

Community Studies in Pollination Ecology in the High Temperate Andes of Central Chile.

I. Pollination Mechanisms and Altitudinal Variation

Author(s): Mary T. Kalin Arroyo, Richard Primack and Juan Armesto

Source: *American Journal of Botany*, Vol. 69, No. 1 (Jan., 1982), pp. 82-97

Published by: Botanical Society of America, Inc.

Stable URL: <http://www.jstor.org/stable/2442833>

Accessed: 12-03-2018 18:18 UTC

REFERENCES

Linked references are available on JSTOR for this article:

http://www.jstor.org/stable/2442833?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://about.jstor.org/terms>



JSTOR

Botanical Society of America, Inc. is collaborating with JSTOR to digitize, preserve and extend access to *American Journal of Botany*

COMMUNITY STUDIES IN POLLINATION ECOLOGY IN THE HIGH TEMPERATE ANDES OF CENTRAL CHILE. I. POLLINATION MECHANISMS AND ALTITUDINAL VARIATION¹

MARY T. KALIN ARROYO,² RICHARD PRIMACK,³ AND JUAN ARMESTO²

ABSTRACT

Pollination mechanisms and pollinators are reported for a total of 137 species (75% of the non-abiotically pollinated flora) as they occur at three altitudinal levels (subandean scrub: 2,200–2,600 m; cushion-plant zone: 2,700–3,100 m; subnival field: 3,200–3,600 m) in the Andean (alpine) zone on the Cordón del Cepo (33°17'S) in central Chile as part of community oriented research in reproductive biology in the high temperate Andes of South America. Only around 4% of the species studied failed to be visited by potential pollinators. Hymenopterans (principally bees) are important pollinators of 50% of the biotically pollinated flora, butterflies of 24% and flies of 46%. Other vectors include beetles, moths, and humming-birds. An estimated 17% of the flora is anemophilous.

Bee species-richness, specialist feeding, and melittophily reach maxima in the subandean scrub; thereafter, bees diminish rapidly in number, with bees pollinating only 13% of the subnival flora as contrasted with 68% of the subandean flora. Although fly and butterfly species-richness also decline with increasing altitude, the proportions of species pollinated by these vectors actually increases. High-altitude populations of melittophilous species with broad altitudinal ranges are invariably serviced by fewer bee species as compared with lower populations.

The rich bee fauna at the lower end of the Andean zone in central Chile appears to have resulted from upward colonization from that of the subtending lowland Mediterranean sclerophyllous woodland vegetation. Altitudinal variation in pollination spectra is discussed in relation to contrasting life history characteristics and different modes of thermoregulation in the insect groups involved.

RECENT STUDIES on the energetics of foraging (e.g., Heinrich, 1974), nectar and pollen con-

stituents (e.g., Baker and Baker, 1979) and relationships with flowering phenology (e.g., Stiles, 1978; Whelan and Burbidge, 1980) have added new dimensions to research in pollination biology. The implications of these studies, nevertheless, have yet to be thoroughly explored at a community level, and as Faegri and van der Pijl (1979) recently stated in reviewing progress in pollination ecology, "until now the evolution of community pollination spectra has only been touched on."

In high-mountain plant communities above timberline, opportunities for growth are restricted to the spring and summer months, and, in temperate regions, prevented during the remainder of the year by low temperatures and associated snow cover. Flowering as a consequence must be limited to a relatively short period of the year, which tends to decrease in length as the upper vegetational limit is approached. Increased low-temperature stress with altitude also affects the distribution and abundance of insects (Mani, 1962). Thus predictably, plant-pollinator relationships might change both quantitatively and qualitatively with altitude. From the work of early naturalists (e.g., Müller, 1880), and more recently that

¹ Received for publication 22 September 1980; revision accepted 4 December 1980.

² Departamento de Biología, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile.

³ Department of Botany, Boston University, Boston, Massachusetts, USA.

Many students, but especially Paulina Uslar and Michaelangelo Trevalli, are thanked for their collaboration with field work. Hymenopterans were identified by Dr. H. Toro, Depto. de Zoología, Universidad Católica, Valparaíso, lepidopterans by Dr. J. Herrera, Fac. de Ciencias, U. de Chile, Santiago and dipterans by Dr. M. Etcheverry, Fac. de Ciencias, U. de Chile, Dr. Raul Cortés, Universidad del Norte, and Dr. Jorge Artigas, Sección de Entomología, Depto. de Zoología, Universidad de Concepción, all in Chile and without whose collaboration this research would have been impossible. We are especially grateful to SDCACI, U. de Chile for providing a special travel grant to R. Primack and to Dr. P. H. Raven, Missouri Botanical Garden, who provided much unavailable literature, and with whom many useful discussions were held during the writing of this paper. The Club Deportivo, Universidad de Chile provided logistic support and Hoteles Portillo granted permission to circulate on high Andean access routes, for which we are most appreciative. This research was supported by Grant No. B388/803 to M.T.K.A. by SDCACI, Universidad de Chile and forms part of MAB-6 (UNESCO/UNEP 1105-77-01).

of Pojar (1974), and Primack (1978), it appears that entomophily predominates in temperate alpine areas. However, there have been no attempts to elucidate the details of changes in pollination spectra as the upper limits of alpine vegetation are met with. In this paper we report the results of a community oriented study on pollination mechanisms in the high temperate Andes of South America in central Chile and discuss how pollination mechanisms vary with altitude.

MATERIAL AND METHODS—Study site—Investigations were conducted in the alpine (more correctly *Andean*) zone in the Cordón del Cepo, a western branch of the main divide of the Cordillera de los Andes in the Mediterranean sector of central Chile between the catchments of the Rio Molina and the Rio San Francisco (33°17'S; 70°16'W) along an altitudinal transect departing from the *Kageneckia angustifolia* D. Don upper limit of the Mediterranean sclerophyllous woodland at approximately 2,200 m below Farellones, passing through the area of La Parva (2,700 m), over onto the summit of Cerro Franciscano (3,600 m) and up onto the base of Cerro Pintor (4,200 m). The Andean vegetation in central Chile is perhaps most striking for its highly zonal character. Immediately above the *Kageneckia* limit, it consists of a floristically rich association of often spiny, low rounded shrubs, with the composite family well represented (e.g., *Chusquea*, *Haplopappus*, *Mutisia*, *Nassauvia*, *Senecio*, *Nardophyllum*), many perennial herbs, and an abundance of annuals and geophytes, which is here referred to as *subandean scrub*. At 2,700 m, the vegetation changes character very abruptly as the semi-woody cushion plants, *Laretia acaulis* (Cav.) Gill. et Hook., three species of *Azorella* (all Umbelliferae), and *Anarthrophyllum gayanum* (A. Gray) Jackson, bearing and interspersed with low perennial herbs and grasses, become dominant. Along the exposed slopes, 500 m above La Parva and encroaching on Cerro Franciscano where feldfield becomes prominent, the umbelliferous *cushion zone* loses its tight-knit physiognomy and intergrades into a sparsely vegetated *subnival area*, constituted predominantly by small tussock species (e.g., *Stipa chrysophylla* Desv.), many cryptically colored, low-growing rosette herbs (e.g., *Viola* spp.), and smaller flat cushions deriving from a variety of plant families. Above 3,600 m, vascular plants are restricted to a few north- and east-facing slopes along the ridge leading to Cerro Pintor. Scattered individuals of *Calandrinia picta* Gill at 3,800 m, and a small pop-

ulation of *Nototriche compacta* (A. Gray) A. W. Hill at 3,850 m, are the highest vascular plant records for the area. Phenological patterns have been detailed for 97 species at six altitudinal levels and on contrasting north- and south-facing slopes (Arroyo, Armesto and Vilagrán, 1981).

The salient features of the climate of the Andean zone, described in greater detail in Arroyo et al. (1981) are the long, snow-free period of 5–8 months, and the ca. 400–800⁴ mm of annual precipitation falling mostly as snow during the winter months in the lower subandean scrub zone, but of which an increasing fraction, perhaps up to 1/5th is received in the form of flash hail and snow storms during the summer months, as the subnival zone is approached. In the subandean scrub zone below 2,700 m, summer days are generally calm and cloud-free during the morning hours, but some cloudiness and a light breeze may develop in the early afternoon at this altitude. The maximum average monthly temperature (recorded at 2,500 m) rises to above 18 C. The temperature depression between the *Kageneckia* woodland limit and the upper limit of the cushion plant zone in January (11–1 p.m.) (from temperatures maintained with pollination observations—see sampling procedure) is in the order of 7 C and, at the higher altitude, afternoon cloud cover tends to be more common. At 3,550 m, the temperature is depressed by a further 2 C, and here there are few days in December and January in which cloud cover and moderately strong winds have not developed by early afternoon with temperature drops to 5–6 C on occasions. February and March, although cooler, tend to be clearer months in the subnival.

Sampling procedure—A sampling procedure was designed which enabled us to assess the relative importance of different pollination vector types to a large and representative number of species in the community, as reported in this first paper, as well as the rates at which flowers are visited (to be discussed elsewhere; Arroyo et al., in prep.). For comparative purposes, the altitudinal transect was subdivided into three 500-m sampling areas: I: 2,200–2,600 m, II: 2,700–3,100 m, and III: 3,200–3,600 m, these roughly corresponding to the vegetation zones previously outlined. Throughout the entire flowering season of 1980–1981, which began in October of 1980 and ended in the following March, two kinds of observations were

⁴ Estimated from 2 yr data at 2,500 m on study site and climate diagrams for areas close to site.

maintained. First, over 1,400 quantified 10-min observation periods were conducted during the morning, midday and afternoon hours, so as to obtain multiple observations on as many species as possible flowering in the three areas. During each 10-min observation period we recorded the number of individuals of the plant species under observation, the total number of flowers being observed, all vectors visiting the flowers, the number of flowers visited by each vector, the exact altitude, a number of weather descriptors, including air temperature at the height pollinators were flying, plus the potential of the vectors as pollinators based on contact possibilities with the stigma and anthers. At the end of each 10-min period, vectors were captured and later pinned for identification. These quantified observations were accompanied by a number of unquantified 10-min observation periods, and a few insect sweeps which are incorporated into the data where appropriate (see Appendix II). As the number of bees and butterflies that were active during any one time was not excessive, these groups could almost always be coded to species level in the field. This task proved to be almost impossible for all but a few very distinct dipterans, which as a consequence have nearly always been grouped according to family in the species observations. The data for each plant were pooled according to the sampling area in which the observations were made, from which the relative importance of each vector class was calculated (Appendix II). As the number of observations per species is too variable for consistently determining the relative importance of individual pollinators at the specific level, in this initial survey we limit ourselves to relative importance of major vector types, leaving the finer analysis at the species level pending the collection of additional field data. Insect determinations were supplied by Chilean specialists. The collection included a number of suspected new species and a great many of doubtful specific affinity (indicated with serial numbers: Appendix I and II). Insect vouchers have been deposited in the collections of entomologists listed in the acknowledgements. Plant vouchers are deposited at the herbaria of the Universidad de Concepción, Concepción, Chile and Missouri Botanical Garden, St. Louis, MO, USA.

