EA
Megachile inimica sayi - Compositae.IV R-OC
Megachile mellitarsis - Compositae?.ZV R-VR
Megachile pugnata pomonae - Compositae, IV
        R - FR
Megachile pugnata pugnata - Compositae, IV
        R - FR
Chelostomoides angelarum - polylectic(Lotus,
        Cordylanthus),IV - EA
Exomalopsis chionura - Grindelia,IV R - AB
Diadasia angusticeps - Clarkia,F - AB
Diadasia bituberculata - Calystegia,F - VA
Diadasia enavata - Helianthus,F - EA
Diadasia laticauda - Malacothamnus.F R-AB
Diadasia nigrifrons - Sidalcea,F R - EA
Diadasia nitidifrons - mallows,F R - AB
Melissodes communis alopex* - polylectic
        (Legumes),F - AB
Melissodes tepida timberlakei - polylectic
        (Legumes),F - EA
Melissodes dagosa*- polylectic,IV - OC
Melissodes lupina - Compositae,F R - EA
Melissodes plumosa*- Compositae(sunflowers),
        F R - R
Melissodes metenua* - Composites?,ZV R - OC
Melissodes clarkiae - Clarkia,F - R
Melissodes nigricauda - Stephanomeria?,IV-R
Melissodes lustra - Compositae,F R - VA
Melissodes glenwoodensis* - Compositae,F R-R
Melissodes stearnsi*- Compositae(+poly?),
        IV - VA
Melissodes menuachus*- Compositae,F R - R
Melissodes bimatris - Compositae,F R - VR
Melissodes bicolorata - Compositae,F R - R
Melissodes expolita* - Compositae,F R - OC
Melissodes robustior - Compositae,F R - EA
Melissodes pallidisignata - Compositae,F -VA
Melissodes hymenoxidis* - Compositae,F R -OC
Melissodes lutulenta - Compositae,F R - IF
Melissodes velutina - Compositae (+
        Eriastrum?),IV R - AB
Melissodes microsticta - Compositae,F R-VA
Melissodes melanura - Compositae.F R - OC
Melissodes moorei - Compositae,F R - IF
Melissodes confusa - Compositae,F R - R
Melissodes micheneri - Compositae,F R-LA
Melissodes monoensis* - Compositae,F R-R
Svastra sabinensis nubila - Compositae,
        F R - IF

Tetralonia acerba - Arctostaphylos?,IV
      R - AB
Tetralonia actuosa - polylectic
      (legumes),F R - EA
Tetralonia angustifrons - polylectic
      IV - AB
Tetralonia cordleyi - polylectic,F -VA
Tetralonia delphinii - polylectic
      (Delphinium?),IV - OC
Tetralonia dorsata - polylectic
      (legumes),IV - AB
Tetralonia edwardsii - polylectic
      (legumes),Iv R - EA
Tetralonia frater albopilosa -
      polylectic(legumes),IV R - VA
Tetralonia frater lata -
      polylectic?,IV R - OC
Tetralonia hurdi - polylectic,IV - OC
Tetralonia lunata - polylectic
      (legumes,Arctostaphylos),IV - VA
Tetralonia monozona - unknown,ZV - VR
Tetralonia stretchii - polylectic?,IV
      R - FR
Tetralonia venusta carinata - Clarkia,
      IV R - VR
Tetralonia virgata - polylectic?,IV -OC
Tetralonia zonata - unknown,ZV - R
Anthophora bomboides stanfordiana -
      polylectic,F - AB
Anthophora californica californica -
      polylectic,F - VA
Anthophora centrifirmis centriformis -
      polylectic,ZV R - VR
Anthophora centroformis vierecki -
      polylectic,ZV R - IF
Anthophora crotchii - polylectic,F - AB
Anthophora edwardsii edwardsii -
      polylectic?,IV R - VA
Anthophora neglecta - polylectic,IV -AB
Anthophora pacifica - polylectic;F - VA
Anthophora urbana - polylectic,F - EA
Anthophora ursina simillima - unknown,
      ZV - R
Anthophora furcata - polylectic,F - FR
Anthophora curta - polylectic (Composi-
      tes),IV - EA
Anthophora exigua - Compositae,IV AB
Anthophora flavocincta - Composites,IV -AB
Anthophora flexipes - unknown,ZV - AB
Anthophora maculifrons* - Compositae,
      IV - OC

Emphoropsis rugosissima - unknown.ZV -OC
Emphoropsis tristissima - unknown.ZV -R
Centris rhodomelas - Psoralea?,IV - R
Ceratina arizonensis - polylectic,F - VA
Ceratina nanula - polylectic,F - EA
Ceratina pacifica - polylectic.F - AB
Ceratina micheneri - polylectic,F - OC
Ceratina tejonensis - polylectic,F - OC
Ceratina acantha - polylectic, F - EA
Ceratina sequoiae - Clarkia,F - OC
Ceratina timberlakei - polylectic,F - OC
Xylocopa brasilianorum varipuncta -
       polylectic, F - VA
Xylocopa californica californica -
       polylectic, F - VA
Xylocopa californica diamesia -
       polylectic, F - VA
Xylocopa tabaniformis orpifex -
       polylectic, F - EA
Bombus appositus - polylectic,F - R
Bombus balteatus - polylectic,F - VR
Bombus californicus - polylectic, F - EA
Bombus nevadensis nevadensis -
       polylectic, F - R
Bombus sonorus - polylectic,F - VA
Bombus occidentalis occidentalis -
       polylectic, F - AB
Bombus bifarius - polylectic, F - AB
Bombus centralis - polylectic,F - EA
Bombus edwardsii - polylectic,F - EA
Bombus flavifrons dimidiatus -
       polylectic, F - AB
Bombus griseocollis* - polylectic.F - VR
Bombus huntii* - polylectic,F - VR
Bombus melanopygus - polylectic,F - R
Bombus mixtus - polylectic,F - AB
Bombus morrissoni - polylectic,F - OC
Bombus rufocinctus - polylectic,F - R
Bombus sylvicola - polylectic.F - OC
Bombus vandykei - polylectic,F - AB
Bombus vosnesenskii - polylectic,F - EA

Anthophora rhodothorax - unknown,ZV-OC
Emphoropsis cineraria - Arctostaphylos?
    IV - OC
Emphoropsis dammersi - Arctostaphylos?,
    IV - R
Emphoropsis depressa - polylectic?,IV-AB
Emphoropsis excellens - unknown,ZV - VR