Local Geographic Distributions of Bumble Bees Near Crested Butte, Colorado: Competition and Community Structure Revisited

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ABSTRACT   Surveys in 1974 of bumble bee species distributions along elevational gradients (Pyke 1982) were revisited to reevaluate the original conclusion that coexistence of bumble bee species can be ascribed to niche differentiation, primarily on the basis of proboscis lengths and the associated corolla lengths of visited flowers. Each bee species largely visited a few plant species, which were preferred relative to other species. Bee proboscis length was correlated with average corolla length of visited flowers, but not when species with relatively long and short proboscises were considered separately. Bumble bee abundance was affected by presence or absence of major plant species and, contrary to the interpretation of Pyke (1982), elevation, with neither factor dominating. Multimodal distributions of proboscis lengths and altitudinal replacement of bee species of similar proboscis length were consistent with the original hypothesis that bumble bee species compete for floral resources, especially nectar, and cannot coexist if proboscis lengths are too similar, unless one species is a "nectar robber" and hence has exclusive use of some floral resources. However, observed overlap in elevational distributions of bumble bee species with similar proboscis length cannot be reconciled with this hypothesis unless other phenomena are invoked.

KEY WORDS   *Bombus*, elevation, competition, proboscis length, corolla length

The results of surveys of bumble bees and the flowers they visit, carried out in 1974 near Crested Butte, CO (Pyke 1982), originally were considered consistent with hypotheses based on competition between bumble bees for floral resources, with coexistence of bumble bee species ascribed to niche differentiation, primarily on the basis of proboscis lengths and the associated corolla lengths of visited flowers (Inouye 1976, 1977, 1978b, 1980; Pyke 1982), and secondarily on nutritional qualities of nectar or pollen (Pyke 1982). It was concluded that the community of coexisting bumble bees at any particular location is determined, after allowing for dispersal between nearby areas, by the plant community at that location and not by other factors such as nesting habitat or climatic variation (Inouye 1976, Pyke 1982). To coexist, bumble bee species apparently had to differ sufficiently in proboscis length and, depending on the array of flower corolla lengths present, up to four nonparasitic bumble bee species could coexist abundantly. Such sets of species comprised up to three species that characteristically take nectar legitimately from flowers, one from each of three different proboscis-length categories (i.e., short,

medium, and long-tongued), and possibly a short-tongued species that robs nectar from flowers with long corollas (Inouye 1976, 1977; Pyke 1982).

A corollary of these original conclusions is that bumble bee assemblages in different locations should be determined by variation in plant communities rather than by elevation (or climate) per se. Plant communities may vary with local conditions, in relation, for example, to soil and moisture, and with elevation, because of its effect on climatic conditions. Bumble bee assemblages are expected to track any such variation in plant communities, but should not show additional variation in relation to elevation. Hence, if plant and bumble bee communities were to change through time, as might result, for example, from climate change, it should be changes in the plants that determine changes in the bumble bees, not the other way around. The original conclusions from the 1974 surveys are therefore significant in terms of understanding local geographic distributions of bumble bee species and their assemblages, and interpreting any observed changes over time in bumble bee and plant communities.

These original conclusions from the 1974 surveys were not, however, based on statistical analyses, but instead the results simply were summarized with tables and graphs and interpretations were based on these (Inouye 1976, Pyke 1982). Hence, the original conclusions were not well substantiated and, as will be seen below, statistical analyses now lead to somewhat different conclusions.

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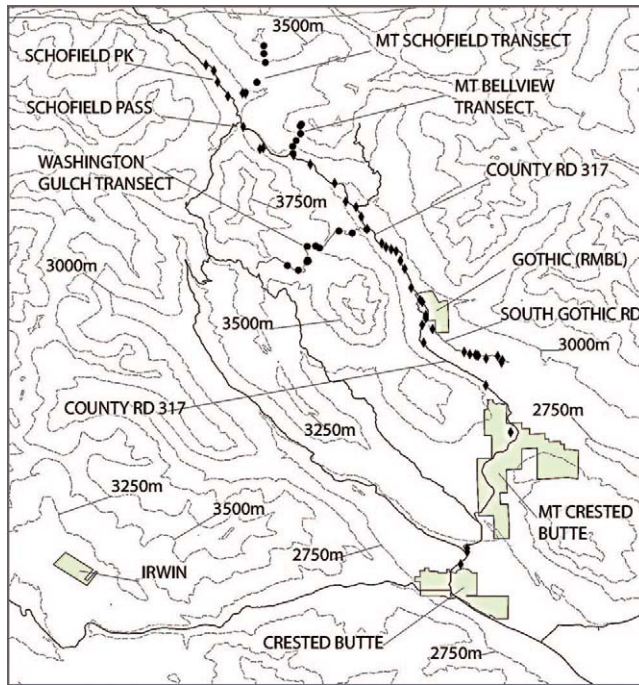[6] Ecology and Evolutionary Biology, University of Toronto, Canada.

Fig. 1. Map of study area showing locations of circular study sites (♦); selected points along walking transects (●); designated roads, track described by us as "South Gothic Rd.;" Washington Gulch Trail (i.e., Forest Service Trail no. 403); and towns. Also depicted are contour lines 250 m apart, some of which are labeled, with the lowest being at 2,750 m. (Online figure in color.)

The data collected during the 1974 surveys provide an excellent opportunity to consider or reconsider seasonal and elevational patterns in bumble bees and the plants they visit. These surveys spanned almost an entire flowering season (i.e., mid-June to early September) along permanent transects that encompassed an elevation range of 2,730–3,730 m, and comprised about 16,000 observations of bumble bees (Pyke 1982 and see Fig. 1; Tables 1 and 2).

Table 1. Numbers of each bumblebee species recorded during surveys, along with the proboscis-length category for each species

Bumblebee species	Proboscis-length category	Number
Nonparasitic spp.		
B. flavifrons	Medium	4,827
B. balteatus (previously B. kirbyellus)	Long	1,838
B. bifarius	Short	1,764
B. sylvicola	Short	1,717
B. appositus	Long	1,431
B. frigidus	Short	1,318
B. occidentalis	Short (nectar robber)	468
B. californicus	Long	170
B. nevadensis	Long	159
B. mixtus	Short	103
B. rufocinctus	Short	101
B. centralis	Medium	19
Total		13,934
Parasitic bumblebees		
Bombus spp. (previously Psithyrus spp.)	Short	1,734

Names adopted in 1974 are included in parentheses if different from current names.

The current study, therefore, aimed to revisit the results and conclusions of the 1974 surveys to provide a statistical basis for comparisons with subsequent surveys at the same locations and to reevaluate the original interpretations. We set out, in particular, to reevaluate the previous conclusion that bumble bee communities in our study area are determined primarily by competition among bumble bees for floral resources and the implication that bumble bee assemblages are determined by the plant communities rather than by elevation per se.

Methods

Strategy. We determined whether bumble bee species showed multimodal frequency distributions (for each caste) of mean proboscis length. Such multimodality is expected if bumble bees compete for floral nectar and if the outcome of this competition depends on interspecific differences in proboscis length (Ranta 1984).

We determined whether plant species showed multimodal distributions of mean corolla depth. Such a pattern might suggest competition between plant species for visits by different pollinators, with the outcome depending on differences in corolla length between different plant species. We also determined whether such a pattern could explain any multimodality in bumble bee proboscis length, independent of competition.

We considered the relationship between average proboscis length for particular bumble bee species or caste combinations and the average corolla length for associ-

Table 2. Numbers of bumblebees, combining parasitic and nonparasitic species, recorded for each of the 30 most frequently visited plant species in decreasing order of bees per plant species, along with the nature and significance of any relationships between presence or absence for each plant species and elevation

Plant species–Current name (Old name)	No. bumblebees	Relationship with elevational region
Delphinium barbeyi	3106	Increase; $P = 0.001$
Hymenoxys (Helenium) hoopesii	1398	Not significant; P's > 0.1
Helianthella quinquenervis	1263	Increase; $P = 0.008$
Mertensia ciliata	947	Increase, then decrease; $P = 0.001$ & 0.004
Aconitum columbianum	880	Decrease, $P = 0.004$
Chamerion (Epilobium) angustifolium	851	Increase, then decrease; P's = 0.001
Senecio triangularis	730	Increase, then decrease; $P < 0.001$ & $P = 0.001$
Senecio bigelovii	657	Not significant; P's $\geq$ 0.05
Senecio crassulus	596	Increase; $P < 0.001$
Viguiera multiflora	501	Increase, then decrease; P's = 0.01
Phacelia hastata (leucophylla)	381	Increase; $P = 0.001$
Senecio serra	346	Not significant; P's > 0.2
Frasera speciosa	337	Not significant; P's > 0.3
Castilleja sulphurea	219	Not significant, P's > 0.1
Gentiana parryi (calycosa)	199	Not significant; P's > 0.1
Solidago (Haplopappus) parryi	194	Not significant; P's > 0.1
Senecio fremontii	186	Increase; $P = 0.004$
Hydrophyllum fendleri	159	Increase then decrease; P's = 0.01
Aster engelmannii	148	Not significant; P's > 0.4
Cirsium sp	143	Not significant; P's > 0.2
Senecio atratus	142	Not significant; P's > 0.4
Pyrrocoma crocea (Haplopappus croceus)	126	Decrease; $P = 0.007$
Arnica sp	115	Increase; $P = 0.001$
Delphinium nuttallianum (nelsonii)	100	Decrease; $P = 0.006$
Senecio amplectens	95	Increase then decrease; P's < 0.001
Gentiana affinis	86	Not significant; P's > 0.1
Vicia americana	78	Decrease; $P < 0.001$
Pedicularis groenlandica	66	Not significant; P's > 0.5
Agoseris sp	60	Not significant; P's > 0.7
Sidalcea candida	57	Only present in region no. 3
Total bumble bees recorded	14,166	

Plant names adopted in 1974 are included in parentheses if different from current names.

ated floral visits. Such a relationship is expected because bumble bees achieve higher rates of net energy gain while foraging at flowers with a particular corolla length than when they forage at flowers with either longer or shorter corollas and this corolla length, at which the rate of net energy gain is maximal, increases with increasing proboscis length (Inouye 1980, Ranta 1984).