RESULTS—Pollinator composition—The most important pollinator groups in the Andean zone in central Chile, considering flower visiting activity, are bees, flies, and butterflies (Appendix I), while secondary groups are beetles, moths, and hummingbirds. Pollen is oc-

asionally transported by ants, but not to any significant extent. Over 50 species of Hymenoptera have been found visiting flowers to date. Bees, 52 spp., are from six families, however more than three-fourths of the species belong to the Megachilidae (4 genera; 16 species), Anthophoridae (7 genera; 12 species) and Colletidae (4 genera; 11 species) with *Megachile* and *Anthidium*, both of the Megachilidae, being the most abundantly represented genera. Considering hymenopterans, lepidopterans, and dipterans together, total species-richness declines with altitude, but when considered separately distinct patterns of altitudinal variation in species-richness and taxonomic composition emerge (Fig. 1). Fifty-three species of Hymenoptera (88% bees), or over 90% of the total in the Andean zone, occur in the lower subandean zone between 2,200–2,600 m. Well over half of these are restricted entirely to this altitudinal range and fail to penetrate higher into the cushion-plant zone between 2,700–3,100 m. Only three new species of Hymenoptera (*Megachile*, sp.-4; *Colletes fulvipes*; *Anthidium*, sp.-1—all bees) turn up in the cushion-plant zone, and thus the total number of hymenopterans in this area is less than half that found 500 m lower in the subandean scrub zone. Above 3,100 m in the subnival zone, wasps cut out entirely and only five species of bees remain. Two of these (*Stenanthidium espinosai* and *Megachile*, sp.-5) were not found below 3,100 m, *Anthidium*, sp.-1 occurs as low as 3,000 m, while *Megachile semirufa* and *Bombus dahlbomii* are wide-ranging bees inhabiting the entire altitudinal range of the Andean zone. Bee species-richness in the subnival zone thus drops to about only one-tenth that encountered originally in the subandean scrub, and whereas six bee families were represented between 2,200–2,600 m, only two (Megachilidae and Apidae) remain in the upper subnival. The drop-off in bee-species number with altitude is also accompanied by size changes. In the subandean scrub zone, large Anthophoridae, Megachilidae, and Apidae persist with many smaller bees, particularly deriving from the Andrenidae, Colletidae, and Halictidae. The small colletid bees still remain to some extent in the cushion-plant zone, but as the subnival zone is reached all small bees have been eliminated.

Fly species-richness (Fig. 1) remains constant in moving from the subandean scrub zone into the cushion-plant zone, but changes in taxonomic composition are evident. Bombyliidae and Tachinidae account for a large proportion of the anthophilous flies in the subandean zone. Tachinidae remain important in the

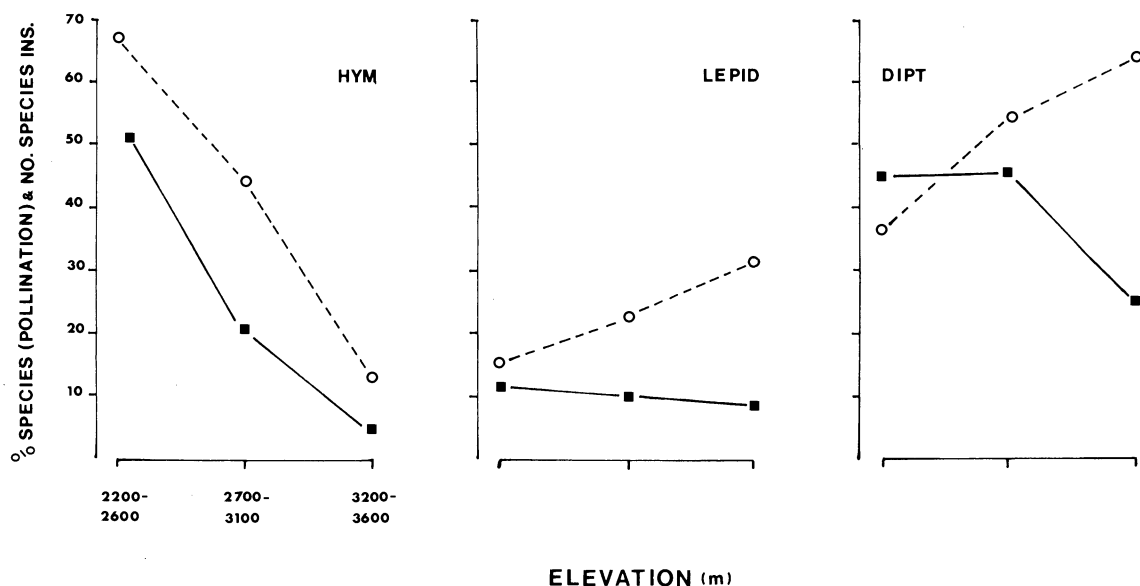


Fig. 1. Percentage of species pollinated by bees and wasps (HYM), butterflies (LEPID) and flies (DIPT), respectively, and insect species-richness according to altitude. The total percentage exceeds 100, given that many species are pollinated by more than one kind of vector (see Table 2). Insect species-richness was determined from flower visitors collected throughout the entire flowering period. Circles: percentage species pollinated. Squares: no. species of insect.

cushion-plant zone, but Bombyliidae diminish and are replaced by Sarcophagidae. Fly species-richness, nevertheless drops very abruptly in the upper subnival zone, and the fly pattern, in contrast with the bee pattern is nonlinear. Most of the subnival flies also occur lower down in the cushion-plant zone.

In sharp contrast with bees and flies, butterfly species-richness does not change markedly from one extreme of the Andean zone to the other (Fig. 1). There are still nine species of butterflies in the subnival as compared with only 12 in the subandean zone. The more abundant Andean butterflies fall into three distinct altitudinal groups: 1) *Yramea modesta*, *Cynthia terpischore*, *Phulia nymphula*, and *Andinus venustus* are restricted primarily to the upper subnival area, and only marginally, if at all penetrate into the cushion-plant zone. 2) *Etcheverrius chiliensis* and *Auca coctei* are most abundant in the subandean scrub zone and only marginally penetrate into the cushion-plant zone. 3) *Faunula leucoglène* is widely distributed altitudinally, as are *Tatochila* spp. and *Hypsochila wagenekti*. The ranges of these latter two species seem to be more closely related to physiographic factors rather than altitude, in particular availability of small exposed summits.

Pollination systems—The total flora of the Andean zone encompassing a broader sector

of the same general area as our study site is estimated to include about 240 species. Of these, 20 are either introduced weeds or truly ecotonal species not penetrating to any real extent into the Andean zone. Anemophilous Cyperaceae, Graminaeae, and Juncaceae constitute around 14% of the species on the study site. When seven additional wind-pollinated dicotyledonous species (2 spp. *Chenopodium*; 2 spp. *Nastanthus*; 2 spp. *Senecio*; *Baccharis petiolata*), and the seemingly largely wind-pollinated gymnosperm *Ephedra breana* are added to these, the anemophilous component of the vegetation stands at around 17%. Flower visitors (Appendix II) have been determined for 137 or 75% of the non-abiotically pollinated species of the region, excluding weeds and ecotonal species, for the most part according to their occurrence in each of the three sampling areas. Using the double criterion that vectors must make contact with the stigmas and anthers and account for at least 10% of the total flower visits to be considered significant for pollination, Appendix II reveals that only six of the species studied (*Chaetanthera pentacaenoides*, *C. planiseta*, *Colobanthus subulatus*, *Gilia lacinata*, *Polemonium micranthum*, *Microsteris gracilis*) failed to be visited, signifying that over 95% of the non-biotically pollinated flora is adapted for animal-mediated pollination, and must engage in cross-pollination to some extent. In accordance with the

TABLE 1. Breakdown of pollination mechanisms in 137 non-abiotically pollinated species studied in the Andean zone (2,200–3,600 m) in the Cordón del Cepo, latitude 33°17'S, Cordillera de los Andes in central Chile. The percentage totals exceed 100, as many species are pollinated by more than one vector class

Pollination mechanism	No. of species	%	Estimated % of total flora ^a
Not visited	6	4.32	3.58
Biotically pollinated	131	95.62	75.94
Bee-pollinated	66	50.38	40.01
Fly-pollinated	60	45.80	36.67
Butterfly-pollinated	31	23.66	18.79
Beetle-pollinated	5	3.81	3.02
Nocturnal moth-pollinated	4	3.05	2.42
Hummingbird-pollinated	2	1.52	1.20

^a Based on the estimate of 17% wind-pollinated and 3.58% nonpollinated.

criterion established above, between Areas I–III, 72.52–88.88% (Table 2) of the species are pollinated by one vector class; 11.11–20.87% are pollinated by two and 0–6.89% are pollinated by three, with an average of 1.32, 1.29 and 1.11 in Area I, II and III respectively.

Melittophily: Hymenopterans (principally bees) pollinate 50% of the biotically pollinated flora studied in the Andean zone (Table 1), or an estimate of 40% of the flora as a whole. This mode of pollination is most strikingly represented in the lower Andean zone (Fig. 2), where 67% of the biotically pollinated species rely exclusively or heavily on bees for pollen transfer. Paralleling the drop in species-richness (Fig. 1), hymenopterans pollinate only 44% of the species in the cushion-plant zone (Fig. 2), and in the upper subnival this figure is reduced to 13% (Fig. 1, 2). All Alstroemeriaceae, Hydrophyllaceae, Iridaceae, Labiatae, Leguminosae, Loasaceae, Scrophulariaceae, Solanaceae, and Tropaeolaceae, and most Amaryllidaceae and many Compositae are bee-pollinated in the Andean zone in central Chile. Important bee-pollinated genera are *Adesmia*, *Anarthrophyllum*, *Astragalus*, *Calceolaria*, *Loasa*, *Phacelia*, *Schizanthus*, *Sisyrinchium*, *Solanum*, and *Stachys*. Bee-pollinated species in the upper subnival are *Adesmia capitellata*, *A. glomerula*, *Caiophora coronata*, all restricted to that altitude, and *Loasa caespitosa*, *Phacelia secunda* and *Tropaeolum polyphyllum*, distributed more broadly in the Andean zone.

Psychophily: Butterflies pollinate 24% of the biotically pollinated flora in the Andean zone (Table 1), the equivalent of 19% of the total

TABLE 2. Percentage of species pollinated by 1, 2 . . . n vector types at three altitudinal levels in the Andean zone on the Cordón del Cepo, latitude 33°17'S, Cordillera de los Andes in central Chile. Mean number of vector types is also given

Altitude	n	No. vector types			\bar{x} vector types per plant
		1	2	3	
I: 2,200–2,600 m	91	72.52	20.87	6.55	1.34
II: 2,700–3,100 m	58	77.58	15.51	6.89	1.29
III: 3,200–2,600 m	45	88.88	11.11	0	1.11

flora. While this figure is not very impressive, this mode of pollination is one of the more interesting in the Andean zone, because of the role butterflies play in the upper subnival. In the lower subandean zone, butterflies pollinate 18% of the biotically pollinated flora, constituting a taxonomically restricted set of species mostly belonging to the composite genera *Senecio*, *Mutisia*, and *Chaetanthera*. Many of these are also heavily visited by bees at this altitude. In ascending into the cushion-plant zone and upper subnival butterflies become increasingly important pollinators, pollinating 31% of the subnival species, or almost 2.5 times the number pollinated by bees. The genera of plants pollinated by butterflies in the subnival (*Viola*, *Junellia*, *Oreopolis*, *Draba*, *Oxalis*, *Nototriche*, *Nassauvia*), moreover, derive from a wide range of plant families and a number of the species appear to have bee-pollinated histories.

