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Activity and abundance of bumble bees near Crested Butte, Colorado: diel, seasonal, and elevation effects

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Abstract. 1. We revisited bumble bee survey data collected by Pyke in 1974 (Pyke, *Ecology*, **63**, 555–573, 1982) to evaluate seasonal changes in abundances of bumble bees and their floral resources, diel patterns of bumble bee activity, and elevation effects on plant and bumble bee phenology.

2. Bumble bee abundance increased during summer as spring queens founded colonies that produced workers, followed by males and autumn queens. The number of plant species visited by bumble bees increased to a peak in midsummer, then declined.

3. The number of bumble bees recorded per person-hour peaked later than the number of flowering plant species used by the bees. Few autumn queens were observed.

4. Despite species differences in emergence times of spring queens, there were no apparent phenological differences among species in worker abundances.

5. Because flowering commences later at higher elevation, abundances of workers and males are also shifted later; therefore elevational comparisons must be seasonally adjusted.

6. These analyses provide basic information about important pollinating insects, and permit future investigations of elevational shifts over time to be properly adjusted for phenological and elevation effects in survey data.

Key words. Bumble bee, climate change, diurnal, elevation, phenology, seasonal.

Introduction

Temporal patterns in bumble bee activity have been widely reported. They often show diel patterns of activity, especially in terms of foraging (Young & Owen, 1989; Bergman *et al*., 1996). Worker bees that forage during the day are relatively inactive in their nests at night (Yerushalmi *et al*., 2006; Stelzer & Chittka, 2010), and generally exhibit a peak in foraging activity during the day (Shelly *et al*., 1991; Yerushalmi *et al*., 2006; Stelzer & Chittka, 2010). Bee activity within areas containing flowers may peak during the day (Teras, 1985a; Bowers, 1986a; Young & Owen, 1989; Williams & Christian, 1991) or be relatively constant (Hatfield & LeBuhn, 2007). There may similarly be variation through the day in terms of the numbers of observed bumble bees at stands of flowers of a particular species or the rates of bumble bee visitation to plants or flowers (Dorr, 1981; Lack, 1982; Tepedino & Stanton, 1982; Posey *et al*., 1986; Elmqvist *et al*., 1988; Potts *et al*., 2001). For example, during 1 day, a focal plant of *Penstemon strictus Benth.* in the West Elk mountains of Colorado received 0.26 bumble bee visits per minute in early morning (07.44–08.39 hours), peaked at 1.28 in the early afternoon (14.09–15.44 hours), and declined to 0.72 by evening (18.44–19.39 hours) (Williams & Thomson, 1998; Fig. 1). Sometimes different plant species may experience peaks in bumble bee activity or numbers at different times of day (Tepedino & Stanton, 1982; Posey *et al*., 1986; Elmqvist *et al*., 1988); other times no such variation is apparent (Catling & Catling, 1989; Utelli & Roy, 2000). Diel patterns may differ among bumblebee species (Teras, 1985a; Elmqvist *et al*., 1988; Young & Owen, 1989) and between different castes of the same bumblebee species (Jennertsen *et al*., 1991).

Diel patterns of bee foraging may affect plant pollination (Jennertsen *et al*., 1991; Wang *et al*., 2009). Plants may have their own diel patterns (for example, of anthesis or stigma receptivity), so interaction with bee periodicity could influence pollen transfer (Potts *et al*., 2001). The magnitude of any temporal separation of visitation to different plant species may also influence pollination as it could affect the frequencies

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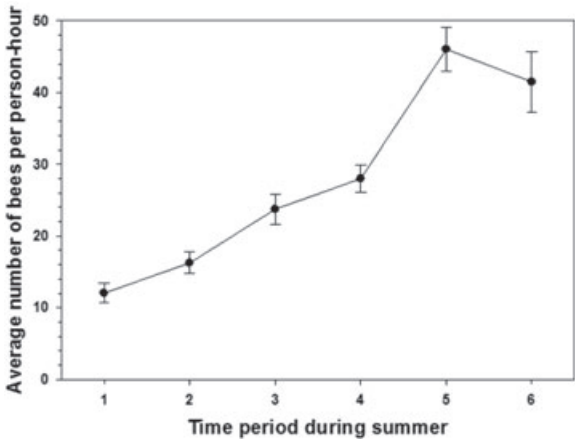

Fig. 1. Average number of bumble bees recorded per person-hour vs. time period during the summer. Vertical lines represent ±1 SE.

of intraspecific and interspecific bee movements. This is of economic significance because the output of crops that require bee pollination may thus be affected by diel patterns of bee foraging (Posey *et al*., 1986; Wang *et al*., 2009). Diel patterns of foraging may also affect the interpretation of bumble bee surveys. Surveys of two sites at different times of day could record different numbers of bees even though diel patterns of activity were identical. Comparison of survey results may therefore require adjustments for time of day.

Bumble bees in temperate climates exhibit seasonal turnover from spring queens to workers to males and autumn queens (Bowers, 1986b; Prys-Jones & Corbet, 1991; de la Hoz, 2006; Charman *et al*., 2009), driving patterns of overall abundance or density (Schmid-Hempel & Durrer, 1991; Hirao *et al*., 2006; Gurel *et al*., 2008; Colla & Dumesh, 2010). Autumn queens, although produced in comparable numbers to males, are rarely observed foraging (Schmid-Hempel & