

**Community Studies in Pollination Ecology in the  
High Temperate Andes of Central Chile  
II. Effect of Temperature on Visitation Rates and Pollination  
Possibilities<sup>1</sup>**

By

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**Key Words:** Angiosperms. – Pollination ecology, visitation rates, pollination along altitudinal gradient. – Flora of Chile, of the Andes.

**Abstract:** Visitation rates and mean numbers of visits per flower per day are determined at three altitudinal levels (2 200–3 600 m) in the high Andes of central Chile from quantified observations of flowers visitors to a total of 134 species of plants, studied over three flowering seasons. Significant altitudinal decreases in the mean no. visits/flower/minute and per day were recorded, with Level III flowers, on the average, being pollinated only about  $\frac{1}{2}$  as frequently and to as low as  $\frac{1}{4}$  as frequently in certain months, as Level I flowers. Visitation rates are generally highest in early and mid-summer at all altitudes. – The lower visitation rates at the higher elevations are due to lower insect abundance relative to plant resources and lower levels of activity for the insects present, stemming from the generally lower ambient temperatures. Seasonal differences in visitation rates may also be related to differences in insect abundance levels. The total probability of ovule pollination cannot be estimated directly from the pollination rates, because stigmas are probably receptive for longer periods at the higher elevations. When differences in the duration of stigma receptivity are estimated from differences in flower life-length, the probability of pollination in Level III is not very different from that expected in Level I. However, for some months, the deficit in Level III may still be substantial. – These results underline the inherent dangers of predicting pollination possibilities directly from pollination rates. They also suggest that the impoverished pollination conditions assumed in hypotheses predicting higher amounts of self-compatibility at high altitudes might not be justified for all high temperate mountains.

Successful pollination depends upon a plant's attractiveness to pollinators as a food source and pollinators transferring sufficient pollen between flowers of genetically compatible genotypes. The rate at which

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<sup>1</sup> First part of this series: ARROYO & al. (1982).

flowers are pollinated, and consequently that at which ovules are fertilized, is a function of the abundance and individual levels of activity of pollinators, and flower density (HEINRICH & RAVEN 1972). Pollinator activity has been shown in several studies to be affected by conditions of weather such as temperature, rainfall and windspeed (e.g., EISIKOWITCH & GALIL 1971, HEINRICH 1975, PRIMACK 1978). Weather may also affect the foraging ability of pollinators because of changes in their energy budgets or their physical inability to fly in rain or wind. It may indirectly affect the foraging rates of pollinators because of changes in the rate of anthesis, quantity of nectar flow and flower duration (ARROYO & al. 1981). However, there are few studies that examine how variation in weather variables affects pollinator activity throughout a whole community. Consequently, we have undertaken a study of pollination levels along an elevation gradient in the high Andes of central Chile, in which temperature is the major variant that materially affects pollination levels.

This study was initiated with a second, and perhaps more important objective in mind. We are currently surveying breeding systems along altitudinal gradients at different latitudes in the Chilean Andes. One of the traditionally accepted arguments for breeding system changes in the direction of non-obligate outcrossing lays its cornerstones on changes in pollinator availability. The abundance of self-compatibility on certain islands (c.f., BAKER 1955, RICK 1966), the evolution of autogamy on continental areas (LLOYD 1965) and more self-compatibility in the early stages of succession (PARRISH & BAZZAZ 1979, SOBREVILA & ARROYO 1982) have all been related to impoverished or uncertain pollinator conditions. With respect to high mountain ecosystems, BILLINGS (1974) has already suggested that there might be large amounts of self-compatibility and apomixis in alpine floras, especially close to the upper limit of the vegetation. MANI's (1962) detailed work on the distributional patterns of high elevation insects, the principal pollinators of alpine floras, and our own work in central Chile (ARROYO & al. 1982, 1983) leaves little doubt of the existence of rapid declines in insect species richness with increasing elevation on high temperate mountains. However, interestingly, the decreases in pollinator activity levels and in the amounts of pollination that supposedly accompany reduced insect species richness, which are implicit in BILLING's (1974) arguments, to our knowledge have never been actually demonstrated. Consequently, this paper, in addition to assessing the effect of decrease in temperature on pollinator activity along an elevational gradient, will address three questions, perhaps of greater importance: 1) Is there any evidence of an *overall* tendency for reduction in the rate at which flowers are pollinated along an elevation gradient? 2) If so, how great are the reductions, and are deficits expected in the number of

ovules pollinated? And finally, 3) if such trends exist, are the decreases in flower visitation rates the result of lower numbers of insects, or lower levels of activity for the insects present?

### Study Sites and Methods

The study site is located in the andean (equivalent of alpine) zone in the Cordon del Cepo (33°17'S, 70°16'W) on the western slopes of the Andes in the Mediterranean sector of central Chile. This area has an estimated 400–500 mm precipitation, mostly in the form of winter snow, and generally clear summer days except for some afternoon cloud above 3 000 m elevation. At 2 500 m the maximum monthly average temperature is 18 °C.

Observations were conducted over three separate flowering seasons (spring–autumn of 1978–1979<sup>1</sup>, 1980–1981 and 1983–1984, respectively) along an altitudinal gradient beginning at the *Kageneckia angustifolia* CAV. treeline at 2 200 m s.m. and ending at 3 600 m s.m., close to the upper vegetation limit. This transect comprises the following three vegetation belts:

I. Subandean scrub (2 200–2 600 m s.m.), a floristically rich area especially abundant in composite shrubs, annual species and geophytes.

II. Cushion plant communities (2 700–3 100 m s.m. and occasionally up to 3 400 m s.m., depending on slope and aspect; ARMESTO & al. 1980), dominated by *Laretia acaulis* (CAV.) GILL. et HOOK. and species of *Azorella*.

III. Subnival fieldfield, sparsely populated with grasses, dwarf rosette herbs and smaller flat cushions (3 200–3 600 m s.m.). At the lower end of the andean zone, flowering is initiated in late-September to mid-October, and some 7 days thereafter for each 200 m s.m. increase in elevation (ARROYO & al. 1981). Flowering continues until April at the lower extreme of the andean zone, but only until late March near the upper vegetation limit. The most important pollinators in the subandean level are bees; however, in the successively higher vegetation belts, butterfly and fly pollination increase proportionately at the expense of bee pollination (ARROYO & al. 1982).

In order to pursue the objectives outlined, it was necessary to develop a sampling procedure providing standard quantitative assessments of the rate at which flowers are visited at a community level. The method we chose involves determining the actual number of visits per flower per unit time on a large and representative sample of plant species occurring at different altitudinal levels, drawn throughout the entire flowering season. This method is extremely useful, as it not only permits the detection of differences in the composition of pollination vectors (ARROYO & al. 1982) and differences in pollination rates, but also differences in pollinator abundance levels and estimates of the expected amount of pollination occurring at different altitudes.

Pollinator activity was sampled for plant species occurring in the three major vegetation belts: Level I: 2 200–2 600 m s.m.; Level II: 2 700–3 100 m s.m.; Level III: 3 200–3 600 m s.m. by a number of observers who constantly moved up and down the overall altitudinal gradient from day to day. Activity was quantified using fixed 10-minute periods of observation. A few 30-minute observations made at the beginning of the first field season when methods were being finalized, have been considered as three 10-minute observation periods. At the start of each observation period, the total number of plants and open flowers of the species

<sup>1</sup> Altitudinal variation in vectors on plant species observed during the 1978–1979 field season is described in detail in ARROYO & al. (1982).

(occasionally more than one species were observed simultaneously) to be observed were counted and the ambient temperature at flower height and the exact altitude were recorded.

Then, each insect visiting flowers on these plants was followed for the number of flowers visited. In order to facilitate the estimation of daily amounts of pollination from the data, a conscious effort was made to spread the observations periods for each species studied over a wide spectrum of the daylight hours. As our objective was to cover the entire altitudinal range and spectrum of habitats occupied by each of as many species as possible, the number of observations per species (Appendix I) is variable. In general, larger numbers of observations were made on species with broad altitudinal ranges and on species with longer flowering periods. The total number of 2341 observation periods accumulated over three field seasons consult a total of 134 plant species. This number excludes all wind pollinated species, nocturally pollinated species and a number of species, probably all autogamous, for which pollinators have never been observed. In species of the *Compositae*, where individual florets cannot easily be observed and counted in the field, the head was considered as the functional pollination unit.

### Altitudinal and Seasonal Variation in Visitation Rates

Fig. 1 compares the mean visitation rates at the three different altitudinal levels (see Table 1 for details). Curve A is based on the means for the total sets of data available at each of the altitudinal levels, while Curve B is the result of averaging the monthly visitation rates (Table 1). The values in Curve B are lower than those in Curve A, because the effect of larger numbers of observations taken in the middle of the flowering season, not only when more species are in flower, but also when rates are higher, is compensated for. Each curve illustrates the same general trend. The mean visitation rate decreases steadily with altitude, that of Level II being approximately  $\frac{2}{3}$  of that at Level I, and that at Level III being approximately  $\frac{3}{4}$  of that at Level II. Considering the altitudinal extremes, over twice as much pollination per unit time is likely to occur in Level I with respect to Level III. These data leave little doubt that pollination rates diminish with altitude in the high Andes of central Chile.

In Fig. 2 the mean number of visits per flower per minute are plotted for each month (see Table 1 for details) at the three altitudinal levels, in order to assess seasonal variation. The seasonal pattern is highly characteristic and similar in general terms at each altitudinal level. As flowering commences, rates are initially low, they then increase, and finally descend again towards the end of the flowering season. Differences between months are significant at the altitudinal extremes except at the beginning of the flowering season in December and for several months of the summer comparing Level I vs. Level II (Table 1).

The month of peak activity, however, varies with the altitudinal level. At the highest level, peak activity occurs early in the flowering season, in December; in Level II and Level I peak activity is seen to occur in the

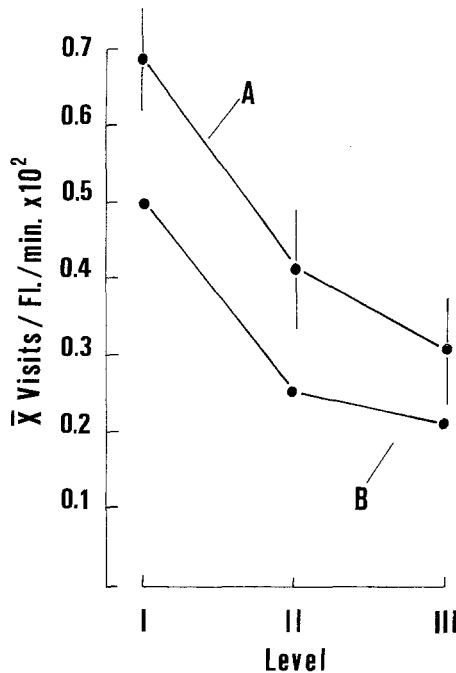


Fig. 1. Mean visitation rate (no. visits per flower per minute  $\times 10^2$ ) at three altitudinal levels in the high Andes of central Chile. Level I: 2 200–2 600 m altitude; Level II: 2 700–3 100 m altitude; Level III: 3 200–3 600 m altitude. The means in Curve A are for the total number of 10-minute observations available at each altitudinal level. The means in Curve B are the averages of the mean monthly visitation rates (see Table 1). Difference between means for Levels I vs. II ( $t = 4.00$ ) and II vs. III ( $t = 2.063$ ) significant for Curve A. Differences between Level I vs. Level III ( $t = 3.407$ ) significant for Curve B. Vertical bars are 95% confidence intervals

middle of the flowering season in January, and February, respectively. In summary a progressive seasonal shift with decrease in altitude in the time of the maximum visitation rate may be seen. Finally, a comparison of the month with the highest pollination rate at each of the three altitudinal levels, indicates that 50% and 40% as much pollination is likely to occur in Level II and Level III respectively, as compared with Level I [differences statistically significant:  $t_{307}$  (Level I vs. Level II) = 3.140,  $p < 0.01$ ;  $t_{298}$  (Level I versus Level III) = 4.119,  $p < 0.001$ ].

#### Factors Responsible for Altitudinal and Seasonal Variation in Visitation Rates

Low visitation rates, such as those observed at higher elevations in the central Chilean Andes, and at certain times of the flowering season, could