We reevaluated the elevational patterns observed by Pyke (1982) by temporally adjusting observations within different elevational regions, to compensate for peak abundances of bumble bees occurring later in the season at higher elevations. This adjustment ensured that elevational comparisons were based on time periods of greatest bumble bee abundance (Pyke et al. 2011).

We developed a method for determining plant utilization indices for each bumble bee species (see Bumble Bee Utilization Regarding Different Plant Species), and used this to identify sets of plant species that are most used by each bumble bee species relative to all other bumble bee species. As these indices seem likely to be approximate measures of bumble bee preferences for the various plant species, we use them below as indices of such preferences. We then assessed how much variation in bumble bee abundance is determined by 1) the presence and absence of these plants and 2) elevation. A significant effect of elevation would require us to revise the conclusion of Pyke (1982) that bee distributions along these transects are driven by plants and competition, with no direct altitudinal effects.

Transects and Sites. As reported by Pyke (1982), surveys of bumble bees and flowers were carried out at sites along road and walking transects in the vicinity of the Rocky Mountain Biological Laboratory (RMBL), Gothic, CO. Roadside sites comprised areas of ≈50-m radius around fixed points alongside of roads. Sites along walking transects comprised areas within ≈25 m of fixed but sometimes unmarked foot trails and within elevational ranges that were generally 500 feet (i.e., 151.5 m). For logistical reasons, there was variation from one time to another in the lengths that were surveyed along the walking routes, and in some cases parts of the walking routes where elevation was relatively constant were surveyed separately. The elevation for each site is taken as the elevation at its center, and sites are considered within elevational regions based on intervals of 152.4 m (500 ft).

A revised description of these transects and sites is presented in Appendix A1. Included now are some sites that were not included in previous analyses (see Pyke 1982 and Appendix A1). The grouping of sites into transects also has changed slightly (see Pyke 1982 and Appendix A1). The locations of all sites and transects now have been recorded with a GPS receiver and this information, along with a copy of the original data, are lodged with the Rocky Mountain Biological Laboratory. The locations of all sites and transects are shown in Fig. 1, and further details are included in Appendix A2, Tables A2–1 (roadside circles) and A2–2 (walking transects).

Survey Methods. As described previously (see Pyke 1982 for further details), one of us (G.H.P.) plus zero to two assistants visited most sites about once every 8 d between 22 June and 8 September 1974. Timing was opportunistic: each site was surveyed at different times of day, with no attempt made to spread survey times per site across times of day. During a visit to a site, the site was surveyed as uniformly as possible. Any observed bumble bees (*Bombus* spp.) or parasitic bumble bees (formerly *Psithyrus* spp., now also *Bombus* spp.) were identified and their behavior recorded. In most cases bumble bees and parasitic bumble bees were observed visiting flowers, but they also occasionally were recorded nest searching (i.e., flying close to ground, stopping to walk into holes in the ground) or in flight. Site visits generally ended after ≈45 min or after at least 20 bumble bees had been recorded for each plant species, whichever came first, or occasionally when halted by inclement weather. The number of visits per site ranged from 1 to 25 and averaged 5.7 ($n = 74$, SE = 0.6). The average visit duration was 40.2 min ($n = 439$, SE = 1.2) or 1.32 person hours ($n = 439$, SE = 0.05).

In almost all cases we identified bumble bees to species and caste on the basis of their size, length of antennae, presence or absence of corbiculae, and patterns of hair coloration (Stephen 1957; Williams 2007; G.H.P., D.W.I., and J.D.T., personal observations). Although Pyke (1982) used the name *B. kirbyellus* for one species, most authors consider *B. balteatus* to be a preferable synonym (e.g., Thorp et al. 1983, Williams 1998), so we adopt it here. We could not confidently distinguish the two species of parasitic bumble bees present in our study area (*Psithyrus insularis* and *P. suckleyi*), and therefore combined them. Since then, the genus *Psithyrus* has been demoted to a subgenus within *Bombus* (Williams 1994, Williams et al. 2008). Voucher specimens were collected and identifications subsequently checked by R. Thorp.

Flowers visited by bumble bees and parasitic bumble bees were identified to the lowest possible taxonomic level. As the names of some plant species have been changed since these surveys, we adopt here the names in the relatively recent checklist of vascular plants of Colorado by Hartman and Nelson (2001) but also report parenthetically the names used by Pyke (1982).

Additional Information. Bumble bees differ in proboscis length and flowers differ in corolla length (here taken to be the distance a bee has to reach with its proboscis to get to the nectar). These measurements combine to determine a bumble bee's ability to extract nectar from flowers (Harder 1983). As a measurement of proboscis length, most authors have taken the length of the labium (e.g., Inouye 1980, Bauer 1983, Williams 1989, Suzuki et al. 2007), which is the prementum and glossa combined, although Harder (1982) has demonstrated that the glossa is actually the functional part of the proboscis in terms of nectar absorption.

We used labium length as our measurement of proboscis length. In most cases, our data on average proboscis lengths were obtained from Macior (1974), for queen and worker bumble bees collected in the Front Range of the Colorado Rockies, and from Inouye (1976, 1980), for males collected around RMBL. Data for workers of *B. rufocinctus* were obtained from Utah in 2008 (J. Strange, personal communication).

In most cases, our data on corolla lengths were obtained from Macior (1974); Inouye (1976, 1980); or Pyke (1982). For a few plant species, corolla lengths were measured within the study area during summer 2008 (Appendix A3; Table A3–1).

Bumble Bee Utilization Regarding Different Plant Species. Patterns of bumble bee utilization regarding different plant species were determined within contiguous areas between which the relative abundances of different bumble bee species showed no appreciable variation. This resulted in the greatest possible sample sizes for determining patterns of floral utilization, while avoiding possible confounding of these patterns with variation in relative abundance of the bumble bees.

We focus on those plant species that accounted for ≈90% of all recorded bumble bee observations. For these plants, which we label as "bumble bee plants," it seems reasonable to assume that the numbers of recorded bees are roughly proportional to plant abundance.

We determined overall levels of utilization for each plant species by simply calculating, for the combined areas described above, the number of recorded observations for each bumble bee species at each plant species. Comparing these numbers across plant species for each bumble bee species would indicate the relative levels of visitation of each plant species by each bumble bee species. However, without some adjustment for floral and plant abundance, these calculations provide no indication of the extent to which each bumble bee differentially uses or prefers the various plant species. Visits to flowers of a particular plant species might be recorded frequently, simply because the plant is relatively common and hence frequently visited by all bumble bees combined, and not because bumble bees exhibit any preference for feeding at its flowers. We therefore combined these numbers with measures of flower abundance.

We assume, as mentioned above, that the abundance of flowers for a plant species, within the group of "bumble bee plants" and within a certain area, is proportional to the total number of recorded bumble bee visits to flowers of that plant species during our surveys within that area, and from this assumption derive a statistic for assessing plant floral preferences exhibited by the different bumble bee species. In other words, we assume that, for our present purposes, the total number of recorded visits to flowers of a particular plant species provides a measure of how florally abundant the plant is. This would seem to be a reasonable assumption for the following reasons: First, during our surveys we walked within sites, pausing to record observed bumble bees and then moving on. Hence, for each plant species, the number of observed flowers should have increased with the number of recorded bumble bees. Second, within what we consider to be the group of "bumble bee plant species," there is good agreement between our subjective assessment of

floral abundance and the total number of bumble bees recorded visiting each plant species (G.H.P., D.W.I., and J.D.T., personal observations). However, we would not expect this approach to work well if extrapolated to include plants that are commonly visited by other kinds of animals (e.g., hummingbirds, butterflies) and are visited rarely by bumble bees.

It follows from this assumption that an index of plant floral preference or rejection for a bumble bee species regarding a particular plant species is provided by the ratio of the percentage of records for each bumble bee species that were of visits to the particular plant species divided by the percentage of all bumble bee records that included the particular plant species. If, for example, a plant species was rare in the environment, and hence generated relatively few recorded bumble bee visits, but accounted for a high proportion of recorded floral visits for a particular bee species, then we would take this to mean that this particular bee species "overuses" or "prefers" the plant species in question relative to alternative species, with the magnitude of the ratio indicating the strength of this preference. Conversely, a low ratio would indicate relative "underutilization," "rejection," or "avoidance." However, if the two percentages were approximately equal, and hence the ratio was approximately equal to one, there would be no indication of relative preference or rejection. In this case, we would categorize the response as "neutral."

This assessment of plant preference and rejection enables different bumble bee species to be compared and also allows identification of those plant species that are most likely to influence the spatial distribution of each bumble bee. It will be seen below that, using this approach, we are able to discern differences in plant preferences that are additional to what would be expected just on the basis of proboscis and corolla lengths. We also are able to examine the extent to which bumble bee distributions are explained by the spatial distributions of their apparently preferred plant species or by elevation. Observed preference ratios range from about four, which we take as an indication of high preference, down to zero, when a particular bumble bee species was never observed to visit the plant species in question, even though other bumble bee species were recorded visiting this plant.