Myophily: Dipterans pollinate a wide spectrum of species in the Andean zone amounting to 46% of the biotically pollinated species, or 37% of the total flora (Table 1). In the lower subandean zone, where bees predominate, Diptera pollinate only 38% of the biotically pollinated species, and, of these, they are the exclusive visitors of relatively few (*Astericum amenocarpum*, *Mulinum spinosum*, *Sanicula graveolens*—all Umbelliferae; *Chaetanthera euphrasioides*, *Nassauvia heterophylla* and *N. axillaris* of Compositae; *Berberis empetrifolia* of Berberidaceae; *Valeriana* spp. of Valerianaceae; *Acaena pinnatifida* and *Tetraglochin alatum* of Rosaceae; and *Viviania marifolia* of the Chilean endemic family Vivianaceae). In the cushion-plant zone, between 2,600–3,100 m (Fig. 1), dipterans pollinate a far greater proportion of the flora than either bees or butterflies. At this altitude, they are the exclusive pollinators of the physiognomically important umbelliferous cushion plants, and species of *Calandrinia*, commonly found on cushion species. Although it was seen that dipteran

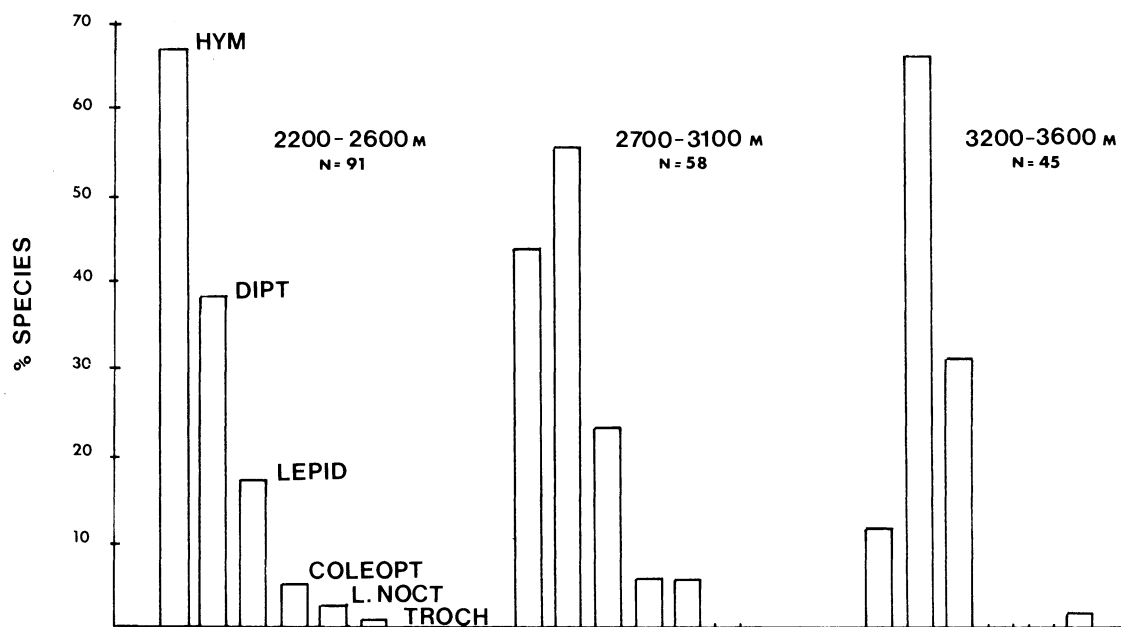


Fig. 2. Percentage of species pollinated by different vector classes at three altitudinal levels in the Andean zone. The total percentage exceeds 100, given that many species are pollinated by more than one vector (see Table 2). n = number of plant species considered at each altitudinal level. LEPID = butterflies only; L. noct. = nocturnal moths.

species-richness dropped very rapidly above 3,100 m, over 60% of the species in the subnival are pollinated by dipterans, often, nevertheless at a very low rate (Arroyo et al., in prep.) and 55% of the biotically pollinated species at this altitude are pollinated by dipterans alone. *Senecio francisci* is visited by bees, flies, and butterflies in the subandean zone, but only by flies in the subnival zone. Like many butterfly-pollinated species at this altitude, those pollinated by dipterans frequently derive from genera pollinated by bees at lower altitudes.

Other mechanisms: Four species, *Leucocoryne ixioides*, *L. pauciflora*, *Tristagma nivale*, and *Oenothera acaulis*, have long-tubed corollas suited to moth-pollination and fail to be visited during the day. *Leucocoryne* flowers are fragrant around 6.00 p.m. Moths have never been observed on any of these species, thus placement in this category is tentative.

Hummingbirds pollinate *Hippeastrum uniflorum* and migrant individuals have also been observed on *Cañaphora coronata*, usually bee-pollinated. Coleopterans transfer pollen in early flowering species of *Oxalis* and *Barneoudia*. Large Buprestidae visit *Hypochaeris*.

Plant-pollinator interactions—Specialist feeding: As Heithaus (1979) has pointed out, oligolecty and polylecty are difficult concepts to apply, since their usage requires knowledge

of the feeding habits of individual insects throughout their entire ranges. In community studies, numerical indices of feeding specialization seem far more appropriate, as small differences in consumer preferences are readily detected. In the Andean zone, specialist feeding, it could be hypothesized, would become increasingly risky as summer weather conditions become less predictable, as occurs on our site with increasing altitude, and opportunistic feeding strategies should be selectively favored, therefore, with increasing altitude. Based on collection data, about one-third of the hymenopterans in the Andean zone appear to be restricted in their feeding to one or a few plant species. Specialist feeders tend to be heavily drawn from the Andrenidae, Colletidae and Halictidae, while anthophorid and megachilid bees are more likely to feed on many plant species. Figure 3 shows the number of bee species feeding on 1, 2 . . . n plant species according to altitude. This comparison shows that narrow specialist feeders occur more frequently in the lower subandean zone, and a clear cut tendency for reduction in specialist feeding with altitude, as we predicted. In Area I, 46% of the bees as far as is known, feed on single plant species; whereas in Area II, the corresponding percentage is only 28.57. In the upper subnival belt, only 1 of five bee species is restricted to a single species. However 3 of the 6 specialists in Area II visit other

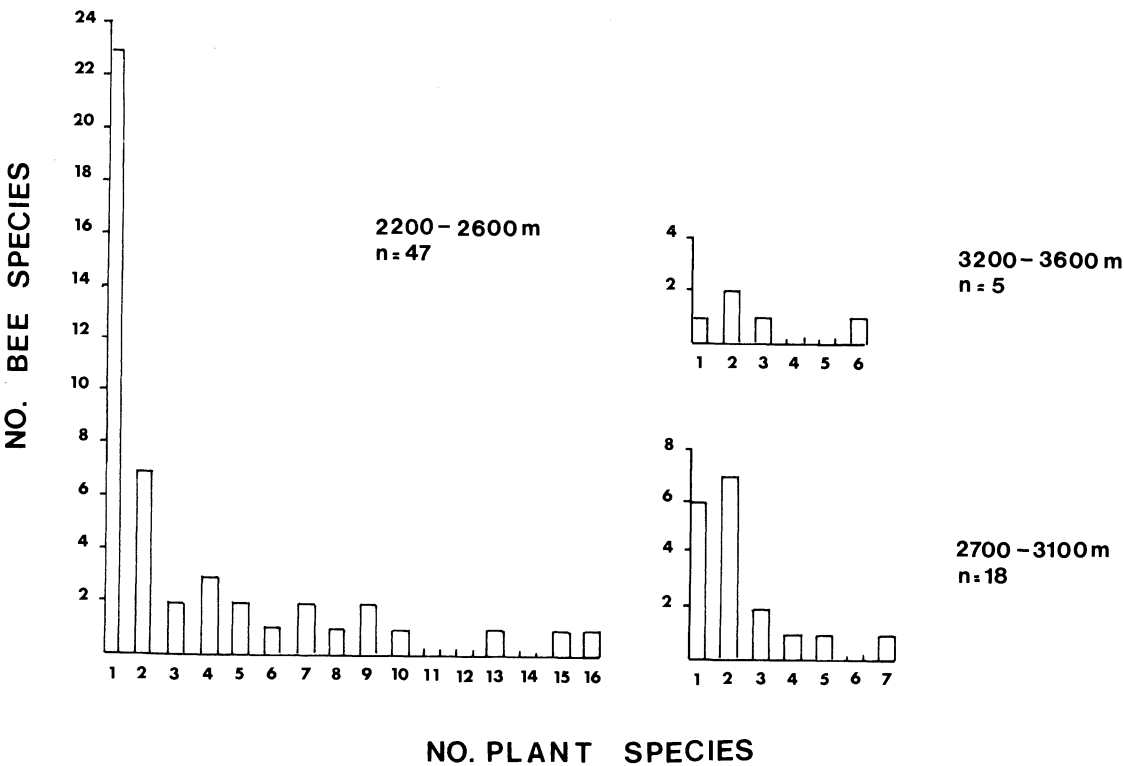


Fig. 3. Number of bee species pollinating 1, 2, . . . n species of plants at three altitudinal levels in the Andean zone. n = number of bee species at each level.

plant species in the subandean zone, while *Megachile semirufa*, which visits a single species in the subnival has several other food plants at lower levels in the Andean zone. Thus, the level of specialist feeding among bees in the cushion-plant zone is even lower than the figures suggest, and, in the subnival, specialist feeders are absent altogether.

The feeding relationships of butterflies tend to be more uniform. Between 40–55% of the butterflies at each altitudinal level feed on sin-

gle species. However, with the exception of *Cynthia terpsichore*, a rare subnival butterfly which thus far has only been observed feeding on *Oxalis* aff. *compacta*, all butterflies are known to visit more than one species when the entire Andean zone is considered. *Faunula leucoglène* tends to be fairly constant on the composite genus *Chaetanthera*. *Yramea modesta* feeds on 12 of the 14 subnival butterfly-pollinated species, while *Etcheverrius chilensis* and *Auca coctei* each feed on ten species.

TABLE 3. Mean, median, and range of bees and wasps, and butterfly species pollinating plants and insect/plant ratios for bee-, butterfly- and fly-pollinated species at three altitudinal levels in the Andean zone^a

	Total insects visiting	Total plants pollinated by these	Insects/pollinating plant				Overall insect/plant ratio
			\bar{x}	SD	Median	Range	
Bee and wasp-pollinated							
I: 2,200–2,600 m	50	43	4.25	4.70	1.0	1–20	1.162
II: 2,700–3,100 m	21	18	2.61	2.40	1.5	1–10	1.166
III: 3,200–3,600 m	5	6	2.33	1.36	2.0	1–5	0.833
Butterfly-pollinated							
I: 2,200–2,600 m	12	14	2.21	1.47	2.0	1–6	0.857
II: 2,600–3,100 m	10	12	2.16	1.52	2.0	1–6	0.833
III: 3,200–3,600 m	9	14	2.07	1.81	2.0	1–8	0.642

^a DIPTERAN Insect/plant ratio: I = 1.293; II = 1.533; III = 0.66.