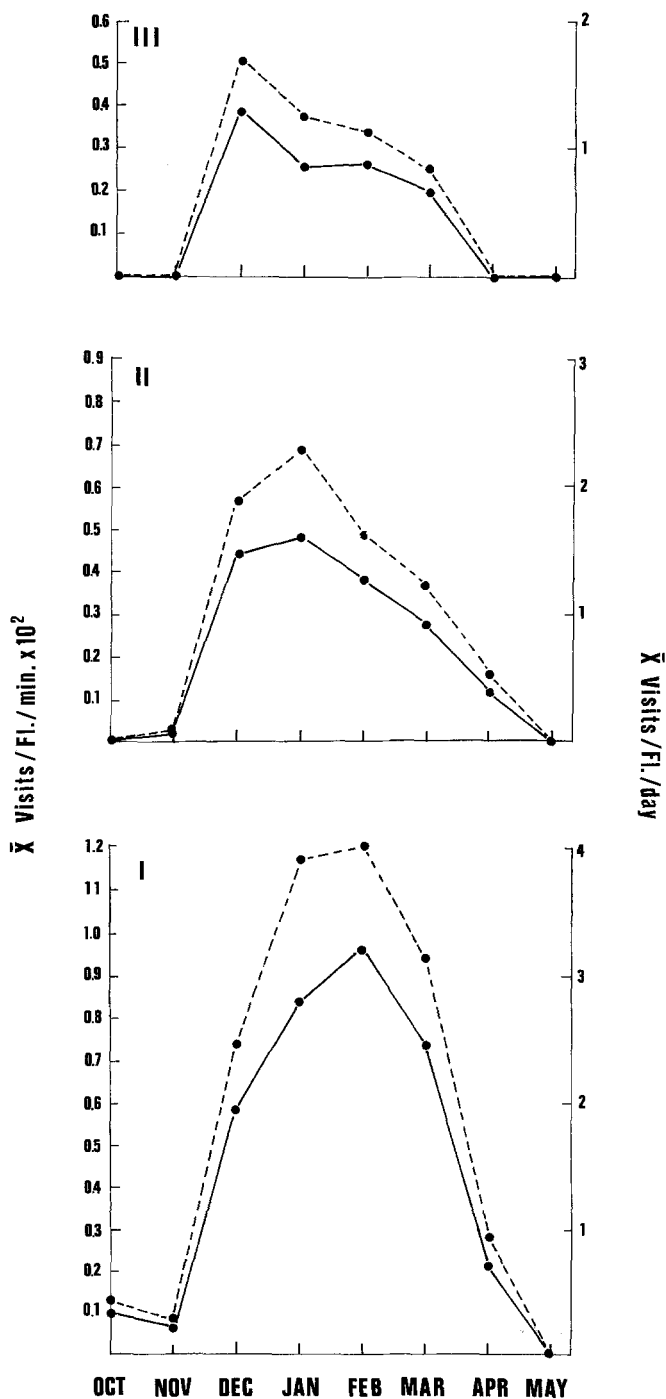


Fig. 2. Seasonal variation in visitation rates at three altitudinal levels in the high Andes of central Chile (—) and estimates of the number of visits per flower per day during each month (---). See also Table 1

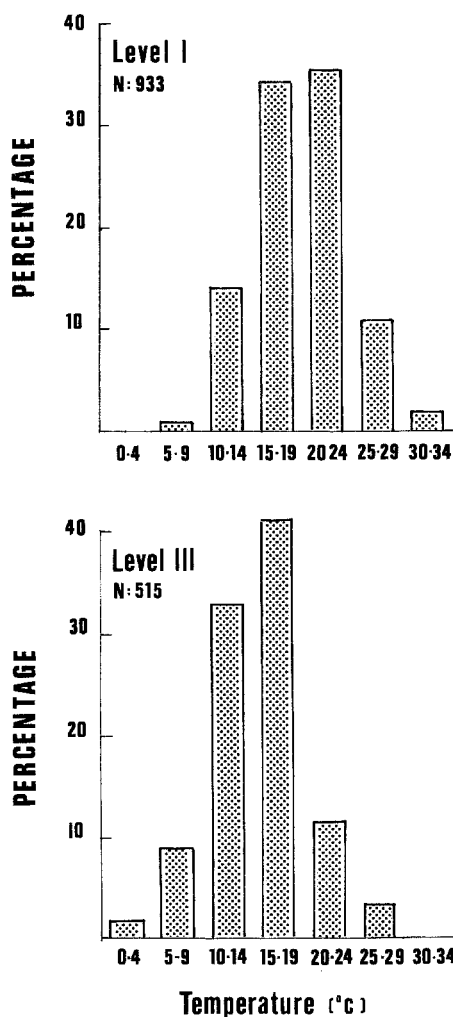


Fig. 3. Distribution of diurnal temperatures at Level I (2 200–2 600 m s.m.) and Level III (3 200–3 600 m s.m.) based on temperature recordings made during observations on pollinators. N = number of 10-minute observations for which discrete temperature readings were taken

result from lower number of insects being present at such elevations or in certain months. However, relative to plant species or floral resource abundance, insect abundance might be relatively constant along the altitudinal gradient and over the entire flowering season, with insect activity been depressed at the higher elevations and in certain months only because of lower ambient temperatures. In the latter case, the lower

Table 1. Mean number of visits per flower per minute ( $\times 10^2$ ) and estimated Andes of

Altitudinal level		Month <sup>1</sup>	No. 10-min. observations	No. spp. observed per month
I:	2 200–2600 m (84 spp.)	Oct.	15	3
		Nov.	132	16
		Dec.	406	52
		Jan.	443	54
		Feb.	106	29
		Mar.	40	5
		Apr.	11	2
(Means, sd for months)				
II:	2 700–3 100 m (63 spp.)	Nov.	9	3
		Dec.	142	22
		Jan.	203	50
		Feb.	124	29
		Mar.	89	13
		Apr.	8	3
(Means, sd for months)				
III:	3 200–3 600 m (41 spp.)	Dec.	194	19
		Jan.	158	29
		Feb.	195	30
		Mar.	66	14
(Means, sd for months)				

<sup>1</sup> No flowering occurred at Level II and III in October and at Level III in April. Some flowering occurred in Level III in November, however, plants were not surveyed for pollinator activity due to the difficulty of reaching that area because of heavy snow drifts. As a consequence the means for the months of Level III is probably higher than it should be.

visitation rates would be a direct effect of low temperatures on insect physiology and behaviour. In order to evaluate whether low activity rates and/or low insect abundance levels are the causes of altitudinal and seasonal variation in visitation rates, the effect of temperature on the latter will be considered. Fig. 3 shows the distribution of diurnal temperatures in Level I and Level III. In Level I, temperatures range from lows in the 5–9 °C range to highs in the 30–34 °C range. Temperatures at this elevation most frequently fall in the 20–24 °C range. In Level III the range and commonly encountered temperatures are shifted 5 °C lower with



average number of visits per flower per day at three altitudinal levels in the high central Chile