Seasonal Adjustments With Elevation. To determine elevational patterns in bumble bee abundance, we considered the time periods when abundance peaked for each elevational region. This enabled different elevations to be compared at corresponding times during the summer season. For workers, we therefore considered time periods 2 and 3 for the elevational region 2,576–2,727 m, periods 3 and 4 for elevational regions between 2,727 and 3,030 m, periods 4 and 5 for the elevational regions between 3,030 and 3,485 m, and periods 5 and 6 for the elevational regions between 3,485 and 3,788 m (Pyke et al. 2011). For males, we considered time period 4 for elevational region 2,576–2,727 m and time periods 5 and 6 for all higher elevations (Pyke et al. 2011).

Analyses. Statistical analyses generally were carried out using Forward Stepwise Linear General model, as provided by the computer software SYSTAT version 11 (Wilkinson 1990), with the log transformed number of bees recorded per person-hour (i.e., log [B + 1] where B is number of bees per person-hour) as the dependent variable. In this case the untransformed variable was strongly right-skewed and the log transformed variable less so, and the frequency distribution of the transformed variable resembled the right half of a Normal distribution with mean zero. Independent variables in the analyses include time period, in half-month units (i.e., period 1: 16–30 June, period 2: 1–15 July, period 3: 16–31 July); elevational region, divided into intervals of 500 ft. (i.e., region 1 is 8,500–9,000 feet; region 2 is 9,000–9,500 feet), and presence or absence of particular plant species (i.e., 0 for absent, 1 for present).

Because our analyses involved multiple tests we used an adjusted threshold P value for significance at each test (Wright 1992, Chandler 1995). To achieve a balance between type I and type II errors, we obtained these adjusted "comparison-wise" P values by applying a Bonferroni correction, but after first setting the overall "experiment-wise" threshold P value at 0.15 rather than the traditional 0.05 (Chandler 1995). We had two "families" of tests, one in which the dependent variable was presence or absence of various plant species and a second in which it was the number of bees recorded per person-hour, so we carried out this procedure separately for each of these families of tests (Chandler 1995). Application of the Bonferroni correction to an experiment-wise P value of 0.05 has been well criticized because of the consequently high expected rate of type II errors (e.g., Perneger 1998, Nakagawa 2004).

For both families of tests, we adopted an adjusted P value for each test of 0.01. In the case of presence or absence of plant species there were 30 tests (see Table 3) with reasonably well known general relationships with elevation, and so the appropriate P value for each test was $(0.15/30) \times 2$, which equals 0.01 (i.e., experiment-wise P value divided by number of tests and multiplied by two to allow for one-tailed tests). In the case of the number of bees per person-hour there were seven tests for workers and seven more for males (see Table 4; males not included), and so the appropriate P value for each test was 0.15/14, which is $\approx$0.01.

Results

Fauna and Flora. Twelve nonparasitic bumble bee species were recorded in the study area, with the seven most commonly recorded species accounting for 96.0% of all those recorded (Table 1). Note that the numbers reported here for each bumble bee species generally are higher than those reported previously because of the additional sites now included. However, the total number of *B. occidentalis* reported here is lower than the number reported previously because of the removal of one site. In addition, two species of parasitic bumble bee were recorded (Table 1).

Bumble bees were recorded visiting flowers of ≈100 plant species in total, but only ≈30 plant species accounted for 90% of all such observations (i.e., 14,166

Table 3. Preference ratios (in parentheses) exhibited by workers of different bumble bee species in relation to different plant species

Elevational regions	Bumble bee species (Proboscis length category)	Plant spp. with short corollas (preference ratio)	Plant spp. with medium corollas (preference ratio)	Plant spp. with long corollas (preference ratio)
4–8[a]	*B. bifarius* (Short)	*Viguiera multiflora* (4.1) *Hymenoxys hoopesii* (3.8) *Phacelia leucophylla* (3.1)		
	B. frigidus (Short)	*Senecio triangularis* (4.2) *Senecio crassulus* (1.9) *Hymenoxys hoopesii* (1.6)	*Mertensia ciliata* (2.8)	
	B. sylvicola (Short)	*Senecio fremontii* (3.2) *Senecio crassulus* (3.2) *Senecio atratus* (2.7) *Senecio amplectens* (2.6) *Helianthella quinquenervis* (1.5)		
4–5[b]	*B. flavifrons* (Medium)	*Senecio bigelovii* (2.0)	*Aconitum columbianum* (2.1) *Chamerion angustifolium* (1.6)	*Vicia americana* (2.3)
	B. appositus (Long)			*Gentiana parryi* (2.7) *Delphinium barbeyi* (2.6)
	B. balteatus (Long)			*Castilleja sulphurea* (4.6) *Gentiana affinis* (3.5) *Gentiana parryi* (3.2) *Delphinium barbeyi* (2.2)
2[c]	*B. flavifrons* (Medium)		*Aconitum columbianum* (3.0) *Mertensia ciliata* (2.8)	
	B. appositus (Long)		*Aconitum columbianum* (1.5)	*Delphinium barbeyi* (3.1)
6–7[d]	*B. flavifrons* (Medium)	*Phacelia leucophylla* (2.3) *Helianthella quinquenervis* (1.5)	*Aconitum columbianum* (3.8)	
	B. balteatus (Long)		*Mertensia ciliata* (1.7)	*Castilleja sulphurea* (4.0) *Delphinium barbeyi* (3.0)

Elevational regions have been chosen so that there is little variation in relative abundance of the considered bumble bee species between the regions (see notes below). Plant species are included if observed preference ratios were ≥1.5. For each bumble bee species the proboscis-length category is included in parentheses.

[a] For elevational regions #'s 4–8 *B. bifarius, B. frigidus* and *B. sylvicola* are all reasonably abundant and their relative abundances change little between regions (Fig. 6).

[b] For elevational regions #'s 4–5 *B. flavifrons, B. appositus* and *B. balteatus* are all common (Fig. 7).

[c] Within elevational region #2, *B. flavifrons* and *B. appositus* were similarly abundant (Fig. 8).

[d] Within elevational regions #'s 6–7, *B. flavifrons* and *B. balteatus* were both abundant and changed little in relative abundance between regions (Fig. 9).

out of 15,751; Table 2). Species counts are not exact because some plants were not identified to species.

Proboscis Lengths and Corolla Lengths. The frequency distributions of numbers of bumble bee species versus average proboscis length show some signs of multimodality, supporting the previous categorization into short, medium, or long-tongued groups (Figs. 2a and b). For queens of nonparasitic species, this frequency dis-

Table 4. Significant relationships between log-transformed numbers of workers observed per person-hour and either elevational region or presence or absence of preferred plant species

Bumblebee species	Workers		
	Plant species	Elevational region	Equation
Short-tongued			
B. bifarius		R^2: Pr < 0.001; R^3: Pr < 0.001	Log B = 2.83–0.24R^2 + 0.03R^3
B. frigidus	*Mertensia ciliata*: Pr = 0.003	R: Pr = 0.001	Log B = 0.18R + 0.57P
B. sylvicola		R^2: Pr < 0.001	Log B = 0.033R^2
Medium-tongued			
B. flavifrons	*Chamerion angustifolium* (*C.a.*): Pr = 0.006 *Mertensia ciliata* (*M.c.*): Pr = 0.009		Log B = 1.15 + 0.58P(*C.a.*) + 0.60P (*M.c.*)
Long-tongued			
B. appositus	*Delphinium barbeyi*: Pr = 0.002	R^2: Pr<0.001	Log B = 0.86–0.035R^2 + 0.93P
B. balteatus		R: P < 0.001	Log B = 0.34R
Nectar-robber			
B. occidentalis	*Ipomopsis aggregata*: P = 0.001	R:P < 0.001; R^2: P = 0.001	Log B = 2.32–0.92R + 0.084R^2 + 0.52P

Abbreviated scientific names are included in parentheses in cases where presence/absence for two plant species were significant. Also included are probability values (Pr) for each test, elevation region (R), the no. of bees recorded per person-hour (B), and presence/absence for each plant species [P or P(abbreviated scientific name)]. Tests included linear, quadratic and cubic powers of elevational region (i.e., R, R^2 & R^3 respectively). Least squares regression equations are presented with the inclusion of any significant terms. Otherwise all relationships are not significant (i.e., Pr's > 0.01).
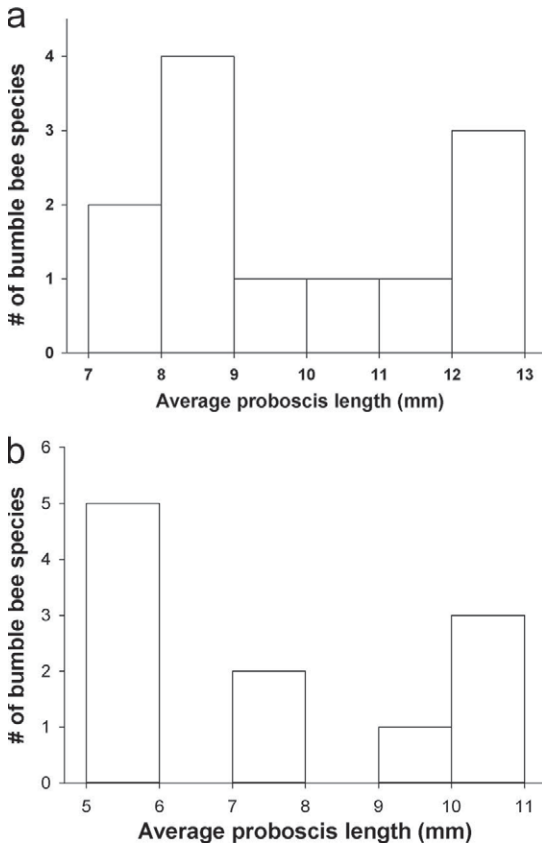
Fig. 2. a: Frequency distribution of average proboscis length (mm) for workers of each bumble bee species, excluding cuckoo bumble bees. b: Frequency distribution of average proboscis length (mm) for queens of each bumble bee species, excluding cuckoo bumble bees.

tribution appeared bimodal, with peaks at ≈8–9 mm and ≈12–13 mm (Fig. 2a), a pattern that is maintained if the parasitic *B. insularis* (formerly *Psithyrus insularis*) is included, as queens of this species from around RMBL have an average proboscis length of 8.2 mm (Macior 1974).