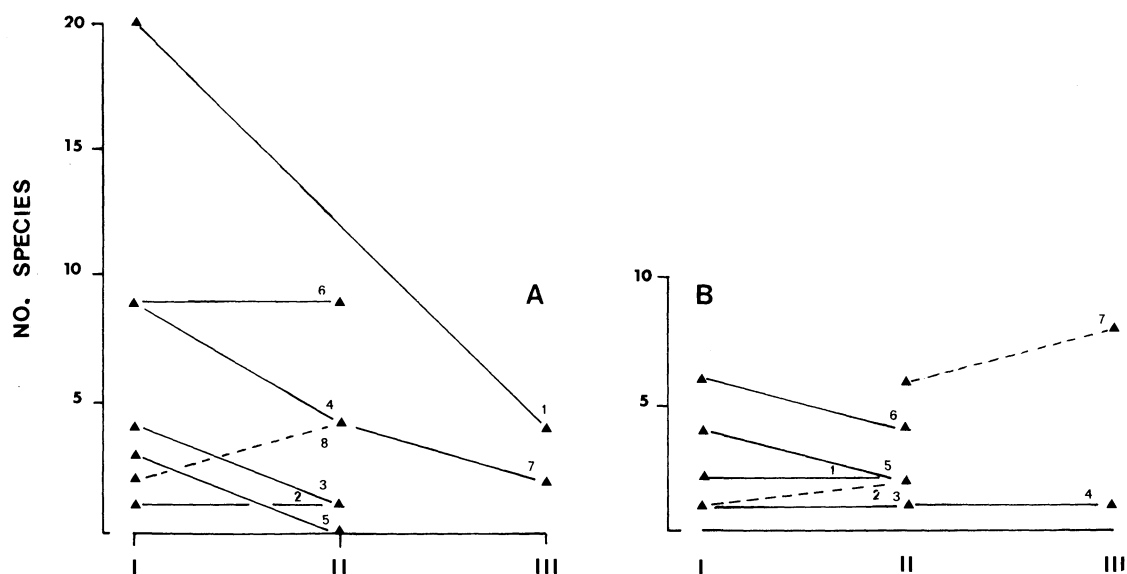


Fig. 4. Number of bees and wasps (A) and butterflies (B) visiting plant species occurring at more than one of the altitudinal levels studied. A: 1 = *Phacelia secunda*; 2 = *Calceolaria arachnoides*, *C. biflora*, *Nothoscordum andinum*, *Rhodophiala montana*, *Tristagma bivalve*; 3 = *Chuquiraga oppositifolia*, *Mutisia sinuata*; 4 = *Senecio bustiosillanus*; 5 = *Senecio francisci*; 6 = *Astragalus curvicaulis*; 7 = *Loasa caespitosa*; 8 = *Anarthrophyllum cumingii*. B: 1 = *Senecio eruciformis*; 2 = *Senecio francisci*; 3 = *Mutisia sinuata*; 4 = *Viola philippii*; 5 = *Senecio bustiosillanus*; 6 = *Chuquiraga oppositifolia*; 7 = *Oxalis* aff. *compacta*.

Pollination-metrics: For plant species using the kinds of pollination vectors not generally well adapted to high altitudes, the potential for cross-pollination will continue to exist so long as *some* of the original vectors are able to colonize higher areas or are replaced by other species. Thus, it becomes of interest to compare the number of insect species and plants they visit at different altitudes, and the relative number of insects visiting particular plant species with broad altitudinal ranges, over different parts of these ranges. The insect/plant ratio is one measure of pollinator availability on a community perspective. This ratio is quite similar for bees and butterflies respectively in the subandean zone and cushion-plant areas (Tables 2, 3). In the subnival, it decreases for both insect groups, but the reduction is far more accentuated for bees. The highest value of the insect/plant ratio for dipterans occurs between 2,600–3,100 m in the cushion-plant zone, where fly-pollinated species also make their largest contribution to total plant cover (Armesto, Arroyo and Villagrán, 1980). The average number of insects visiting each plant species for a given vector class is another way of comparing pollinator availability. This measure (Table 2) is also lower in the subnival zone for both bee- and butterfly-pollinated species; however, as with the insect/plant ratio, the reduction is far more substantial for bees.

The patterns just outlined hold up well for bee-pollinated species with broad altitudinal ranges, when compared for number of visitors along different parts of their ranges (Fig. 4), but the situation for butterfly-pollinated species is distinct. The general trend in the bee-pollinated plants is a decrease in the number of visiting bees per plant species with altitude, most clearly exemplified by *Phacelia secunda* which is pollinated by 20 species of bees in the subandean zone between 2,200–2,600 m and only five species in the subnival. Many species visited by a single bee retain the same species in Area I and II. *Astragalus curvicaulis* is visited by nine species in both Area I and II. The like number is not surprising, as the *Astragalus* plants in Area I and II are continuous. In the only species that seems not to obey the trend (*Anarthrophyllum cumingii*) December cold weather held up bee emergence as this species came into peak flower in Area I.

For butterfly-pollinated species there are two cases of increase in visitors with altitude, in two it decreases and there are three cases with no change. Thus, on balance, decrease in visitors with altitude is not a characteristic of butterfly-pollinated species on our study site. On face value, this result seems contradictory to the lower mean number of butterfly species per plant and the lower butterfly/plant ratio seen

in the subnival. However, in the subnival these last values are heavily influenced by neo-psychophilous species that apparently have only recently shifted to butterfly-pollination (Arroyo, unpubl.) and are only visited by a few species. When species of this nature (e.g., *Tropaeolum polyphyllum*, *Nassauvia lagascae*, and *Nototriche compacta*) are excluded, the mean number of butterflies per plant (2.27) and the butterfly/plant ratio (0.81) fall very close to the values in Area I and II.

DISCUSSION—An abundance of entomophily, as in the Andean zone in central Chile, seems to be the prevailing situation for alpine areas in temperate mountains in general (cf., Schroeter, 1926—Caucasus mountains; Müller, 1880—European Alps in general; Heine, 1937; Primack, 1978—New Zealand mountains; Mani, 1962—Himalayas; Pojar, 1974—British Columbia mountains). The single most outstanding characteristic of the Andean zone in central Chile, as opposed to many other temperate mountain areas, is the richness of the bee fauna and the great abundance of bee-pollination systems, especially in the lower Andean scrub zone between 2,200–2,600 m. This particularly contrasts with New Zealand, also in the Southern Hemisphere, where bee-pollination is very poorly represented in alpine areas (Heine, 1937; Primack, 1978). The rich bee fauna in Chile is a consequence of a number of interrelated climatic and biogeographic features, among which Chile's position in relation to the semi-arid, bee-rich regions of the world (Michener, 1979) is clearly very relevant. Another very important point is that bee-diversity tends to be very high in the lower Mediterranean sclerophyllous scrub zone, the main source area for many of the high Andean bees. Upward migration of bees into the Andean zone at this latitude in the Andes, moreover has also been greatly facilitated by the very gradual nature of the ecotone connecting the Andean zone to the lower Mediterranean vegetation. Finally, excellent summer weather conditions in the high Andes would also have favored the establishment of bees in the Andean zone as the latter came into existence during the final phases of the Andean orogeny in the Quarternary. Moldenke (1976) cites 65 species of bees for all alpine areas in the central and southern Andes in Chile, or only one-third that occurring in the alpine zone in the climatically equivalent Sierra Nevada of California. During the course of this study we have collected 52 species of bees at one site in the Cordón del Cepo alone. Thus the Chile-California gap in alpine bee species-richness is possibly not as great as it is presently envisaged, and only as

the higher areas in Chile are more intensively collected will it be possible to determine its real magnitude.

While bees pollinate a very high proportion of the total Andean flora at 33°S, we have shown that melittophily ceases to be the dominant pollination mode above 2,600 m. Here, not only does bee species-richness fall very rapidly, but also the bee/melittophilous plant ratio and the mean number of bee species per melittophilous species go down, progressively fewer bee families are represented at the higher altitudes, and specialist feeding, which was seen to be substantially represented in the subandean scrub zone, is eventually eliminated as the subnival zone is reached. In contrast, the proportions of plants relying on flies and butterflies, respectively, increase with altitude, even in the face of greatly reduced dipteran species-richness in the subnival. Butterflies and flies, moreover, pollinate increasingly broader taxonomic spectra of plants as altitude increases, and, as it was argued, recent shifts from bee- to butterfly-pollination seem to have been a common tendency in the evolution of the subnival flora. This vertical sequence in the relative importance of different pollination modes apparently is not unique to the Andes in central Chile, but in fact it is revealed by the literature to be rather general on high temperate mountains. Müller (1880), long ago stated that lepidopterans, principally butterflies, are more frequent visitors and pollinators above treeline in the European Alps than in adjacent lowland areas. Mani (1962) reports that bee-pollinated species disappear completely above 4,000 m in the Himalayas and are thereafter replaced by species with brilliantly colored flowers pollinated by flies and butterflies, just as we have encountered in central Chile. Pojar (1974) intimates that lepidopterans are of major significance in the subalpine meadow he studied in British Columbia, and Primack (1978) has pointed out how important moth-pollination is in the bee-depauperate alpine of New Zealand. There is also some suggestion for similar changes in species-richness as alpine zones intergrade into tundra at higher latitudes. According to Downes (1965), dipterans and lepidopterans are far better represented than hymenopterans in the Arctic in general. This is also implicit in Mosquin and Martin's (1967) list of flower visitors to Melville Island, Canada, and in Kevan's (1972) study of Lake Hazen Arctic plants, although at Lake Hazen the few species of bumblebees seem to pollinate proportionately more of the plants studied than the lepidopterans. Unfortunately, there are no comparative data for the subantarctic region

at this stage. Cruden (1972) found birds to be more efficient pollinators than bees with increasing altitude at high elevations in Mexico. Thus, again, it is of great interest that bees become less important pollinators at high elevations in the tropics. Cruden (1972) relates lack of bees to the cloudy weather conditions which are unsuitable for bee flight.

The controlling factors for changes in pollinator spectra on high mountains, as in central Chile, are evidently of great interest for understanding the evolution of high-altitude floras, yet at this point nothing is very clear, and there is evidently much need for studies on the comparative energetics of the insect groups involved. Butterflies (Watt, Hoch and Mills, 1974), and presumably flies, are less energy-demanding pollinators than bees (Heinrich and Raven, 1972), and thus granting that these insect groups increase their population levels to the extent that their pollinating efficiency matches or exceeds that of bees, it might be advantageous for plants to turn away from bees. However, this does not answer the ultimate question as to why bees excel less than butterflies and flies at high elevations. Towards a preliminary analysis of the problem, we discuss two quite different factors, both ultimately tied to peculiarities of the high-elevation environment that might be contributing to the altitudinal patterns observed. Firstly, such patterns might be the result of different ecological responses by bees, butterflies, and flies to summer daytime temperatures as they affect the net energy budget of the insects in question. In continental mountains in general, temperatures decrease by approximately 6.5 C per 1,000-m increase in elevation. In the subandean scrub zone on our study site, for example, the mean temperature at the height insects fly during the month of January (11–1 p.m.) of 1980 was 23 C, whereas, the corresponding temperature in the upper subnival zone was only 14 C, and temperature drops to 6–12 C in the afternoon were quite common at this last altitude. It is now well established that hymenopterans (Heinrich, 1975), lepidopterans (Heinrich, 1972) and dipterans (Heinrich and Pantle, 1975) must elevate their thoracic temperature considerably above ambient temperature to engage in flight activity. For bumblebees T_{Th} can be in the range of 36–45 C (Heinrich, 1975), for syrphid flies T_{Th} of 26–32 C has been recorded (Heinrich and Pantle, 1975), and some butterflies (Watt, 1968) require T_{Th} above 30 C. As these temperature ranges are well above those registered in the Andean zone in the Andes of Chile, and significantly above in the upper subnival zone, this means

that all of the insect groups must be resorting to some form of thermoregulation, which if by endothermy, would involve increasingly large energy expenditures as elevation increases. A seemingly very important and relevant difference in behavior of bees as compared with butterflies and flies, stems from the fact that since the latter do not engage in feeding their young and in nest warming activities, they are able to engage in energetically free behavioral thermoregulation. In the high Andes this is most readily appreciated in the contrasting foraging patterns of these insect groups. Butterflies and flies tend to begin pollinating relatively early in the morning in the subnival zone (9–10 a.m.) and continue their activities until wind or cloud cover appears in the early afternoon. The typical behavioral pattern consists of low flight, foraging at a small number of flowers alternating with sun-basking stops on warm stones on the part of the butterflies, or actually among flowers themselves in the case of the flies, much in the same way described by Hocking and Sharplin (1965) and Kevan (1975) for Arctic Diptera. During intermittent periods of cloud cover, butterflies change from foraging to seeking protection under loose stones. Watt (1969) and Heinrich (1972) have shown that the high thoracic temperatures required to keep butterflies in flight can be achieved largely through such sun-basking alone, and Kevan's (1975) work demonstrates how flies may benefit immensely from the heat emitted by flowers. The high subnival bees in the Andes of central Chile, in contrast, invariably begin pollinating later in the day (11–1 p.m.), evidently requiring more time to warm up initially. Foraging tends to be continuous for 5–10 min, punctuated by trips away from the floral resource, presumably for nest provisioning. As the activity of bees tends to be continuous, therefore, all thermoregulation is probably endothermic, and given the low ambient temperatures, this must involve enormous energetic costs on their part. If this last point is added to the fact that bees must collect enough nectar and pollen to sustain themselves as well as their young over a very limited time period in the day suitable for pollination, whereas flies and butterflies need only collect for their own consumption (which will be significantly lower because of possibilities for behavioral thermoregulation), then the energy demands on bees could become so great with increasing altitude as to prevent the exploitation of high cold areas.