Total no. flowers observed	No. visits/flower/min. ( $\times 10^2$ )		Estimated mean no. visits/flower/ day <sup>2</sup>
	$\bar{X}^3$	S.E.	
1 566	0.101	0.031	0.424
26 607	0.061	0.016	0.256
52 195	0.588	0.082	2.470
35 802	0.831	0.071	3.989
14 053	0.955	0.141	4.011
4 858	0.746	0.175	3.133
1 055	0.217	0.082	0.911
	<b>0.500 (0.342)</b>		<b>2.170 (1.634)</b>
723	0.013	0.013	0.055
38 624	0.446	0.101	1.873
41 003	0.484	0.080	2.323
38 903	0.390	0.085	1.638
7 903	0.296	0.041	1.243
1 101	0.124	0.078	0.521
	<b>0.292 (0.171)</b>		<b>1.276 (0.858)</b>
37 505	0.399	0.067	1.676
50 147	0.264	0.096	1.267
58 248	0.277	0.057	1.163
7 067	0.206	0.068	0.865
	<b>0.287 (0.081)</b>		<b>1.243 (0.335)</b>

<sup>2</sup> Estimates are based on a 7-hour day in October, November, December, February, March, and April, and an 8-hour day in January.

<sup>3</sup> Differences between Level I vs. Level III (t-test) significant for January ( $p < 0.01$ ), February ( $p < 0.001$ ) and March ( $p < 0.001$ ). Differences between Level I vs. Level II significant for December ( $p < 0.05$ ), February ( $p < 0.001$ ) and March ( $p < 0.001$ ). Differences between Level II and Level III not significant.

respect to Level I. If temperature affects foraging rates through a direct effect on insect physiology, a comparison of insect activity at different temperatures under similar environmental conditions, should yield variation in the visitation rates. If, additionally, differences in insect abundance levels are contributing to the altitudinal and seasonal variation in visitation rates, the activity levels should be consistently lower at the higher elevation, for any one temperature considered. Fig. 4, which compares visitation rates at different temperatures in Level I and Level III, indicates that both high and low temperatures reduce foraging rates at

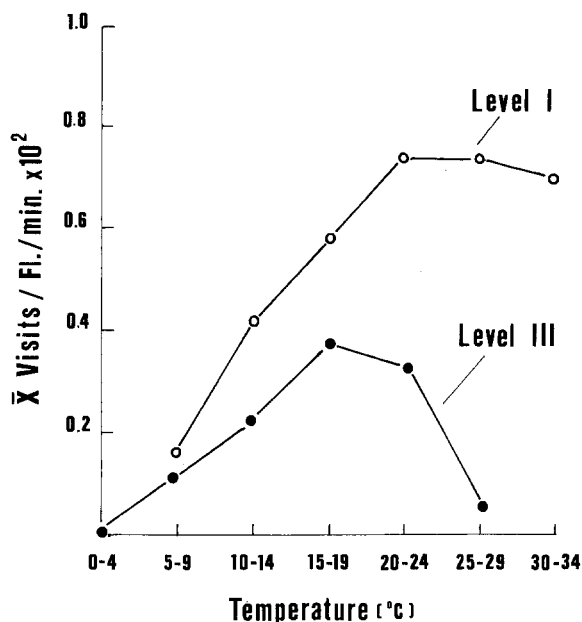


Fig. 4. Comparison of the mean visitation rate at different temperatures in Level I (2 200–2 600 m s.m.) and Level III (3 200–3 600 m s.m.). Curves are based on the same sets of data used in Fig. 3

both altitudinal levels. In Level I the optimal temperature for foraging is in the 20–24 °C range, whereas in Level III highest foraging rates occur in the 15–19 °C range. Temperatures below the foraging optima probably affect visitation rates by reducing the velocity of flight, rate of warm up, and ability of an insect of initiate flight. At temperatures beyond the optima for foraging, the limiting factor is probably overheating. Irrespective of the fact that temperature affects foraging, a comparison of the visitation rates at the two altitudinal levels for any given temperature prove that there is a clear tendency for higher visitation at the lower altitudinal level (Fig. 4). The latter could only come about if insect abundance, relative to plant abundance is lower at the higher elevation. It may be concluded therefore, that the lower visitation rates at higher elevations in the high Andes of central Chile are due to two causes: i) lower insect abundance relative to plant abundance, and ii) lower activity levels in the insects present, because of lower temperatures on the average. It is interesting, nevertheless, that as lower temperatures are reached, the difference in the visitation rates between Level I and Level III is less notorious. Evidently, and not surprisingly, high altitude populations of

insects in the subnival belt are better adapted to flying at low temperatures than their subandean counterparts. As very high temperatures are met with, contrarilywise, the difference between the Level I and Level III visitation rates is more exaggerated. The same heat conserving adaptations (e.g., hairiness; dark color in the case of Diptera) present in the higher insect populations apparently result in their overheating more rapidly than the lower populations.