For workers of species other than *B. rufocinctus*, for which data from around RMBL are not available, the frequency distribution appeared trimodal with peaks at ≈5- 6 mm, 7–8 mm, and 10–11 mm (Fig. 2b). This pattern should be maintained if *B. rufocinctus* are included, as workers of this species have relatively short tongues in Utah (i.e., average ≈5.2 mm; J. Strange, personal communication).

Considering both queens and workers, the short-tongued species are *B. bifarius*, *B. frigidus*, *B. mixtus*, *B. occidentalis*, and *B. rufocinctus;* the medium-tongued species are *B. centralis* and *B. flavifrons;* and the long-tongued species are *B. appositus*, *B. californicus*, *B. balteatus*, and *B. nevadensis*. We do not consider proboscis lengths for males because we have local data for only seven species.

We therefore follow previous studies (Inouye 1976; 1977; 1978a,b; 1980; Pyke 1982) in recognizing four proboscis categories: short-, medium-, and long-tongued

species that feed legitimately at flowers, plus a short-tongued species (*B. occidentalis*) that legitimately visits some flower species, especially those with short corollas, but characteristically robs nectar from some flowers with long corollas (Table 2; Figs. 2a and b).

The frequency distribution of numbers of plant species versus corolla length shows little or no evidence of multimodality (Fig. 3), but to facilitate analysis and discussion we divide corolla lengths into the following four categories (Fig. 3): zero, short (<7.5 mm); medium (7.5–10.5 mm); long (10.5–20 mm); and very long (>20 mm). These categories correspond to the peaks exhibited by the frequency distribution of corolla lengths (Fig. 3).

Bumble bees primarily visited short-, medium-, and long-corolla flowers, seldom appearing on flowers with either zero or very long corollas (Fig. 4). Visits to flowers with very long corollas either involved pollen collection from accessible anthers by species of various tongue-lengths or nectar-robbing by *B. occidentalis.*

Across all combinations of bumble bee species and caste, excluding the nectar-robbing species *B. occidentalis*, there was the expected positive relationship between bumble bee proboscis length and the average corolla length for recorded flower visits ($r^2 = 0.7$, $P < 0.001$; Fig. 5).

Elevational Distributions of Bumble Bees and Flowers. Each bumble bee species had its own distinct elevational distribution. For each of the seven commonly-recorded species, except *B. bifarius*, the average numbers of workers recorded per person-hour peaked at a particular elevation and decreased with progressively higher and lower elevations (Figs. 6 and 7). However, as was noted previously (Pyke 1982), *B. bifarius* showed a major peak in worker abundance at relatively low elevation and a second, smaller peak at the highest elevations (Fig. 6).

Within each proboscis length category, most bumble bee species had quite different elevational distributions in terms of worker and male abundances, but there was considerable overlap between proboscis-length categories. Within the long-tongued species, *B. appositus* was a distinctly low-elevation species, whereas *B. balteatus* occurred at relatively high elevation (workers: Fig. 7; males: unpublished). Considering workers and males of the short-tongued, non-nectar-robbing species, *B. bifarius* predominated at relatively low elevations, *B. sylvicola* at relatively high elevations, and *B. frigidus* at mid elevations (Figs. 6 and 8). The nectar-robbing species *B. occidentalis* reached peak abundance, in terms of workers and males, in elevational region 2 or 3 (Figs. 6 and 8). Across proboscis categories, workers of *B. bifarius, B. appositus*, and *B. occidentalis* all peaked in abundance in the second-lowest elevational region (Figs. 6 and 7). The only common species of intermediate proboscis length was *B. flavifrons;* its broad elevational distribution of workers overlapped with all other species (Fig. 7).

Most frequently visited plant species occurred non-randomly across elevational regions, providing a basis for considering relationships between bumble bee and plant distributions. For the 30 plant species that each
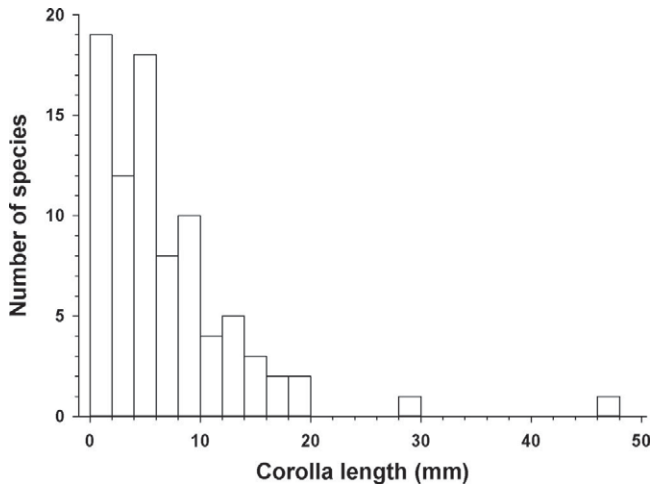
Fig. 3. Frequency distribution of flower corolla lengths (mm) across all plant species for which visitation by bumble bees was recorded.

received at least 50 visits, six species increased in frequency with elevation, four decreased, and seven peaked at intermediate elevations (Table 2; Fig. 9).

Floral Resources Preferred by Different Bumble Bee Species. The bumble bee species within each proboscis length category generally exhibited preferences for plant species in the corresponding corolla length category. Workers of bumble bees with short or long proboscises were recorded preferentially on plant species with short and long corollas respectively, as indicated by preference ratios >3 (Table 3). Workers of *B. flavifrons*, which has a medium-length proboscis, either showed relatively strong preferences for plant species with medium-length corollas or exhibited moderate preferences (i.e., 2–3) for plant species that spanned the range from short- to long-corollas (Table 3). Similar patterns are evident when queens and males are considered (G.H.P., unpublished data). These foraging preferences are reflected in the ob-

served relationship between bumble bee proboscis length and the average corolla length for visited plants (see above and Fig. 5).

However, within each bumble bee proboscis-length category, different bee species exhibited different plant preferences, with these preferences showing no apparent relationship with corolla length. Within the group of bumble bee species with short proboscises, the strongest preferences were for *Viguiera multiflora* and *Hymenoxys hoopesii* by *B. bifarius*, *Senecio triangularis* by *B. frigidus*, and other *Senecio* spp, especially *Senecio fremontii* and *Senecio crassulus*, by *B. sylvicola* (Table 3). These patterns accord with the previous, less comprehensive report that *B. bifarius* preferred *Hymenoxys (Helenium) hoopesii*, *B. frigidus* preferred *Senecio triangularis*, and *B. sylvicola* preferred *Senecio crassulus* (Pyke 1982). For the group of bumble bee species that have relatively short proboscises (i.e., <9 mm), including all castes but excluding the nectar-rob-
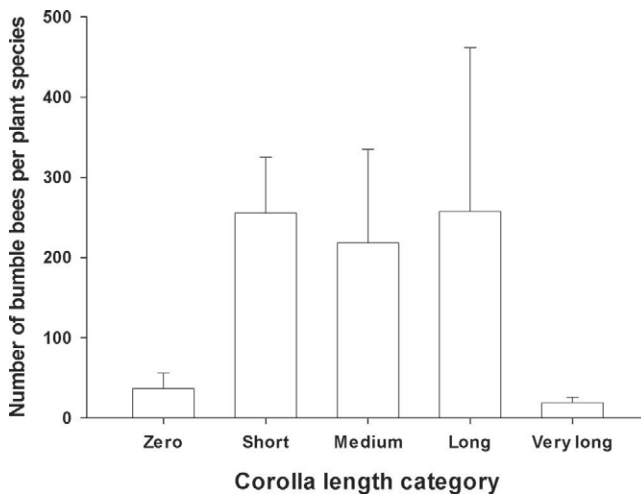

Fig. 4. Average number (+1 SE) of bumble bees recorded per plant species versus corolla length category.
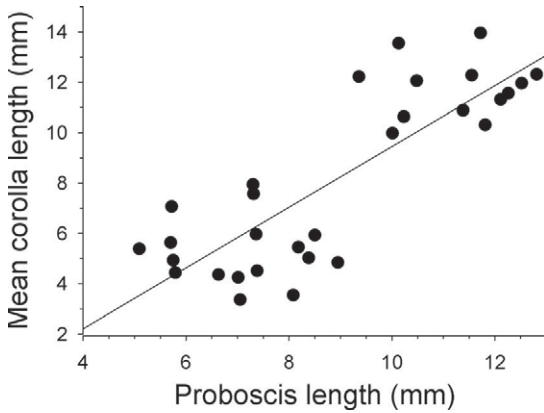
Fig. 5. For each combination of bumble bee species and caste (excluding *B. occidentalis*), the average corolla length (mm) for recorded plant visits is plotted against bumble bee proboscis length (mm). Also shown is the linear regression line fitted to these points (i.e., Y = −2.6 + 1.2X where X is proboscis length and Y is corolla length).

bing species *B. occidentalis*, there was no significant relationship between proboscis length and average corolla length of visited plants ($r^2 = 0.005$, $P = 0.8$; Fig. 5).