A second reason why bees might be less able to persist in high cold areas stems from their overwintering habits. Lepidopterans overwinter in the larval stage, protected between the

leaves of the larval host plant, or simply on the ground. In the subnival in central Chile, megachilid bees, at least, are ground nesters. The latter, unless located on exposed shelves where snow blows away early in the spring, would especially be at a disadvantage in early spring, because the substrate usually remains saturated for over a month or so after snow melt. Under these conditions, butterflies could complete their life cycles more rapidly than bees, and butterfly populations would certainly be less subject to such environmental hazards as local avalanching and the like. In this respect we know that the high subnival bees do not emerge until mid-January above 3,100 m, whereas butterflies begin flying by late November at the same altitude. It is not known whether high Andean butterflies are univoltine or bivoltine.

The high level of specialist feeding detected in the subandean scrub zone at our study site is fairly typical of bee species-rich areas in semi-arid climates (Moldenke, 1976; Michener, 1979; Heithaus, 1979). Evolutionarily speaking, the subandean situation seems to be a carry-over from that prevailing lower down in the Mediterranean scrub communities, from whence, as was mentioned earlier, most high Andean bees have been derived. Heithaus (1979) examined a number of alternate hypotheses for specialist feeding and concluded that competitive pressures between consumer species could explain some of the variation seen between tropical and temperate communities. According to competition theory, lack of specialist feeding at the high altitudes in the Andean zone would be due to relaxation of competition where the number of consumers is now low. We hypothesized that specialist feeding would also be far too risky under the increasingly unpredictable weather conditions characterizing our particular altitudinal gradient. There is no way at present of distinguishing between these two alternatives, and indeed, there is some reason to suspect that neither would be validated. In the subandean zone, it is notable that specialist feeders tend on the average to be smaller than polylectic species. Thus, the dropout in specialist feeding we have observed with altitude might be reflecting selection against smaller bees, which because of greater heat loss through convection would be even less adapted to high cold environments than larger-sized bees.

Finally, we recall again the interesting tendency for melittophilous species with wide altitudinal ranges in the Andean zone to be visited by decreasing numbers of bee species with altitude. This tendency seems to be indicating that bee-pollination must in fact remain rela-

tively profitable for some plants at high altitudes, despite the very large amounts of energy they would have to offer. Viewing the development of the Andean community over evolutionary time, it is also evident that upward range extensions in self-incompatible species serviced by many bees should be more possible than in self-incompatible species pollinated by a small number of bees, for the probability that at least one will be able to adapt to the higher altitude as a plant species increases its altitudinal range will increase as a function of the original bee number. Expressed in another fashion, self-incompatible species that have managed to colonize high areas where pollination rates are exceedingly low (Arroyo et al., in prep.) are more likely to be generalists in terms of the pollinators they attract.

LITERATURE CITED

- ARMESTO, J., M. T. KALIN ARROYO, AND C. VILLAGRÁN. 1980. Altitudinal variation, cover and size structure of umbelliferous cushion plants in the high Andes of central Chile. *Oecol. Gen.* 1(4): 331-336.
- ARROYO, M. T. KALIN, J. ARMESTO, AND C. VILLAGRÁN. 1981. Plant phenological patterns in the high Andean cordillera in central Chile. *J. Ecol.* 69: 205-223.
- BAKER, H. G., AND I. BAKER. 1979. Sugar analyses of floral nectars and their significance. In T. S. Elias and B. A. Bentley [eds.], *The biology of nectars*. Columbia University Press, New York.
- CRUDEN, R. W. 1972. Pollination in high elevation ecosystems: relative effectiveness of birds and bees. *Science* 176: 1439-1440.
- DOWNES, J. A. 1965. Adaptations of insects in the Arctic. *Ann. Rev. Entomol.* 10: 257-274.
- FAEGRI, K., AND L. VAN DER PIJL. 1979. *The principles of pollination ecology*, 3rd ed. Pergamon Press, Oxford.
- HEINE, E. M. 1937. Observations on the pollination of New Zealand flowering plants. *Trans. Proc. R. Soc. N.Z.* 67: 133-148.
- HEINRICH, B. 1972. Thoracic temperatures of butterflies in the field near the equator. *Comp. Biochem. Physiol.* 43A: 459-467.
- . 1974. Thermoregulation in endothermic insects. *Science* 178: 747-756.
- . 1975. Thermoregulation in bumblebees. II. Energetics of warm up and free flight. *J. Comp. Physiol.* 96: 155-166.
- , AND C. PANTLE. 1975. Thermoregulation in small flies (*Syrphus* sp.) basking and shivering. *J. Exp. Biol.* 62: 599-610.
- , AND P. H. RAVEN. 1972. Energetics and pollination ecology. *Science* 176: 597-602.
- HEITHAUS, R. 1979. Flower feeding specialization in wild bee and wasp communities in seasonal neotropical habitats. *Oecologia* 42: 174-194.
- HOCKING, B., AND D. SHARPLIN. 1965. Flower basking by Arctic insects. *Nature* 206: 215.
- KEVAN, P. G. 1972. Insect pollination of high Arctic flowers. *J. Ecol.* 60: 831-847.
- . 1975. Sun-tracking furnaces in High-Arctic flowers: significance for pollination and insects. *Science* 189: 723-726.

- MANI, M. S. 1962. Introduction to high altitude entomology: insect life above timberline in the north-western Himalayas. Methuen, London.
- MICHENER, C. D. 1979. Biogeography of the bees. *Ann. Mo. Bot. Gard.* 66: 277–347.
- MOLDENKE, A. R. 1976. Evolutionary history and diversity of the bee faunas of Chile and Pacific North America. *Wash. J. Bot.* 34: 147–177.
- MOSQUIN, T., AND J. E. H. MARTIN. 1967. Observations on the pollination biology of plants on Melville Island, N. W. Canada. *Can. Field Nat.* 81: 201–205.
- MÜLLER, H. 1880. The fertilisers of alpine flowers. *Nature* 21: 275.
- POJAR, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. *Can. J. Bot.* 52: 1819–1834.
- PRIMACK, R. 1978. Variability in New Zealand montane and alpine pollinator assemblages. *N.Z. J. Ecol.* 1: 66–73.
- SCHROETER, C. 1926. *Das Pflanzenleben der Alpen* Zürich verlag von albein. Raststein.
- STILES, F. G. 1978. Temporal organization of flowering among the hummingbird food-plants of a tropical wet forest. *Biotropica* 10: 194–210.
- WATT, W. B. 1968. Adaptive significance of pigment polymorphism in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution* 22: 437–458.
- . 1969. Adaptive significance of pigment polymorphism in *Colias* butterflies. II. Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*. *Proc. Nat. Acad. Sci. U.S.A.* 63: 767–774.
- , P. C. HOCH, AND S. G. MILLS. 1974. Nectar resource by some *Colias* butterflies. *Oecologia* 14: 353–374.
- WHELAN, R. J., AND A. H. BURBIDGE. 1980. Flowering phenology, seed set and bird pollination of five western Australian *Banksia* species. *Aust. J. Ecol.* 5: 1–7.

APPENDIX I. Inventory of pollinating insects collected in the high Andes of central Chile (33°17'S); families are arranged according to species abundance^a

DIPTERA

BOMBYLLIIDAE (19 spp.): *Lycophlaeba infumata*; *L. lugubris*; *Sericosoma turva*; *Truphoechus bellus*; *Villa arenarius*; *V. discolor*; *V. durvillei*; *V. flavicula*; *V. gayi*; *V. guttapennis*; *V. hypoxantha*; *V. semifuscata*; *V. sp. prox. verdensis*; indet., 6 spp.

SYRPHIDAE (17 spp.): *Allograpta*, sp.-1; *Atelogluta*, sp.-1; *Carpocallis chalconatata*; *Copestylum scutellatum*; *Dolicogyna nigripes*; *Dolicogyna*, sp.-1; *Dolicogyna*, sp.-2; *Eristalis tenax*; *Habromyia lipoflava*; *Mesogramma*, sp.-1; *Mesogramma*, sp.-1; *Scaeva melanostoma*; *Syrphus simulus*; *Volucella escomeli*; indet., 4 spp.

TACHINIDAE (13 spp.): *Admontia communis*; *Actia*, sp.-1; *Atelogluta*, sp.-1; *Prosopochaeta caliginosa*; *Psecacera*, sp.-1; *Ruiziella luctuosa*; *Spathipalpus australis*; *Steatosome rufiventris*; indet., 4 spp.

SARCOPHAGIDAE (11 spp., all indet.)

ANTHOMYIIDAE (5 spp., all indet.)

TABANIDAE (5 spp.): *Dasybasis*, sp.-1; *Dasybasis*, sp.-2; *Mycteromyia fusca*; *Scaptia atra*; 1 sp., indet.

AGROMYZIDAE (2 spp., indet.); BIBIONIDAE (2 spp., indet.); NEMISTRINIDAE (2 spp.): *Eurygostomyia philippii*; 1 sp., indet.; ASILIDAE (1 sp., indet.); CALIFORNIDAE (1 sp., indet.); MUSCIDAE (1 sp., indet.); FAMILY UNKNOWN (2 spp.).

LEPIDOPTERA

PIERIDAE (6 spp.): *Colias vauthierii*; *Hypsochila wagenknekti*; *Phulia nymphula*; *Tatochila blanchardii*; *T. mercedis*; *T. theodice*.

NYMPHALIDAE (4 spp.): *Cynthia terpsichore*; *Yramea cytherys*; *Y. lathonoides*; *Y. modesta*.

LYCAENIDAE (3 spp.): *Andinus venustus*; *Pseudolucia chilensis*; *Thecla bicolor*.

SATYRIDAE (3 spp.): *Auca coctei-pales*; *Etcheverrius chilensis*; *Faunula leucoglène*.