Table 2. Mean visitation rates [no. visits./fl./min ( $\times 10^3$ )] at two different temperature ranges for different periods of the flowering seasons

	0-19 °C		20-39 °C	
	n	$\bar{x}$	n	$\bar{x}$
<i>Level III</i>				
Early <sup>1</sup>	126	0.437	41	0.403
Mid	254	0.234	35	0.122
Late	59	0.230	— <sup>2</sup>	
<i>Level I</i>				
Early	180	0.199	211	0.517
Mid	287	0.743	224	0.956
Late	12	0.274	21	1.378

<sup>1</sup> Early: Oct.–Dec.; Mid: Jan.–Feb.; Late: March–April.

<sup>2</sup> Temperature readings in this range were not recorded.

Table 2 sheds light on the same questions posed with respect to seasonal differences in visitation rates. Visitation rates are compared for the early (up to December), mid (January and February) and late (March onwards) months of the flowering season, according to two discrete temperature ranges. If differences in insect abundance were not a casual factor of seasonal variation in visitation rates, then, again, for any given temperature, the visitation rates should be invariant throughout the flowering season. Table 2 shows that there is conspicuous seasonal variation in the visitation rates when considered by temperature range, at both altitudinal levels compared. The direction of these differences, is generally consistent with highest visitation rates early in the flowering season in Level I and in late in the flowering season in Level III, respectively. Variation in insect abundance levels relative to floral resource levels, thus must also be contributing to the observed seasonal differences in visitation rates.

### Estimates of Amounts of Pollination per Day

Up to this point, significant altitudinal and seasonal differences in visitation rates have been revealed for the high Andes in central Chile, and these have been related to differences in insect abundance levels and in activity levels. We now turn to the question as to whether such trends result in differences in the probability of a flower being pollinated over a day.

The expected amount of pollination occurring daily at each altitudinal level may be calculated from the mean number of visits per flower per minute and the number of hours for which insects are active each day. The total probability of a flower being pollinated, on the other hand will be a function of the expected amount of pollination occurring daily, and the number of days stigmas remain receptive.

Estimates of the mean number of visits per flower per day are given in Table 1 and plotted in Fig. 2. At Level I, flowers are pollinated on the average of at least once daily, except at the very beginning and end of the flowering season. Between December and March, flowers at this level could be pollinated more than twice daily, and during January and February as much as four times daily. In Level II, again, at the beginning and end of the flowering season, flowers receive an estimated average of less than one visit daily. At this level the highest number of visits per day occurs in January, however, this is only around  $\frac{2}{3}$  the number received in the same month in Level I. In Level III, flowers receive less than one visit per day in March, and if data had been taken in November, possibly the same trend would have been observed for this month (see footnote to Table 1). The highest number of visits per flower per day, is seen in early summer, in December, where however flowers receive only around  $\frac{2}{5}$  of the visits seen in Level I. Comparing the month of maximum pollination for each of Level I and Level III, it is seen that Level I flowers may be pollinated close to 2.5 times as frequently as those in Area III. In certain months (January, February and March), moreover, Level I flowers can be expected to receive more than 3 to 4 times as many visits daily as Level III flowers. Thus as seen previously in comparisons of the visitation rates, again it may be firmly concluded that the frequency of pollination decreases along the altitudinal gradient studied.

### Discussion

For the same altitudinal gradient studied here, we have previously shown that insect species richness relative to plant species richness and the mean number of insect species visiting each individual plant species decrease with altitude (ARROYO & al. 1982). These trends, moreover, occur

in spite of no discernable difference in the attractiveness of flowers along the altitudinal gradient. The results analysed in this paper establish that the above trends are accompanied by significant altitudinal reductions in visitation rates and in the estimated amounts of pollination occurring daily. Comparisons of insect activity for different temperatures at the same altitude, and for the same temperatures at different altitudes suggest that the reduced visitation rates at higher altitudes are caused in part by reduced insect abundance relative to plant abundance and partially by lower activity in the insects because of the lower temperatures on the average. The decline in insect-species richness, therefore, has not been compensated for by an increase in population size in the insect species that live at the higher, colder altitudes. Consequently, the hitherto untested prediction of reduced insect activity with altitude is fully warranted for this latitude in the Chilean Andes.

An interesting question which may be asked is whether the observed lower insect abundance levels at higher elevations are the result of insufficient caloric output on the part of the resident plant populations. Theoretically, insect abundance should increase up to an equilibrium value in which floral resources are totally utilized, and up to the point at which maximum numbers of ovules are pollinated and mature to seed. As insects require higher caloric intakes for survival in habitually cold environments (DOWNES 1965, HEINRICH & RAVEN 1972, HEINRICH 1974, 1975), the number of pollinators any given floral resource can sustain will decrease as ambient temperature falls (HEINRICH 1975). The metabolic intake of a bumblebee weighing 0.5 gm increases from 85–850 cal (gm hr)<sup>-1</sup> over the 0–30 °C temperature range. Consequently the size of the insect population a plant species pollinated by a bee species with these characteristics could support, would differ by a factor of 10, if additional caloric rewards were not offered at the lower end of the temperature range (HEINRICH 1974).