Similarly, within the group of bumble bee species with long proboscises, different species exhibited different plant preferences, with no apparent relationship between these preferences and corolla length. Within this group, *B. appositus* exhibited its strongest preferences for *Delphinium barbeyi* and *Gentiana parryi*, whereas *B. balteatus* most strongly preferred *Castilleja sulfurea*, *Gentiana affinis*, and *Delphinium barbeyi* (Table 3). In addition, *B. appositus* showed a moderate preference for *Aconitum columbianum* (Table 3), whereas *B. balteatus* was not recorded visiting this plant species at all. Similarly, *B. balteatus* showed

a moderate preference for *Mertensia ciliata* (Table 3), a plant species not visited by *B. appositus*. In addition, there were no visits by *B. appositus* to *Castilleja sulfurea*, which, as just mentioned, was highly preferred by *B. balteatus*. These results accord with the conclusions in (Pyke 1982) regarding these two bumble bee species. For the group of bumble bee species that have relatively long proboscises (i.e., >9 mm), including all castes, there was no significant relationship between proboscis length and average corolla length of visited plants ($r^2 = 0.005$, $P = 0.8$; Fig. 5).

The species that robs nectar from a number of plant species, *B. occidentalis*, visits a wide array of different plant species with a wide array of corolla lengths. For workers of this bumble bee species, the most commonly visited plant species ($n = 370$) are the long-corolla *Delphinium barbeyi* (9%); the medium corolla *Aconitum columbianum* (13%) and *Penstemon strictus* (3%); and the short-corolla *Epilobium angustifolium* (15%), *Ligusticum porteri* (8%), *Senecio bigelovii* (8%), and *Haplopappus croceus* (5%), thus requiring seven plant species to account for 60% of recorded flower visits, compared with four or fewer species required for the other bumble bee species. At medium- and long-corolla plants, *B. occidentalis* either collects pollen or robs nectar (G.H.P., personal observations). It is also sometimes observed robbing nectar from the long-corolla *Ipomopsis aggregata* and *Corydalis caseana* (Maloof 2001; G.H.P, D.W.I., and J.D.T., personal observations), although this was not recorded during the current study, and it visits some zero-corolla-length plant species that are rarely if ever visited by other bumble bee species (e.g., *Ligusticum porteri*: 100% of recorded flower visits, $n = 28$; *Heracleum lanatum*: 93%, $n = 15$). *Ipomopsis aggregata* was identified previously as an important plant species for *B. occidentalis* (Pyke 1982) and will be included in subsequent analyses.

Fig. 6. Average numbers (±1 SE) of bumble bee workers recorded per person-hour versus elevational region for three short-tongued legitimately-feeding species (i.e., *B. bifarius*, *B. frigidus*, *B. sylvicola*) and one nectar-robbing species (i.e., *B. occidentalis*). Included time periods are two and three for elevational region 2,576–2,727 m; 3 and 4 for elevational regions between 2,727 and 3,030 m; 4 and 5 for the elevational regions between 3,030 and 3,485 m; and 5 and 6 for the elevational regions between 3,485 and 3,788 m (Pyke et al. 2011).
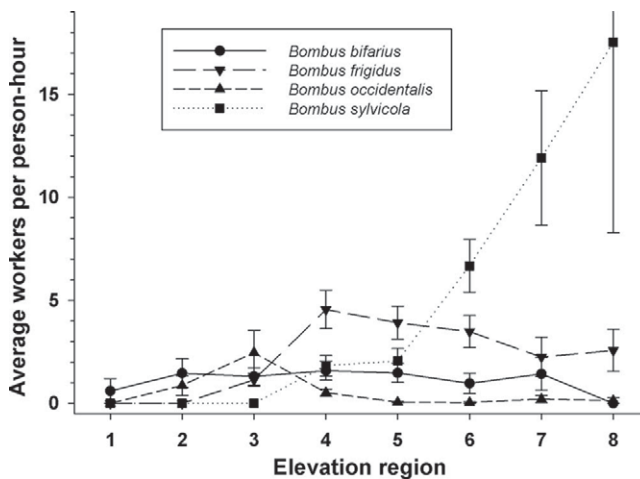
Fig. 7. Average numbers (±1 SE) of bumble bee workers recorded per person-hour versus elevational region for two long-tongued species (I.e., *B. appositus* and *B. balteatus*) and one medium-tongued species (i.e., *B. flavifrons*). Included time periods are 2 and 3 for elevational region 2,576–2,727 m; 3 and 4 for elevational regions between 2,727 and 3,030 m; 4 and 5 for the elevational regions between 3,030 and 3,485 m; and 5 and 6 for the elevational regions between 3,485 and 3,788 m (Pyke et al. 2011).
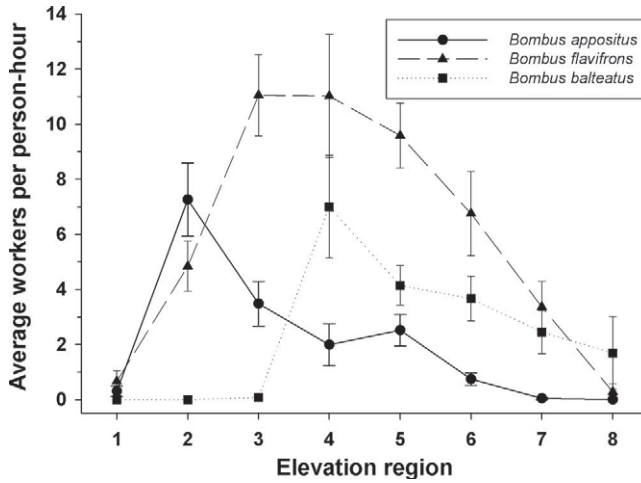
Bumble Bee Distributions Versus Plant Distributions and Elevation. For the seven most commonly recorded bumble bee species, the log transformed numbers of workers and males recorded per person-hour generally were related to both elevational region and presence or absence of their major floral resources (i.e., plant species indicated as preferred floral resources by above analysis). In the case of workers, both elevational region and presence or absence of a major plant species significantly affected abundance for three bumble bee species, elevational region alone for three species, and two of the major plant species but not elevational region for one species (Table 4). In the case of males, both elevational region and presence or absence of a major plant species were significant for two bumble bee species, elevational region alone for three species,

and one of the major plant species but not elevational region for one species (Table 4). Essentially the same results are obtained if the analyses are repeated using the untransformed number of worker bumble bees as dependent variable (G.H.P., unpublished data).

Discussion

Assessing Bumble Bee Abundance. Although originally dismissed as a dependent variable, because of likely differences between observers in ability to observe and identify bumble bees and a tendency for each observer to concentrate on patches of particular plant species (Pyke 1982), bees per person-hour now appears to be the most suitable dependent variable in assessing bumble bee abundance (current study and
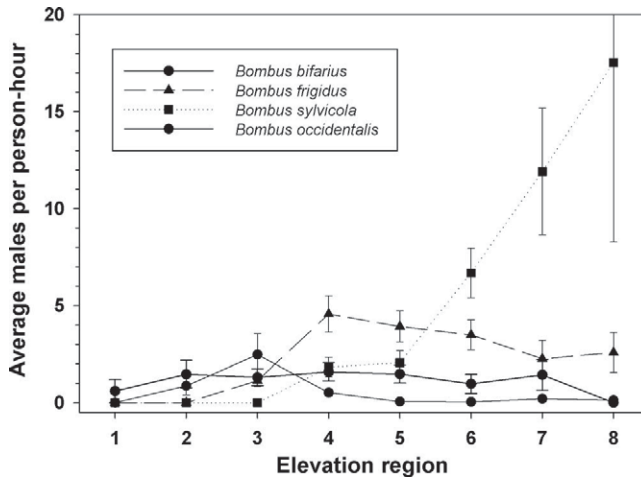

Fig. 8. Average numbers (±1 SE) of bumble bee males recorded per person-hour versus elevational region for three short-tongued species that feed legitimately (i.e., *B. bifarius, B. frigidus, B. sylvicola*). Included time periods are 4 for elevational region 2576–2727 m and time periods 5 and 6 for all higher elevations.
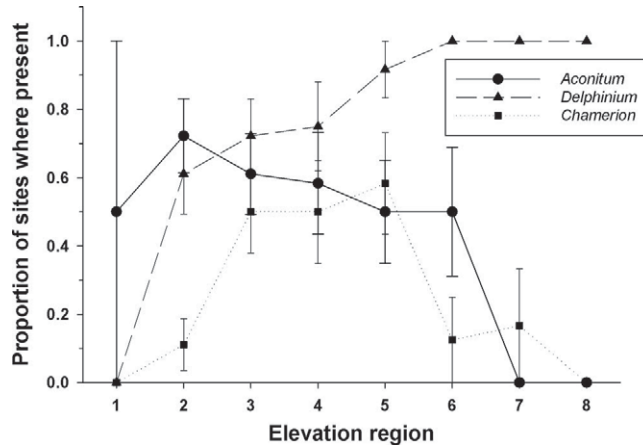
Fig. 9. Proportion of sites where present (±1 SE) versus elevational region for *Aconitum columbianum*, *Delphinium barbeyi*, and *Chamerion* (formerly *Epilobium*) *angustifolium*.

Pyke et al. 2011). At the time of the original surveys, Pyke (1982) attempted to minimize interobserver differences; furthermore, combining the records of three observers should "average over" residual differences among observers. Other analytical approaches, such as using relative abundances of different species and castes, would be subject to similar biases, and possible effects on relative abundance are more difficult to analyze and interpret than effects on bees per person-hour, which may be considered an index of "absolute" abundance.