HYMENOPTERA

MEGACHILIDAE (16 spp.): *Anthidium adriani*; *A. chilensis*; *A. decaspilum*; *A. funereum*; *A. gayi*; *Anthidium*, sp.-1; *Coelioxys*, sp.-1; *Lithurgomma wagenknekti*; *Megachile sauleyi*; *Megachile semirufa*; *Megachile* 5 spp., indet.; *Stenanthidium espinosai*.

ANTHOPHORIDAE (12 spp.): *Alloscirtetica gayi*; *A. rufitarsis*; *Alloscirtetica*, sp.-1; *Anthophora incerta*; *Anthophora*, sp.-1; *Centris cineraria*; *C. nigerrima*; *Isepeolus niveiventris*; *Mesonychium gayi*; *Svatrides melanura*; *Tapinotaspis caerulea*; *T. herbsti*.

COLLETIDAE (11 spp.): *Cadeguala occidentalis*; *Caupolicana dimidiata*; *Chilicola*, 2 spp. indet.; *Chilimelissa*, sp.-1; *Colletes araucariae*; *C. fulvipes*; *Colletes*, sp.-1; *Hemicolletes ruizi*; *Xanthocolletes incahuasi*; *X. sicheli*.

HALICTIDAE (6 spp.): *Caenohalictus*, 3 spp. indet.; *Corynura*, sp.-1; *Dialictus*, sp.-1; *Ruizantheda mutabilis*.

VESPIDAE (5 spp.): *Gayella reedi*; *Hypodynerus chilotus*; *Hypodynerus*, 3 spp. indet.

ANDRENIDAE (4 spp.): *Lipanthus sabulosus*; *Lipanthus*, 2 spp. indet.; *Panurginae*, sp.-1.

APIDAE (1 sp.): *Bombus dahlbomii*.

ICHNEUMONIDAE (1 sp.) indet.

TIPIDAE (1 sp.) *Elaphroptera relicta*.

^a Number undetermined species include new taxa, taxa of dubious affinity and taxa for which names have not been obtainable.

APPENDIX II. Flower visitors and relative proportions of flowers visited by each vector class for high Andean species in central Chile (33°17'S); I = 2,200–2,600 m; II = 2,700–3,100 m; III = 3,200–3,600 m elevation, respectively

- ALSTROEMERIACEAE: *Alstroemeria pallida* Grah. I (14, 1,419)* HYM (1.000): *Alloscirtetica*, sp.–1, *A. gayi*, *Anthidium funereum*, *Megachile semirufa*, Panurginae sp.–1.
- AMARYLLIDACEAE: *Hippeastrum uniflorum* (Phil.) Baker I (10, 41)* TROCH (1.000): n.i.; *Leucocoryne ixioides* (Hook.) Lindl. I (11, 220)* LEPID: n.i.; *L. pauciflora* Phil. I (11, 429)* LEPID: n.i.; *Nothoscordum andinum* Poepp Kunth I (4, 159) HYM (0.856): *Caenohalictus*, sp.–1; *DIPT*^d (0.035): *Scaeva melanostoma*, n.i.^b (0.056); II (14, 868) HYM (0.964): *Caenohalictus* sp.–1; *DIPT* (0.035): *Scaeva melanostoma*; *Rhodophiala montana* Phil. I (3, 69) HYM (1.000): *Megachile* sp.–1; II (2, 29): HYM (1.000): *Megachile* sp.–1; *Tristagma bivalve* (Lindl.) Traub. I (2, 195) HYM (0.333): *Caenohalictus* sp.–1; *DIPT* (0.666): n.i.; *T. nivale* Peopp. I (4, 206)* LEPID: n.i.; II (4, 353) LEPID: n.i.; *T. sessile* (Phil.) Traub. I (2, 68) *DIPT* (1.000): n.i.
- BERBERIDACEAE: *Berberis empetrifolia* Lam. I & II (11, 3981) HYM (0.010): *Caenohalictus* sp.–1, *Hypodynerus* sp.–1; *DIPT* (0.990): Sarcophagidae, *Scaeva melanostoma*, Tachinidae; *B. montana* Gay I (2, ca. 2,000)* HYM: n.i.; *DIPT*: n.i.
- BORAGINACEAE: *Cynoglossum creticum* Mill I (8, 163) HYM (1.000): *Megachile* sp.–1.
- CACTACEAE: *Trichocereus chiloensis* Br. & Rose I (2, 10)* HYM (1.000): *Lipanthus* sp.–1 & 2.
- CALYCERACEAE: *Nastanthus aglomeratus* Miers III (5, 1,500) HYM (1.000)*: ants; *N. spathulatus* (Phil.) Miers II & III (7, ca. 4,000) HYM (1.000)*: ants.
- CARYOPHYLLACEAE: *Cerastium arvense* L. I (26, 1,029) *DIPT* (0.920): Bibionidae sp. 1 & 2, *Habromyia lipoflava*, *Scaeva melanostoma*, n.i. (0.136); *COLEOPT*: (0.070): n.i.; II (31, 2,296) HYM (0.053): *Bombus dahlbomii*, *Caenohalictus* sp.–1, *Hypodynerus* sp.–1; *LEPID* (0.067): *Pseudolucia chilensis*; *DIPT* (0.483): Bombyliidae, Tachinidae, n.i. (0.108); *COLEOPT* (0.398): n.i.; III (16, 804) *DIPT* (1.000): Bombyliidae, n.i. (0.080); *C. montioides* Naud. II *(2, 135) *DIPT* (1.000): n.i.; III *DIPT*: n.i.; *Colobanthus subulatus* (D'Urv.) Hook. f. III (6, 498) no visitors.
- COMPOSITAE: *Chaetanthera apiculata* (Remy) Meyen (6, 27)* III *LEPID* (1.000): *Faunula leucoglène*, *Yramea modesta*; *C. euphrasoides* (DC) Meigen I & II (13, 492) HYM (0.184): *Caenohalictus* sp.–1; *DIPT* (0.818): *Lycophlaeba lugubris*, *Scaeva melanostoma*, *Spathipalpus philippii*, *Villa arenarius*, *V. gayi*, *V. flavicura*, *V. hypoxantha*, *V. semifuscata*, *Villa* spp.; *C. flabellata* D. Don III* *LEPID* (1.000): *Faunula leucoglène*; *C. lycopodioides* (Remy) Cabr. III (9, 602) *LEPID* (1.000): *Faunula leucoglène*, *Yramea modesta*; *C. microphylla* (Cass.) H. & A. I (2, 178) *LEPID* (0.429): *Faunula leucoglène*; *DIPT* (0.571): *Euryglostromyia philippii*, *Scaeva melanostoma*; *C. pentacaenoides* Cabr. III (6, 345): no visitors; *C. planista* I & II no visitors; *C. pusilla* (D. Don) H. & A. II (30, 1,462) *LEPID* (0.897): *Faunula leucoglène*, *Yramea modesta*; *DIPT* (0.101): Tabanidae; *Chuquiraga oppositifolia* D. Don I (31, 3,937) HYM (0.227): *Anthidium funereum*, *Bombus dahlbomii*, *Centris nigerrima*, *Megachile* sp.–1; *LEPID* (0.545): *Auca coctei-pales*, *Etcheverrius chiliensis*, *Faunula leucoglène*, *Tatochila blanchardii*, *T. mercedis*; *DIPT* (0.228): *Scaeva melanostoma*, *Villa semifuscata*; II (12, 5,305) HYM (0.206): *Bombus dahlbomii*; *LEPID* (0.578): *Andinus venustus*, *Auca coctei-pales*, *Etcheverrius chiliensis*, *Faunula leucoglène*; *DIPT* (0.215): *Scaeva melanostoma*, n.i. (0.080); *Erigeron andicola* DC II & III*(2, 146) *DIPT* (1.000): n.i.; *Haplopappus chysanthemifolius* (Less.) DC I (6, 184) **DIPT* (0.710): *Scaeva melanostoma*; *LEPID* (0.090): n.i.; HYM (0.290): n.i.; *H. sericeus* Phil. I (4, 149) HYM (0.328): *Megachile semirufa*, Panurginae sp.–1; *LEPID* (0.546): *Auca coctei-pales*, *Etcheverrius chiliensis*, *Yramea lathonoides*; *DIPT* (0.124): *Scaeva melanostoma*; *Hypochoeris* sp. indet. I (9, 171) HYM (0.219): *Centris cineraria*, *Ruizantheda mutabilis*; *LEPID* (0.028): *Tatochila mercedis*; *DIPT* (0.479): *Scaeva melanostoma*, *Villa* spp.; *COLEOP* (0.274): Buprestidae; *Leuceria landbeckii* (Phil.) Reiche I (5, 120) HYM (0.750): *Megachile* sp.; *DIPT* (0.250): *Scaeva melanostoma*; *L. salina* (Remy) Hieron. III (5, 176) *DIPT* (1.000): *Scaeva melanostoma*; *Madia sativa* Mol. I (10, 357) HYM (0.574): *Centris cineraria*, *Hemicolletes ruizii*, *Corynurus* sp., *Dialictus* sp.^a *DIPT* (0.425): Bombyliidae; *Mustisia acerosa* Poepp. ex Less. I (6, 204) *LEPID* (1,000): *Auca coctei-pales*, *Etcheverrius chiliensis*, n.i. (0.444); *M. sinuata* Cav. I (11, 319) HYM (0.568): *Bombus dahlbomii*, *Isepeolus niveiventris*, *Megachile* sp.–1, *M. semirufa*; *LEPID* (0.372): *Etcheverrius chiliensis*; *DIPT* (0.059): *Scaeva melanostoma*; II (2, 39) HYM (0.400): *Bombus dahlbomii*; *LEPID* (0.600): *Etcheverrius chiliensis*; *M. subulata* R. & P. I (7, 121) HYM (0.603): *Anthidium chilensis*; *LEPID* (0.395): *Auca coctei-pales*, *Etcheverrius chiliensis*; *Nardophyllum lanatum* (Meyen) Cabr. I (5, ca. 1,200) *LEPID* (0.214): *Auca coctei-pales*; *DIPT* (0.786): n.i.; *Nassauvia axillaris* (Lag.) D. Don II (9, 818) HYM (0.098): *Hypodynerus* sp.; *DIPT* (0.902): Bombyliidae, Sarcophagidae, *Scaeva melanostoma*; *N. heterophylla* (Phil.) Reiche I & II (22, 1,119) *DIPT* (1.000): Bombyliidae, *Dasybasis* sp.–1, *Vibrissomyia* sp., *Villa verdensis*, *Villa* spp.; *N. lagascae* (D. Don) var. *lagascae* III (19, 258) *LEPID* (0.429): *Phulia nymphula*, *Yramea modesta*; *DIPT* (0.569): Sarcophagidae, n.i. (0.297); *N. pinnigera* D. Don III (8, 189) *DIPT* (1.000) n.i.; *N. pungens* Phil. III (6, 1,144) HYM (0.093): *Bombus dahlbomii*; *DIPT* (0.906): Bombyliidae, *Scaeva melanostoma*; *Perezia carthamoides* (D. Don) H. & A. I (14, 132) HYM (0.001): n.i.; *LEPID* (0.181): *Auca coctei-pales*, *Etcheverrius chiliensis*; *DIPT* (0.187): *Ruiziella luctuosa*, *Truphloeuchus bellus*; *Senecio bustillosianus* Remy I (25, 2,513) HYM (0.504): *Anthidium chilensis*, *A. funereum*, *Anthophora incerta*, *Bombus dahlbomii*, *Centris cineraria*, *Hypodynerus* sp. 3, *Megachile* sp.–1; *M. semirufa*, Panurginae sp.–1, n.i. (0.050); *LEPID* (0.826): *Auca coctei-pales*, *Etcheverrius chiliensis*, *Faunula leucoglène*, *Tatochila mercedis*; *DIPT* (0.289): *Eristalis tenax*, Sarcophagidae, *Scaeva melanostoma*, *Spathipalpus philippii*, *Ruiziella luctuosa*, *Villa verdensis*, *Villa* spp., n.i. (0.002); II (7, 517) HYM (0.814): *Bombus dahlbomii*, *Anthidium funereum*, *Megachile* sp.–1, *Megachile semirufa*; *LEPID* (0.108): *Auca coctei-pales*, *Etcheverrius chiliensis*; *DIPT* (0.084): *Scaeva melanostoma*, Sarcophagidae, Tachinidae, n.i. (0.003); *S. crithmoides* H. & A. III (9, 457) no visitors *S. erucaeformis* Remy I & II (15, 2,547) HYM (0.520): *Anthidium funereum*,

APPENDIX II. Continued.