Proof that pollinator abundance levels in the high Andes of central Chile are limited by energetic or such intrinsic considerations, would come from a demonstration that foraging costs increase with altitude and that floral resources are indeed limiting. The first may be inferred directly from the observation that maximum foraging in the subnival zone occurs in a physiological suboptimal temperature range (HEINRICH 1975), where insects are required to engage in energy consuming, active endothermy. Such shifts in temperature optima for foraging at the expense of higher caloric requirements have also been reported for many Arctic insects (DOWNES 1965). It is not entirely clear, at this point, however, whether floral resources are limiting. The fact that subnival flowers are visited far less frequently per day as compared with flowers in the subandean belt

might suggest that flowers in the subnival belt are not being completely exploited for their caloric rewards. But this last argument would only be valid if rates of nectar production are invariant with altitude. As it is highly likely that nectar secretion is considerably slower under the lower temperatures experienced in the subnival belt, it is not inconceivable that proportionately speaking the amount of nectar per day removed from subnival and from subandean flowers is similar. If the last were true, the question as to whether floral resources are limiting at higher elevations is still an open one.

The observed altitudinal trend for increase in insect abundance relative to plant abundance, alternatively, might be the result of extrinsic factors. Considering the quarternary age of the Andean belt in the Andes (SIMPSON 1979), it may be assumed that the plant and insect species occurring near the upper vegetation limit have been present in their habitats for relatively less time than those occurring lower down in the andean zone, close to the tree-line. Plant species should be able to disperse onto newly available high mountain surfaces with relative ease, since their initial survival, in the face of unpredictable climatic and weather conditions, can be secured by vegetative propagation (GRIME 1979). For insects, in which sexual reproduction is obligate for survival, in contrast, the colonization of high altitude environments should be a much slower process, as entire generations could be locally eliminated in unfavorable years, or with freak weather conditions. Indeed, it is not surprising that some Arctic insects have secondarily evolved the capacity to survive through a series of unfavorable summers in the juvenile phases (DOWNES 1965). Consequently, the altitudinal reduction in insect versus plant abundance in the Andes might be as much a result of different degrees of preadaptedness of plants and insects to the peculiarities of the high altitude environment, as an effect of limitations in caloric output on the part of the plants.

The estimates of numbers of visits per flower per day, lead to the surprisingly result that subandean flowers may be pollinated as much as four times daily, with subnival flowers being pollinated, on the average, only half as frequently, to as low as close to  $\frac{1}{4}$  as frequently in certain months. These results are difficult to interpret, as little information is available on the number of flower visits required for full ovule pollination in natural circumstances. Such large numbers of visits per day, as found in the andean zone (Level I) might be necessary in order to compensate for ineffectual visits such as those to flowers on the same plant in genetically self-incompatible species. If the latter were true, it may be safely concluded that there are significant differences in the number of ovules pollinated daily at the altitudinal extremes of the gradient studied. However, can it be deduced from the data presented here, that the probability of an ovule

being pollinated on the whole is also lower in the subnival belt? The total probability of ovule pollination will be directly proportional to the daily visitation rates, when the above arguments on ineffectual visits are correct, or when the number of visits per day per flower occurring in the subandean zone is at least not twice in excess of that required for full pollination, and if there is no significant difference in the time stigmas remain receptive at each of the altitudinal extremes. Preliminary work on seed set in the andean zone suggests that excess pollination is highly unlikely (ARROYO & al., unpubl. data). Although no information is available on stigma

Table 3. Relative total amounts of pollination expected at different elevations in the andean zone in the high Andes of central Chile assuming stigmas in Level III remain receptive 2.2 times as long as those in Level I. For comparative purposes, the expected amount of pollination in Level I is given the value of 1

	Level I	Level II	Level III
Average for all values	1	0.946	0.927
Month with maximum deficit	1	0.635	0.607

receptivity for the species studied, it is dubious as to whether the second condition will hold up. ARROYO & al. (1981), in a comparison of flower life-length in the subnival and subandean zones, were able to show that subnival flowers remain open for an average of 2.2 times as many days as flowers in the subandean zone. If such slower floral development in the subnival zone is reflected in longer periods of stigma activity, then it may be expected that subnival flowers will be available for pollination for twice as much time as flowers occurring 1 000 m lower in the subandean belt. Once this difference in stigma receptivity duration is taken into account (Table 3), then, interestingly, in spite of the significantly lower pollination rates at higher elevations, the probability of an ovule being pollinated, or the relative number of ovules pollinated, should on the average, not be very different at the altitudinal extremes of the andean zone. At the most, in the month of maximum differences in pollination rates, the deficit will be in the order of  $\frac{2}{5}$ , and not  $\frac{3}{4}$  as suggested by direct inspection of the pollination rates. These results demonstrate that much caution should be exercised in interpreting pollination rate data, and more significantly, they call for a critical re-examination of the pre-requisites of certain hypotheses predicting higher levels of self-compatibility and apomixis at higher elevations.