Bumble Bee Floral Preferences. Our assessment of bumble bee preferences regarding the various plant species is based on the assumption that the total number of bumble bees recorded visiting flowers of a particular plant species provides a measure of the relative floral abundance of that plant species within our survey sites, and it is possible to imagine situations in which this assumption does not hold. Future studies similar to ours should, therefore, include quantitative assessments of plant and floral abundances.

Bumble Bee Distributions. As reported earlier (Pyke 1982), the most abundant bumble bee species within a proboscis-length category tended to have different elevational distributions. The two long-tongued species in the current study showed altitudinal replacement of one species by the other; so too did the three short-tongued species (Pyke 1982). Few other studies have considered such geographic replacement or turnover of bumble bee species (but see Inouye 1977). Similarly consistent with what was reported earlier, each bumble bee species had a small number of plant species, generally from within the associated corolla-length category, that constituted a large proportion of observed flower visits and were preferred relative to other plant species. For both long-tongued bee species, the long-corolla *Delphinium barbeyi* was both a highly-visited and preferred plant species. *B. balteatus* also favored *Castilleja sulfurea*, another long-corolla plant species, and *Mertensia ciliata*, a medium-corolla species. The plant species favored by the three short-tongued bumble bee spe-

cies all have short corollas (i.e., *Phacelia leucophylla*, *Helenium hoopesii*, *Senecio triangularis*, *Senecio crassulus*, and *Helianthella quinquenervis*) except for the medium-corolla *Mertensia ciliata*, which is favored by one bumble bee species (i.e., *B. frigidus*). The medium-tongued *B. flavifrons* favored two medium-corolla plant species (i.e., *Mertensia ciliata* and *Aconitum columbianum*). The preferences for *Delphinium* by *B. appositus* and for *Aconitum* by *B. flavifrons* also were reported by Inouye (1978b), whose experimental manipulations demonstrated that competitive interactions between the bumble bee species are in part responsible for the resource use patterns.

Also consistent with what was reported earlier, the bumble bees showed flower preferences, indicating that factors in addition to corolla length are involved. It was concluded previously, for example, that each of the three short-proboscis bumble bee species appeared to prefer a different plant species: *Helenium hoopesii* for *B. bifarius*, *Senecio triangularis* for *B. frigidus*, and *Senecio crassulus* for *B. sylvicola* (Pyke 1982). In the current study we extended these conclusions, showing that these bumble bee species exhibited preferences in regard to additional plant species.

It is possible that such differences between the bumble bee species could be the result of nutritional differences between the pollens of the different plant species with each bumble bee adapted to the pollen from a different plant (Pyke 1982). Though the above three bumble bee species probe the flowers of their preferred flower species, thus collecting nectar and generally collecting pollen only incidentally, they do accumulate pollen from these plants in their corbiculae (G.H.P., D.W.I., and J.D.T., personal observations). Pollens are known to be nutritionally diverse, different bumble bee species prefer some pollens over others, and the kind of pollen available affects the growth and development of bumble bee larvae (Rasheed and Harder 1997, Genissel et al. 2002, Goulson et al. 2005, Hanley et al. 2008).

However, the present analysis did not support the original conclusion that bumble bee distributions are determined by plant distributions, rather than by elevation *per se* (Pyke 1982). By applying multiple regression, we now find that some of the covariation of bumble bee abundance with elevation remains unaccounted for by the presence or absence of major plant species. Key plant species are important but do not dominate over other unspecified elevational correlates (Table 4). Of course, plant presence or absence, averaged over a number of sites, is at best a crude measure of plant abundance, and it is possible that a more quantitative assessment of plant abundance would have generated different results.

The new analyses, although generally consistent with what was reported earlier, are equivocal regarding the role of interspecific competition in structuring bumble bee communities around RMBL. The relationships between average numbers of bumble bees recorded per hour and presence or absence of major plant species were no stronger for males than for workers (Table 4), whereas stronger relationships might be expected if there is competition for floral resources between worker bumble bees, as such competition is likely to affect the food resources collected by the workers and subsequently converted into production of males. Given the time lag between egg laying and bee emergence, it seems likely that male numbers would be more affected by interspecific competition between workers than the numbers of workers themselves.

That bumble bee species replace one another altitudinally could reflect interspecific competition between bumble bees, but could also result from differential adaptation to altitude, and its associated climate, by each bumble bee species. Of course, each bumble bee species is likely to have become adapted to both the plant species with which it co-occurs and the climate it typically encounters, thus increasing the difficulty of separating these factors.

Bumble Bee Community Structure. Attempts to understand community structure have frequently hypothesized that bumble bee species compete for floral resources, most importantly nectar, and therefore cannot coexist if there is too much similarity in proboscis length, unless one of the species is a "nectar robber" and hence has sole access to some floral resources (Inouye 1977, 1978b, 1980; Pyke 1982; Ishii et al. 2008). This hypothesis has been supported by observations that, in some cases, 1) the proboscis lengths of coexisting and common species appear to be "spaced out" on the continuum of possible proboscis lengths (Inouye 1977, 1978b; Pyke 1982; Bauer 1983; Ishii et al. 2008); 2) the frequency distribution of proboscis lengths for regionally co-occurring species is multimodal (this study); and 3) species with similar proboscis lengths replace one another geographically (this study; Inouye 1977). Also consistent with this hypothesis is the likelihood that individual bumble bees may forage in or disperse to areas some distance from where they nest and successfully breed (Pyke 1982, Bauer 1983, Osborne et al. 2008, Lepais et al. 2010, O'Connor et al. 2010), as this may explain observed overlapping distributions of bumble bees with similar proboscis lengths and the presence of relatively uncommon bumble species with similar proboscis lengths to common species (Pyke 1982, Bauer 1983).

However, this competition hypothesis has been contradicted by a number of observations. For example, in some studies, when bumble bee species in a community have been ordered by increasing (or decreasing) proboscis length, the observed average ratio of proboscis length for neighboring species (a measure of "spacing" between adjacent species in the list) has not been significantly different from what would be expected if the members of this community were chosen at random from the pool of available species in the region (Ranta 1982, 1984; Ranta and Tiainen 1982). Furthermore, this conclusion is not altered when the probability that a particular species is chosen is weighted by its observed relative abundance (Ranta 1982, 1984; Ranta and Tiainen 1982). The hypothesis also is contradicted by the observation that some bumble bee communities apparently include more species than expected, with coexisting species sometimes being similar in proboscis length (Ranta and Lundberg 1980, Ranta 1982, Williams 1989, Goulson and Darvill 2004, Iserbyt et al. 2008).

It is difficult to reconcile this difference between observed community-level patterns re proboscis length and what is expected under the hypothesis of competition for nectar. Of many possible explanations for this, the following stand out. First, spatial–temporal variability enables coexistence of bumble bee species with similar proboscis lengths because one species is favored in terms of competition at one point in time or in one patch of flowers, whereas another is favored elsewhere or at another time (Ranta and Lundberg 1980, Ranta and Vepsalainen 1981). This could lead to the coexistence of species with similar proboscis lengths and hence to a relatively large number of coexisting species (Ranta and Lundberg 1980, Ranta and Vepsalainen 1981), and could also result in a multimodal frequency distribution of proboscis lengths.

Alternatively, different species, with similar proboscis lengths, are favored in geographically distinct areas that are nevertheless close enough for significant numbers of individuals to move between areas (Pyke 1982). Our observations of how individual bumble bee species and bumble bee communities vary with elevation are consistent with this.

To understand better the factors that determine bumble bee communities and, in particular, to be able to separate the effects of interspecific competition from the effects of other factors, it may therefore be necessary to consider study sites where the level of spatio–temporal variability is minimal, or at least measurable, and sites that are sufficiently isolated that immigration should not be significant.

It is also possible that bumble bee species with similar proboscis length can coexist if different plant species with similar corolla lengths favor different bumble bee species by virtue of nutritional differences between their pollen (Pyke 1982, Goulson et al. 2005). Differences in floral preferences between bumble bee species with similar proboscis length could reflect

such nutritional differences between different pollens, with each bumble bee species preferring and favored by different plant species (Goulson et al. 2005, Hanley et al. 2008). Further research on the nutritional values of different pollens to different bumble bee species will be necessary to measure this possibility (Goulson et al. 2005).

Long-Term Changes. Our reanalysis of the 1974 data, along with other available information, provides a basis for considering how the distributions of bumble bees and plants, and relationships between them, may have changed since then. There are clear spatial and temporal patterns in terms of both bumble bee species and the plants they visit, and possible changes in these patterns can now be considered. Of course, climate change since 1974 is one factor that may have affected the bumble bees and the plants they visit, and information is available with regard to the nature and magnitude of climate change in the area as well as how climatic variation and change affects plant distribution and phenology for plant species that occur in the area (Inouye and McGuire 1991; Inouye 2000, 2008). Integrating these different kinds of information should help in understanding the effects of climate change on bumble bees and the flowers they visit.

Acknowledgments

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Appendix A1: Revised description of transects and study sites

1. Gothic Road Transect (GRT): This transect comprised 11 sites along Gunnison County Road 317 from Crested Butte (elevation 2693 m) to Gothic (elevation 2874 m), a distance of 12.4 km. The site closest to Gothic (i.e., SRT #01; Table A1) was previously included in what was called the 'Gothic Transect', but the other sites were not included (Pyke 1982).

2. South Gothic Road (SGR): This transect comprised 12 sites along a small side road (also locally known as the Kettle Pond Road) that leaves the Crested Butte-Gothic Road just south of Gothic and runs south-easterly for about 2.8 km. This transect was previously included as the lowermost part of the 'Gothic Transect' (Pyke 1982).