- Bombus dahlbomii*, *Chilicola* sp.-1, *Megachile* sp.-1, *M. semirufa*, *Hypodynerus* sp.-1 & 3, *Caenohalictus* sp.-1, *Panurginae* sp.-1; LEPID (0.439): *Andinus venustus*, *Auca coctei-pales*, *Etcheverrius chiliensis*, *Tatochila* sp.; DIPT (0.021): n.i.; *S. francisci* Phil. I (6, 373) HYM (0.501): *Anthidium funereum*, *Megachile semirufa*, *Panurginae* sp.-1; LEPID (0.097): *Auca coctei-pales*, *Hypochila wagenknechti*; DIPT (0.402): *Bombyliidae*, *Tachinidae*; II (8, 623); LEPID (0.664): *Faunula leucoglène*, *Etcheverrius chiliensis*, n.i. (0.124); DIPT (0.334): *Scaeva melanostoma*, *Vibrissomyia* sp., *Villa* spp.; III (5, 130)* DIPT (1.000): *Scaeva melanostoma*; *S. lithostaurus* Cabr. I (1, 69) HYM (0.555): *Alloscirtetica* sp.-1; LEPID (0.333): *Auca coctei-pales*; DIPT (0.110): *Scaeva melanostoma*; *S. Looseri* Cabr. III (7, 862) no visitors; *Senecio* sp. indet. II (10, 1,540) HYM (0.306): *Anthidium funereum*, *Bombus dahlbomii*; LEPID (0.124): *Etcheverrius chiliensis*, *Faunula leucoglène*, *Pseudolucia chilensis*; DIPT (0.569): *Bibionidae* sp.-1, *Bombyliidae*, *Scaeva melanostoma*, *Tachinidae*, *Villa* spp. n.i., (0.086); *Werneria pygmaea* Gill. ex Hook. et Arn. II (3, 231) DIPT (1.000): *Sarcophagidae*, n.i. (0.170).
- CRUCIFERAE: *Draba gilliesii* H. & A. III (17, 9,059) LEPID (0.652): *Phulia nymphula*; DIPT (0.348): *Sarcophagidae*, *Scaeva melanostoma*; *D. tenuis* Barn. III (18, 1,932) HYM (0.240): ants; DIPT (0.518); *Syrphidae*, *Tachinidae*, n.i. (0.022); COLEOPT (0.240): n.i.; *Cardamine nivalis* Gill. ex Hook. I, II & III DIPT*: n.i.; *Lepidium suffruticosum* Phil. I (2, 42) DIPT (1.000): *Ruizella luctuosa*; *Stenodraba stenophylla* (Leyb.) O. E. Schulz II (12, 410) DIPT (1.000): *Anthomyiidae*, n.i. (0.254).
- EUPHORBIACEAE: *Euphorbia portulacoides* L. emend. Spreng. I & II (14, 2,978) HYM (0.169): *Vespidae*; DIPT (0.830): *Scaeva melanostoma*, *Tabanidae*, *Tachinidae*, n.i. (0.302).
- GERANIACEAE: *Erodium circutarium* (L.) L'Herit. ex Aiton I (5, 99) DIPT (1.000): *Scaeva melanostoma*, n.i. (0.864).
- HYDROPHYLLACEAE: *Phacelia secunda* J. F. Gmel. I (43, 4,605) HYM (0.930): *Alloscirtetica* sp.-1, *A. rufitarsis*, *Anthidium chilensis*, *A. adriani*, *A. decapsilum*, *A. gayi*, *Anthophora incerta*, *Anthophora* sp.-1, *Bombus dahlbomii*, *Cadeguala occidentalis*, *Caenohalictus* sp.-1, *Centris cineraria*, *Colletes araucariae*, *Hypodynerus* sp.-3, *Lithurgomma wagenknechti*, *Megachile* sp. 1 & 2, *M. semirufa*, *Ruizantheda mutabilis*, *Svastrides melanura*, n.i. (0.003); DIPT (0.069): *Scaeva melanostoma*, *Scaptia atra*, *Truphloechus bellus*, *Villa verdensis* III: HYM (0.979): *Anthidium* sp.-1, *Bombus dahlbomii*, *Megachile* sp.-5, *M. semirufa*; *Stenanthidium espinosai*; DIPT (0.021): *Scaeva melanostoma*.
- IRIDACEAE: *Sisyrinchium arenarium* Poepp. I (21, 2,370) HYM (1.000): *Anthidium chilensis*, *Caenohalictus* sp. 1, 2, & 3, *Megachile* sp.-2, *Tapinotaspis caerulea*, *T. herbsti*, n.i. (0.057); *S. junceum* E. Mey. ex K. Presl. var. *junceum* I (17, 816) HYM (0.990): *Caenohalictus* sp.-1, *Elaphroptera relicta*; DIPT (0.009): *Sarcophagidae*, *Tachinidae*; COLEOPT (0.001): n.i.; *S. philippii* Klatt I (21, 1,587) HYM (0.527): *Caenohalictus* sp.-1, *Centris cineraria*; DIPT (0.054): *Scaeva melanostoma*; COLEOPT (0.417): n.i.; *Solenomelus sisyrinchium* (Griseb.) Pax. ex Diels I (4, 24)* HYM (1.000): n.i.
- LABIATAE: *Stachys albicaulis* Lindl. I (55, 9,676) HYM (0.957): *Alloscirtetica* sp.-1, *A. gayi*, *A. rufitarsis*, *Anthidium gayi*, *Anthophora* sp.-1, *A. incerta*, *Bombus dahlbomii*, *Cadeguala occidentalis*, *Centris cineraria*, *C. nigerrima*, *Megachile* sp. 1 & 2, *M. semirufa*; DIPT (0.043): *Eurygostromyia philippii*, *Scaeva melanostoma*.
- LEGUMINOSAE: *Adesmia* affin. *aconcaguensis* Burk. I (22, 1,455) HYM (0.541): *Chilimelissa* sp.-1, *Xanthocolletes sicheli*; DIPT (0.457): *Scaeva melanostoma*, *Villa semifusca*, *Villa* spp. n.i. (0.311); *A. brachysemon* I (4, 237) HYM (0.803): *Anthidium decapsilum*, *Centris cineraria*, *Megachile semirufa*, *Xanthocolletes sicheli*; DIPT (0.135): *Scaeva melanostoma*; *A. capitellata* (Clos) Hauman III (12, 312) HYM (1.000): *Anthidium* sp.-1, *Stenanthidium espinosai*; *A. conferta* H. & A. I (24, 7,265) HYM (0.900): *Alloscirtetica* sp.-1, *A. rufitarsis*, *Anthidium chilensis*, *A. decapsilum*, *A. gayi*, *Cadeguala occidentalis*, *Centris cineraria*, *Chilicola* sp.-2, *Lithurgomma wagenknechti*, *Mesonychium gayi*, *Megachile* sp.-2; DIPT (0.083): *Scaeva melanostoma*; LEPID (0.017): *Pseudolucia chilensis*; *A. exilis* Clos I (15, 16,662) HYM (1.000): *Xanthocolletes incahuasi*, *X. sicheli*, *Xanthocolletes* sp.; *A. glomerula* Clos var. *glomerula* III (13, 549) HYM (0.959): *Anthidium* sp.-1; LEPID (0.040): *Faunula leucoglène*; *A. montana* Phil. I (15, 1,979) HYM (1.000): *Lipanthus sabulosus*; *A. radicefolia* Clos I (19, 4,078) HYM (0.819): *Alloscirtetica* sp.-1, *Anthidium decapsilum*, *Cadeguala occidentalis*, *Caupolicana dimidiata*, *Centris cineraria*, *Megachile semirufa*, *Xanthocolletes incahuasi*, *X. sicheli*; DIPT (0.181): *Scaeva melanostoma*; *Anarthrophyllyum cumingii* H. & A. F. Phil. I (12, 6,107) HYM (0.979): *Centris cineraria*, *Hypodynerus* sp.-2; LEPID (0.020) *Etcheverrius chiliensis*, *Yramea lathonoides*, II (13, 8,012) HYM (1.000): *Alloscirtetica rufitarsis*, *Centris cineraria*, *Gayella reedi*, *Hypodynerus* sp.-2, *Megachile* sp.-2; *A. gayanum* (A. Gray) Jackson II (11, 3194) HYM (0.375): *Alloscirtetica* sp.-1, *Centris cineraria*, *Hypodynerus* sp.-1, n.i. (0.149); LEPID (0.625): *Pseudolucia chilensis*; *Astragalus curvicaulis* (Clos) Reiche I (15, 4,804) HYM (0.971): *Alloscirtetica* sp.-1, *Anthidium gayi*, *Centris cineraria*, *Caenohalictus* sp.-1, *Colletes* sp.-1, *C. fulvipes*, *Megachile* sp.-1, *M. semirufa*, *Mesonychium gayi*; DIPT (0.033): *Sarcophagidae*; II (14, 6,891) HYM (0.998): *Alloscirtetica* sp.-1, *Caenohalictus* sp.-1, *Centris cineraria*, *Colletes* sp.-1, *C. fulvipes*, *Gayella reedi*, *Hypodynerus* sp.-1, *Megachile* sp.-1, *M. semirufa*; DIPT (0.002): *Sarcophagidae*; *Astragalus*, sp. indet. I (9, 1,483) HYM (0.956): *Alloscirtetica* sp.-1, *Anthidium gayi*, *Megachile* sp.-2, n.i. (0.163); LEPID (0.045): *Pseudolucia chilensis*; *Lathyrus subandinus* Phil. I (1, 62) HYM (1.000): *Centris cineraria*; *Lupinus microcarpus* I (4, 2,094)*HYM (1.000): n.i.
- LOASACEAE: *Caiophora coronata* (Gill.) ex Arn.) H. & A. III (9, 317) HYM (0.566): *Anthidium* sp.-1, *Bombus dahlbomii*; TROCH (0.434): n.i.; *Loasa caespitosa* Phil. II (10, 420) HYM (1.000): *Anthidium* sp.-1, *Bombus dahlbomii*, *Megachile* sp. 4 & 5, *M. semirufa*; III (12, 742) HYM (1.000): *Anthidium* sp.-1, *Megachile* sp.-5; *L. heterophylla* I (1, 426) HYM (1.000): *Anthidium chilensis*, *Bombus dahlbomii*, *Megachile semirufa*, *Megachile* sp.-