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### Appendix

Numbers of species per genus and numbers of 10-minute observations made in these.  $\frac{1}{23}$  signifies that one species of the named genus was studied and 23 10-minute observations were made;  $\frac{3}{46}$  signifies that 3 species of the named genus were studied, with a total of 46 10-minute observations made in these.

*Alstroemeriaceae*: *Alstroemeria*  $\frac{1}{23}$ ; *Hippeastrum*  $\frac{1}{5}$ ; *Nothoscordum*  $\frac{1}{24}$ ; *Rhodophiala*  $\frac{1}{29}$ ; *Tristagma*  $\frac{2}{12}$ . — *Berberidaceae*: *Berberis*  $\frac{1}{36}$ . — *Caryophyllaceae*: *Cerastium*  $\frac{2}{103}$ . — *Compositae*: *Calopappus*  $\frac{1}{4}$ ; *Chaetanthera*  $\frac{8}{103}$ ; *Chuquiraga*  $\frac{1}{89}$ ; *Erigeron*  $\frac{1}{11}$ ; *Haplopappus*  $\frac{3}{45}$ ; *Hypochaeris*  $\frac{3}{17}$ ; *Leuceria*  $\frac{2}{21}$ ; *Madia*  $\frac{1}{12}$ ; *Mutisia*  $\frac{3}{30}$ ; *Nardophyllum*  $\frac{1}{17}$ ; *Nassauvia*  $\frac{6}{105}$ ; *Perezia*  $\frac{2}{45}$ ; *Senecio*  $\frac{6}{183}$ ; *Taraxacum*  $\frac{1}{1}$ ; *Werneria*  $\frac{1}{3}$ . — *Cruciferae*: *Draba*  $\frac{1}{17}$ ; *Lepidium*  $\frac{1}{5}$ ; *Menonvillea*  $\frac{1}{2}$ ; *Thlaspi*  $\frac{1}{10}$ . — *Euphorbiaceae*: *Euphorbia*  $\frac{1}{25}$ . — *Geraniaceae*: *Erodium*  $\frac{1}{7}$ ; *Geranium*  $\frac{1}{5}$ . — *Hydrophyllaceae*: *Phacelia*  $\frac{1}{89}$ . — *Iridaceae*: *Sisyrinchium*  $\frac{4}{80}$ ; *Solenomelus*  $\frac{1}{5}$ . — *Labiatae*: *Stachys*  $\frac{1}{58}$ . — *Loasaceae*: *Caioophora*  $\frac{2}{14}$ ; *Loasa*  $\frac{2}{44}$ ; *Scyphanthus*  $\frac{1}{1}$ . — *Malesherbiaceae*: *Malesherbia*  $\frac{1}{11}$ . — *Malvaceae*: *Nototriche*  $\frac{1}{23}$ . — *Onagraceae*: *Epilobium*  $\frac{1}{2}$ . — *Oxalidaceae*: *Oxalis*  $\frac{7}{147}$ . — *Papilionaceae*: *Adesmia*  $\frac{9}{231}$ ; *Anarthrophyllum*  $\frac{2}{71}$ ; *Astragalus*  $\frac{2}{57}$ ; *Lathyrus*  $\frac{1}{1}$ . — *Polemoniaceae*: *Collomia*  $\frac{1}{5}$ . — *Portulacaceae*: *Calandrinia*  $\frac{5}{50}$ . — *Ranunculaceae*: *Barneoudia*  $\frac{2}{20}$ ; *Ranunculus*  $\frac{1}{11}$ . — *Rhamnaceae*: *Discaria*  $\frac{1}{10}$ . — *Rosaceae*: *Acaena*  $\frac{1}{13}$ . — *Rubiaceae*: *Galium*  $\frac{1}{1}$ ; *Oreopolus*  $\frac{1}{24}$ ; *Relbunium*  $\frac{1}{11}$ . — *Santalaceae*: *Quinchamalium*  $\frac{2}{10}$ . — *Scrophulariaceae*: *Calceolaria*  $\frac{4}{22}$ . — *Solanaceae*: *Salpiglossis*  $\frac{1}{8}$ ; *Schizanthus*  $\frac{2}{29}$ . — *Tropaeolaceae*: *Tropaeolum*  $\frac{2}{30}$ . — *Umbelliferae*: *Asteriscium*  $\frac{1}{1}$ ; *Azorella*  $\frac{2}{43}$ ; *Bowlesia*  $\frac{1}{10}$ ; *Laretia*  $\frac{1}{42}$ ; *Mulinum*  $\frac{1}{8}$ ; *Pozoa*  $\frac{1}{12}$ ; *Sanicula*  $\frac{1}{4}$ . — *Valerianaceae*: *Valeriana*  $\frac{2}{8}$ . — *Verbenaceae*: *Junellia*  $\frac{1}{30}$ ; *Verbena*  $\frac{1}{16}$ . — *Violaceae*: *Viola*  $\frac{4}{92}$ . — *Vivianaceae*: *Viviania*  $\frac{1}{8}$ .