3. Schofield Road Transect (SRT): This transect comprised 18 sites in Gunnison National Forest along County Road 317 from Gothic (elevation 2730 m) to Schofield Pass (3240 m), a distance of about 14.3 km. All but the two highest of these sites were previously included in the 'Gothic Transect'. The third and second highest sites (i.e., SRT #16 & SRT #17) were located close to Emerald Lake (elevation 3180m) and were previously considered as a separate 'Emerald Lake' site (Pyke 1982). The highest site was located at Schofield Pass (elevation 3240m) and was previously omitted (Pyke 1982).

4. Washington Gulch Transect (WGT): This transect comprised 11 segments along a foot-trail (United States Forest Service [USFS] Trail 403) from the USFS 'Gothic' Campground (2940 m) on County Road 317 to the saddle (3440m) between Gothic Mountain and Mount Baldy. From this point the foot-trail leads down into Washington Gulch. The segments overlapped (Table A2) because there was variation from one time to another in the lengths of trail that were surveyed. In some cases parts of the trail where elevation was relatively constant were surveyed separately (Table A2). This transect was previously referred to by the same name (Pyke 1982).

5. Mt. Bellview Transect (MBT): This transect comprised 12 segments along a regular but unmarked walking route from County Road 317 to near the summit of Mt. Bellview. These segments overlapped because of variation from one time to another in the lengths that were surveyed (Table A2). The uppermost segment was only 65 m in elevational range because it ended near the summit (i.e., 3635–3700m). These segments were previously included as the uppermost part of the 'Gothic Transect' (Pyke 1982).

6. Schofield Park (SP): There were four sites along the road through Schofield Park (3180 m), which lies just north of Schofield Pass, in the White River National Forest. These sites were previously combined and included as the lowermost site along the 'Schofield Transect' (Pyke 1982).

7. Mt. Schofield Transect (MST): This transect consisted of two sites at the bottom (i.e., MST #01 & MST #2) plus seven segments at higher elevations along a regular but unmarked walking route from Schofield Park to near the summit (3760 m) of the unnamed mountain which rises at the eastern edge of the park, north of the trail to West Maroon pass. These segments overlapped because of variation from one time to another in the lengths that were surveyed (Table A2). The upper most segment was only 90 m in elevational range because it reached the summit (i.e., 3635–3725m). This mountain is the nearest mountain to the north of Mt. Bellview. This transect previously formed all but the lowermost part of the 'Schofield Transect' (Pyke 1982).

Appendix Table A2–1. Location details for 1974 circular study sites. These were almost all relocated in 2007 and had their locations recorded in 2007 or 2010. Name(s) 1974 refers to the name(s) used in field notebooks containing the original data. These notebooks have been scanned to pdf copies that have been lodged with the Rocky Mountain Biological Laboratory

Code	Name(s) 1974	Elev. (s) 1974 (ft)	Region 1974 (ft)	Relocated 2007	GPS Unit	GPS_Date	GPS_Time	GPS Datafile	GPS Latitude	GPS Longitude	GPS Height (m)
GRT #01	Near dump	8,900	8,501–9,000	Yes	GEOXT	05-Jul-10	10:41:31am	PYKE070520101130.cor	38.876114265	−106.977772502	2701
GRT #02	Slate River Road	9,000	8,501–9,000	Yes	GOOGLE-MAP				38.880086000	−106.975681000	2710
GRT #03	Near bend in road	9,100	9,001–9,500	Yes	GEOXT				38.881237910	−106.975716166	2713
GRT #04	Below (old) C.B. stables	9,550	9,501–10,000	Yes	GARMIN RINO 110	01-Jul-10	03:03:26 pm	DAVENDONISJ070115B.c	38.918016667	−106.961916667	
GRT #05	Near Rosy Point	9,550	9,501–10,000	Yes	GARMIN RINO 110				38.932833333	−106.969816667	
GRT #06	Below Snodgrass	9,500	9,001–9,500	Yes	GARMIN RINO 110				38.946416667	−106.989483333	
GRT #07	Just south of East River bridge	9,500	9,001–9,500	Yes	GEOXT	19-Jul-10	04:23:08 pm	PYKE071920101700.co	38.952071314	−106.989942932	2874
GRT #08	Between S.Gothic turnoff & Kettle ponds turnoff	9,500	9,001–9,500	Yes	GOOGLE-MAP				38.954203000	−106.988818000	2879
GRT #09	David's study plot south of Gothic	9,500	9,001–9,500	Yes	GEOXT	19-Jul-10	04:05:58 pm	PYKE071920101700.co	38.954822602	−106.988795601	2877
GRT #10	Near turnoff to S.Gothic cabins	9,500	9,001–9,500	Yes	GEOXT	19-Jul-10	04:02:38 pm	PYKE071920101700.co	38.955208702	−106.988756350	2879
GRT #11	Gothic	9,550	9,501–10,000	Yes	GOOGLE-MAP				38.959335000	−106.989905000	2593
MST #01	In front of cabin	10,500	10,001–10,500	Yes	GEOXT	12-Jul-10	01:54:31 pm	PYKE071220101500.cor	39.025533507	−107.046890864	3202
MST #02	Old mining road	10,600	10,501–11,000	Yes	GEOXT	12-Jul-10	01:58:06 pm	PYKE071220101500.cor	39.025421888	−107.045942335	3211
SGR #01	Below cabin	9,200	9,001–9,500	Yes	GEOXT	01-Jul-10	12:32:56 pm	DAVENDONISJ070113A.c	38.940128319	−106.964816134	8640
SGR #02	Near cabin	9,400	9,001–9,500	Yes	GEOXT	05-Jul-10	01:16:21 pm	PYKE070520101400.cor	38.940441170	−106.964917473	2837
SGR #03	Near stream	9,400	9,001–9,500	Yes	GEOXT	05-Jul-10	01:13:21 pm	PYKE070520101400.cor	38.940852630	−106.964557772	2833
SGR #04	Near stream above cabin	9,450	9,001–9,500	Yes	GEOXT	05-Jul-10	01:20:26 pm	PYKE070520101400.cor	38.942143377	−106.966050195	2838
SGR #05	Dried kettle pond south of gate/S of gate & kettle pond N of cabin	9,425	9,001–9,500	Yes	GOOGLE-MAP				38.941372000	−106.969712000	2867
SGR #06	Just south of gate	9,450	9,001–9,500	Yes	GEOXT	05-Jul-10	01:39:46 pm	PYKE070520101400.cor	38.942308255	−106.972171296	2863
SGR #07	Near gate	9,350	9,001–9,500	Yes	GEOXT	01-Jul-10	01:06:26 pm	DAVENDONISJ070114A.c	38.942424709	−106.972691364	2863
SGR #08	Just north of gate	9,450	9,001–9,500	Yes	GEOXT	05-Jul-10	01:42:21 pm	PYKE070520101400.cor	38.942566566	−106.973129913	2866
SGR #09	Dried kettle pond north of lower gate	9,400	9,001–9,500	Yes	GEOXT	01-Jul-10	01:21:56 pm	DAVENDONISJ070114A.c	38.942741015	−106.974867793	2859
SGR #10	Kettle pond - near power/phone line	9,500	9,001–9,500	Yes	GEOXT	01-Jul-10	01:42:11 pm	DAVENDONISJ070114A.c	38.943342594	−106.976663224	2863
SGR #11	Near Aspen Grove	9,500	9,001–9,500	Yes	GEOXT	01-Jul-10	02:03:21 pm	DAVENDONISJ070115A.c	38.950732314	−106.986658687	2873
SGR #12	1/5 mile E of road	9,540	9,501–10,000	No							
SP #01	At southern edge	10,500	10,001–10,500	Yes	GEOXT	12-Jul-10	02:35:56 pm	PYKE071220101500.cor	39.024607150	−107.051532815	3170
SP #02	Near turnoff to Northpole Basin	10,500	10,001–10,500	Yes	GEOXT	12-Jul-10	02:31:46 pm	PYKE071220101500.cor	39.029038561	−107.054795343	3159
SP #03	Between bridge & turnoff to Northpole Basin	10,450	10,001–10,500	Yes	GEOXT	12-Jul-10	02:24:41 pm	PYKE071220101500.cor	39.032686678	−107.056003890	3160
SP #04	Near bridge	10,400	10,001–10,500	Yes	GEOXT	12-Jul-10	02:17:06 pm	PYKE071220101500.cor	39.034516237	−107.058502794	3147
SRT #01	North Gothic	9,600	9,501–10,000	Yes	GEOXT	18-Jul-10	02:20:36 pm	PYKE071820101430.cor	38.959983913	−106.990579130	2900
SRT #02	Just north of Gothic	9,650	9,501–10,000	Yes	GEOXT	18-Jul-10	02:15:31 pm	PYKE071820101430.cor	38.963842652	−106.993420226	2918
SRT #03	Near beaver pond (on E side of road)	9,650	9,501–10,000	Yes	GEOXT	18-Jul-10	02:10:26 pm	PYKE071820101430.cor	38.969892032	−106.995503132	2920
SRT #04	Just south of Avery Pk Campground	9,650	9,501–10,000	Yes	GEOXT	18-Jul-10	02:06:16 pm	PYKE071820101430.cor	38.972389671	−106.996859288	2923
SRT #05	In front of Avery Pk Campground	9,700	9,501–10,000	Yes	GEOXT	18-Jul-10	02:02:16 pm	PYKE071820101430.cor	38.975465349	−106.998198408	2925
SRT #06	Just north of Avery Peak Campground	9,700	9,501–10,000	Yes	GEOXT	18-Jul-10	01:58:01 pm	PYKE071820101430.cor	38.976035033	−106.999748238	2923