APPENDIX II. *Continued.*

- 1; *L. sigmoidea* Urb. et Gilg. I (4, 438)* HYM (1.000) n.i.; *Scypanthus elegans* D. Don I (3, 203) HYM (1.000): *Anthidium chilensis*, *A. funereum*, *Megachile* sp.-1, *M. semirufa*, *Megachile* sp.-2, *Alloscirtetica* sp.-1, *Coelioxys* sp.-1.
- MALESHERBIACEAE: *Malesherbia linearifolius* (Cav.) Pers. I (6, 414) *HYM (1.000): *Centris* sp.
- MALVACEAE: *Nototriche compacta* (A. Gray) A. W. Hill III (19, 1,245) LEPID (0.660): *Phulia nymphula*, *Yramea modesta*; DIPT (0.430): Sarcophagidae, n.i. (0.100).
- ONAGRACEAE: *Clarkia tenella* (Cav.) Lewis & Lewis I (6, 604) HYM (1.000): n.i.; *Oenothera acaulis* *Cav. I LEPID: n.i.
- OXALIDACEAE: *Oxalis* affn. *compacta* Gill. ex H. & A. II (35, 6,539) HYM (0.081): *Bombus dahlbomii*, *Megachile* sp.-5; LEPID (0.886): *Andinus venustus*, *Faunula leucoglène*, *Phulia nymphula*, *Tatochila mercedis*, *Yramea modesta*, *Y. lathonoides*, n.i. (0.001); DIPT (0.031): *Habromyia lipoflava*, *Prosopochaeta caliginosa*, Sarcophagidae; III (51, 9,998) HYM (0.059): *Anthidium* sp.-1; LEPID (0.941): *Andinus venustus*, *Cynthia terpsichore*, *Phulia nymphula*, *Hypsochila wagenknechti*, *Tatochila mercedis*, *Yramea modesta*; *O. cinerea* Zucc. I (9, 310) HYM (0.544): n.i.; DIPT (0.002): *Scaeva melanostoma*; COLEOPT (0.453): n.i.; *Oxalis geminata* H. & A. I (8, ca. 400) HYM (0.596): n.i.; DIPT (0.057): Muscidae sp.-1; COLEOPT (0.346): n.i.; II (17, 662) HYM (0.368): n.i.; DIPT (0.257): n.i.; COLEOPT (0.373): n.i.; *Oxalis* sp.-1 indet. III (6, 496) DIPT (1.000): n.i.; *Oxalis* sp.-2 indet. I (4, ca. 200) DIPT: n.i., COLEOPT: n.i., HYM: n.i.
- POLEMONIACEAE: *Collomia biflora* (R. & P.) Brand. I (5, 417) LEPID (1.000): *Yramea lathonoides*; *Gilia lacinata* R. & P. II (2, 69) no visitors; *Microsteris gracilis* (Hook.) Greene I (8, 378) no visitors; II (7, 530) no visitors; *Polemonium micranthum* Benth. I (6, 345) no visitors.
- PORTULACAEAE: *Calandrinia affinis* Gill. I & II (9, 758) HYM (0.184): *Caenohalictus* sp.-1, *Hypodynerus* sp.-2, n.i. (0.183); LEPID (0.016): *Phulia nymphula*; DIPT (0.799) Agromyzidae sp.-1 & 2, Anthomyiidae sp.-2, *Habromyia lipoflava*, *Prosopochaeta* sp., Sarcophagidae, *Scaeva melanostoma*, *Villa hypoxantha*, n.i. (0.595); III (5, 156) DIPT (1.000): *Scaeva melanostoma*; *C. dianthoides* Phil. II (2, 42) DIPT (1.000): n.i.; *C. caespitosa* Gill. ex Arn. var. *caespitosa* III (2, 106)* DIPT (1.000): n.i.; *C. occulta* Phil. III DIPT: *n.i.; *C. picta* Gill. ex Arn. III (2, 53)* DIPT (1.000): n.i.; *C. sericea* H. & A. II (12, 1,392) DIPT (1.000): Sarcophagidae, *Scaeva melanostoma*; III (18, 2,079) DIPT (1.000): Sarcophagidae, *C. upallatensis* Phil. I (5, 353) HYM (0.349): *Anthidium chilensis*, *Lipanthus sabulosus*, *Megachile semirufa*; DIPT (0.652): *Scaeva melanostoma*, *Villa* sp., n.i. (0.536).
- RANUNCULACEAE: *Barneoudia chilensis* Gay I (6, 198) HYM (0.884): ants; DIPT (0.115): n.i.; *B. major* Phil. var. *major* (13, 230) DIPT (1.000): *Dasybasis* sp.-1 & 2, Sarcophagidae, *Scaeva melanostoma*, n.i. (0.177); *Ranunculus peduncularis* J. E. Smith var. *erodiifolius* (Gay) Reiche II (5, 39) HYM (0.500): *Caenohalictus* sp.-1; DIPT (0.500): n.i. III DIPT: n.i.
- RHAMNACEAE: *Discaria nana* (Clos) B. & H. ex Weberb. var. *nana* II (8, 3966); DIPT (0.992): *Ateloglutis* sp., *Habromyia lipoflava*, *Prosopochaeta* sp., Sarcophagidae, Tachinidae; LEPID (0.008): n.i.
- ROSACEAE: *Acaena pinnatifida* R. & P. I (7, ca. 3,400) DIPT (1.000): *Scaeva melanostoma*; II (6, 243) DIPT (1.000): *Scaeva melanostoma*; III: DIPT: *Scaeva melanostoma*; *Tetraglochin alatum* (Gill. ex H. & A.) O. K. I (3, ca. 1,500)* DIPT (1.000): *Scaeva melanostoma*.
- RUBIACEAE: *Oreopolis glacialis* (R. & P.) Ricardi. var. *glacialis* III (24, 9,277) LEPID (1.000); *Phulia nymphula*, *Pseudolucia chilensis*, *Yramea modesta*.
- SANTALACEAE: *Quinchamalium chilensis* Mol. I (5, 619) LEPID (0.114): DIPT (0.886): *Lycophlaeba lugubris*, *Scaeva melanostoma*, *Villa hypoxantha*, n.i. (0.036).
- SCROPHULARIACEAE: *Calceolaria arachnoides* Grah. I & II (7, 275) HYM (1.000): *Centris nigerrima*, *C. biflora* Lam. var. *obtusifolia* (Kze. et Walp.) Clos; II (9, 813) HYM (1.000): *Centris nigerrima*; *C. cana* Cav. I (6, 263)* HYM (1.000): *Centris* sp.; *C. montana* Cav. I (6, 1,043) HYM (1.000): *Centris nigerrima*, *Megachile* sp.-2, n.i. (0.247); *Calceolaria* sp. indet. HYM: *n.i.
- SOLANACEAE: *Schizanthus grahamii* Gill. ex Grah. I (3, 501) HYM (1.00): *Centris cineraria*; *S. hookeri* Gill. ex Grah. I (21, 2,035) HYM (1.000): *Anthidium funereum*, *Centris cineraria*, *Megachile semirufa*; DIPT (0.006): *Villa verdensis*; *Solanum tomatillo* Remy I HYM: *n.i.; *Salpiglossus* sp. HYM: *n.i.
- TROPAEOLACEAE: *Tropaeolum polyphyllum* Cav.* I (2, 653) HYM (1.000): *Megachile semirufa*; II & III (18, 2,238) HYM (0.466): *Anthidium* sp.-1, *Megachile* sp.-5; LEPID (0.368): *Yramea modesta*; DIPT (0.014): *Scaeva melanostoma*; TROCH (0.149): n.i.; *T. sessilifolium* P. & E. (8, 798) HYM (1.000): *Megachile* sp.-1, n.i. (0.345); *T. tricolor* Cav. I HYM: *n.i.
- UMBELLIFERAE: *Asteriscium aemocarpon* Clos I (6, ca. 1,500) DIPT (1.000): *Villa hypoxantha*, n.i. (0.363); *Azorella bolacina* Clos II (6, ca. 5,000) DIPT (1.000): Sarcophagidae, Tachinidae, n.i. (0.368); *A. madreporica* Clos III (38, ca. 42,000) HYM (0.221): ants; DIPT (0.779): *Dasybasis* sp., *Habromyia lipoflava*, *Scaeva melanostoma*, Sarcophagidae, n.i. (0.107); *A. monantha* Clos II (11, 12,420) DIPT (1.000): *Habromyia lipoflava*, *Prosopochaeta* sp., Sarcophagidae, Tachinidae, n.i. (0.110); *Bowlesia tropaeolifolia* Gill. ex Hook. I (5, ca. 500) DIPT (1.000): *Scaeva melanostoma*, Sarcophagidae, n.i. (0.247); *L. acaulis* (Cav.) Gill. et Hook. II (22, ca. 32,300) DIPT (1.000); *Habromyia lipoflava*, *Prosopochaeta caliginosa*, Sarcophagidae, Tachinidae, *Scaeva melanostoma*, n.i. (0.015); III (15, ca. 40,

APPENDIX II. *Continued.*

200) DIPT (1.000): *Habromyia lipoflava*, *Vibrissomyia* sp., *Villa* spp. n.i. (0.414); *Mulinum spinosum* (Cav.) Pers. I (7, 5,682) HYM (0.037): Panurginae sp.–1; LEPID (0.001): *Auca coctei-pales*; DIPT (0.963): *Scaeva melanostoma*, *Villa flavicura*, *V. guttapennis*, *V. hypoxantha*, *V. verdensis*, *Villa* spp., n.i. (0.221); *Pozoa coriacea* Lag. III DIPT:* n.i.; *Sanicula graveolens* Poepp. ex DC I & II* DIPT: Anthomyiidae sp.–2, *Prosopochaeta caliginosa*, *Scaeva melanostoma*, n.i.

VALERIANACEAE: *Valeriana gracileps* Clos I (9, 1,669) DIPT (1.000): Anthomyiidae sp.–4, *Scaeva melanostoma*, n.i. (0.365); *V. radicalis* Clos III (3, 189)* DIPT (1.000): n.i.

VERBENACEAE: *Junellia uniflora* (Mol.) Mold. III (24, 1,852) LEPID (0.999): *Phulia nymphula*, *Yramea modesta*; DIPT (0.001): n.i.; *Verbena scoparia* Gill. et Hook. I (11, 5,215) HYM (0.106): n.i.; DIPT (0.894): *Chaetodemoticus chilensis*, *Lyphlaeba lugubris*, *Truploecheus bellus*, *Villa durvillei*, *Villa* spp., n.i. (0.091).

VIOLACEAE: *Viola atropurpurea* Leyb. III (26, 6,058) LEPID (0.971): *Yramea modesta*; DIPT (0.028): n.i.; *V. montagnei* Leyb. III (2, 63)* LEPID (1.000); *Yramea modesta*; *V. philippii* Leyb. II & III (6, 348) LEPID: *Yramea modesta*.

VIVIANACEAE: *Viviania marifolia* Cav. I (3, 251) DIPT (1.000): *Chaetodemoticus chilensis*, n.i. (0.250).

^a Number of 10-min observation periods and total number of flowers observed; observations are unquantified where these numbers are lacking.

^b n.i. = not identified in the field; number refers to the proportion of flower visits by that vector class which was not identifiable in the field.

^c Population observed was continuous over the boundary of the two areas indicated.

^d Noneffective and unimportant pollinators are indicated in italics.

* Observations not quantified. Frequency of 1.00 with asterisk indicates that only the one vector type was observed.