Appendix Table A2–1. Continued

Code	Name(s) 1974	Elev. (s) 1974 (ft)	Region 1974 (ft)	Relocated 2007	GPS Unit	GPS_Date	GPS_Time	GPS Datafile	GPS Latitude	GPS Longitude	GPS Height (m)
SRT #07	Just S of East River bridge near camp	9,700	9,501–10,000	Yes	GOOGLE-MAP				38.976700000	−107.001412000	
SRT #08	Near bridge over East River near camp	9,700	9,501–10,000	Yes	GEOXT	18-Jul-10	01:49:06 pm	PYKE071820101430.cor	38.977870578	−107.002762289	
SRT #09	Near our camp	9,650	9,501–10,000	Yes	GEOXT	18-Jul-10	01:39:46 pm	PYKE071820101430.cor	38.982488195	−107.007376141	
SRT #10	Near Rustler Gulch Turnoff	9,750	9,501–10,000	Yes	GEOXT	18-Jul-10	01:33:26 pm	PYKE071820101430.cor	38.989457849	−107.010913945	
SRT #11	Near campsite north of ours	9,750	9,501–10,000	Yes	GEOXT	05-Jul-10	03:41:11 pm	PYKE070520101400.cor	38.986383981	−107.009301575	
SRT #12	Steep hillside	9,800	9,501–10,000	Yes	GEOXT	05-Jul-10	03:17:26 pm	PYKE070520101400.cor	38.991175034	−107.014168254	
SRT #13	Less steep hillside	9,900	9,501–10,000	Yes	GEOXT	05-Jul-10	03:00:16 pm	PYKE070520101400.cor	38.996989742	−107.017695152	
SRT #14	No name	10,150	10,001–10,500	Yes	GEOXT	05-Jul-10	02:34:31 pm	PYKE070520101400.cor	39.002958185	−107.025430785	
SRT #15	Chicken Place	10,350	10,001–10,500	Yes	GEOXT	05-Jul-10	02:16:56 pm	PYKE070520101400.cor	39.005588330	−107.030697537	
SRT #16	Emerald Lake	10,500	10,001–10,500	Yes	GEOXT	12-Jul-10	03:06:41 pm	PYKE071220101500.cor	39.008137895	−107.040355094	
SRT #17	Above Emerald Lake	10,600	10,501–11,000	Yes	GEOXT	12-Jul-10	03:10:31 pm	PYKE071220101500.cor	39.007792822	−107.041359178	
SRT #18	Schofield Pass	10,700	10,501–11,000	Yes	GEOXT	02-Jul-07	01:48:31 pm	MILLERT070214B.cor	39.014899961	−107.046703288	3267

Appendix Table A2–2. Location details re 1974 transect surveys. Various points along these transects were relocated in 2007 and their locations recorded with a GEOXT GPS Unit. Name 1974 refers to the name used in field notebooks containing the original data. These notebooks have been scanned to pdf copies that have been lodged with the Rocky Mountain Biological Laboratory

Code	Name 1974	Region 1974 (ft)	GPS Location 2007	GPS_Date	GPS_Time	Datafile	GPS Latitude	GPS Longitude	GPS Height (m)
MBT #01	10,200-10,800 ft	10,001-10,500							
MBT #02	10,400-10,700 ft	10,501-11,000	MBT #02 Bottom (10,400 ft)	09-Jul-07	08:03:01 am	MILLERT070909A.cor	39.006416042	-107.030930035	3167.0
MBT #03	10,501-11,000 ft	10,501-11,000							
MBT #04	10,700-11,000 ft	10,501-11,000	MBT #04 Bottom/MBT #02 Top (10,700 ft)	09-Jul-07	08:45:21 am	MILLERT070909B.cor	39.008641644	-107.030982350	3268.3
MBT #05	10,800-11,200 ft	10,501-11,000							
MBT #06	11,000-11,500 ft	11,001-11,500	MBT #06 Bottom/MBT #03 Top (11,000 ft)	09-Jul-07	09:19:11 am	MILLERT070910A.cor	39.010461664	-107.029931745	3341.7
MBT #07	11,200-11,500 ft	11,001-11,500							
MBT #08	11,500-11,700 ft	11,501-12,000							
MBT #09	11,500-12,000 ft	11,501-12,000	MBT #09 Bottom/MBT #06 Top (11,500 ft)	09-Jul-07	10:10:01 am	MILLERT070911A.cor	39.012651546	-107.028501480	3484.3
MBT #10	11,600-12,000 ft	11,501-12,000							
MBT #11	11,700-12,100 ft	11,501-12,000							
MBT #12	12,000-12,200 ft	12,001-12,500	MBT #12 Bottom/MBT #09 Top (12,000 ft)	09-Jul-07	11:00:31 am	MILLERT070912A.cor	39.015059492	-107.028622925	3659.2
			MBT #12 Top (12,200 ft)	09-Jul-07	11:12:51am	MILLERT070912BA.cor	39.015639925	-107.028242118	3700.9
MST #03	10,600-11,000 ft	10,501-11,000	MST #03 Bottom (10,00 ft)	28-Jun-07	09:04:46 am	MILLERT062810A.cor	39.025755951	-107.046054761	3220.3
MST #04	11,000-11,500 ft	11,001-11,500	MST #04 Bottom/MST #03 Top (11,000 ft)	28-Jun-07	09:42:41 am	MILLERT062810B.cor	39.028950567	-107.042347855	3336.8
MST #05	10,700-11,600 ft	11,001-11,500							
MST #06	11,500 ft	11,001-11,500							
MST #07	11,500-12,000 ft	11,501-12,000	MST #07 Bottom (11,500 ft)	28-Jun-07	10:31:56 am	MILLERT062811A.cor	39.035212655	-107.039689189	3495.9
MST #08	11,600-12,200 ft	11,501-12,000							
MST #09	12,000-12,300 ft	12,001-12,500	MST #09 Bottom/MST #07 Top (12,000 ft)	28-Jun-07	11:40:06 am	MILLERT062812A.cor	39.038035582	-107.040127768	3654.0
	12,000-12,300 ft		MST #09 Top (12,300 ft)	28-Jun-07	12:41:21 pm	MILLERT062813A.cor	39.040528582	-107.040181401	3763.7
WGT #01	9,700-10,200 ft	09,501-10,000	WGT #01 Bottom (9,700 ft)	29-Jun-07	08:06:16 am	MILLERT062909A.cor	38.982297627	-107.007526750	2945.3
WGT #02	9,700-10,500 ft	10,001-10,500							
WGT #03	10200 ft	10,001-10,500							
WGT #04	10,200-10,500 ft	10,001-10,500	WGT #04 Bottom/WGT #01 Top (10,200 ft)	29-Jun-07	08:51:11 am	MILLERT062909B.cor	38.981134248	-107.012145496	3100.7
WGT #05	10,500-10,700 ft	10,501-11,000	WGT #05 Bottom/WGT #04 Top (10,500 ft)	29-Jun-07	09:24:06 am	MILLERT062909C.cor	38.981796596	-107.016337837	3193.0
			WGT #05 Top (10,700 ft)	29-Jun-07	10:19:56 am	MILLERT062910A.cor	38.976432509	-107.022528329	3257.8
WGT #06	10,700 ft	10,501-11,000	WGT #06	29-Jun-07	10:25:31 am	MILLERT062911A.cor	38.977033676	-107.023733990	3265.7
WGT #07	10,700-11,000 ft	10,501-11,000	WGT #07 Bottom (10,700 ft)	29-Jun-07	10:39:41 am	MILLERT062911B.cor	38.976906929	-107.026439812	3273.0
			WGT #07 Top (11,000 ft)	29-Jun-07	10:59:01 am	MILLERT062911C.cor	38.972564702	-107.026247405	3349.0
WGT #08	11,000 ft	10,501-11,000	WGT #08	29-Jun-07	11:01:31 am	MILLERT062912A.cor	38.972224676	-107.026071512	3347.7
WGT #09	11,000-11,200 ft	11,001-11,500	WGT #09 Bottom (11,000 ft)	29-Jun-07	11:08:26 am	MILLERT062912B.cor	38.972006670	-107.026501061	3363.2
WGT #10	11,000-11,350 ft	11,001-11,500	WGT #11 Bottom/WGT #09 Top (11,200 ft)	29-Jun-07	11:28:46 am	MILLERT062912C.cor	38.969372749	-107.029215150	3403.3
WGT #11	11,200-11,350 ft	11,001-11,500	WGT #11 Top (11,350 ft)	29-Jun-07	12:33:06 pm	MILLERT062912D.cor	38.970856929	-107.03721631	3471.2

Appendix Table A3–1.   Average corolla lengths (mm) not previously available with 1974 plant species names as well as current species names

Plant species–Current name (Old name)	Average corolla length (s.e.) in mm
Achillea millefolium	2.4 (0.1)
Agastache urticifolia	8.7 (0.2)
Agoseris glauca	8.8 (0.4)
Aquilegia coerulea (caerulea)	45.3 (1.2)
Campanula rotundifolia	0 (0)
Castilleja miniata	14.4 (0.3)
Castilleja rhexifolia	11.6 (0.3)
Chaenactis douglasii	5.8 (0.1)
Ericameria (Chrysothamnus) parryi	4.7 (0.1)
Erigeron speciosus	3.9 (0.1)
Eriogonum umbellatum	0 (0)
Geranium richardsonii	0 (0)
Lupinus sp	0 (0)
Pedicularis procera (grayi)	15.9 (0.6)
Penstemon strictus	8.4 (0.3)
Polemonium foliosissimum	2.31 (0.01)
Potentilla fruticosa	0 (0)
Potentilla gracilis	0 (0)
Senecio wootonii	4.6 (-)
Sidalcea candida	0 (0)
Trifolium hybridum	2.34 (0.05)
Trifolium nanum	7.6 (0.5)
Wyethia amplexicaulis	6.3 (0.1)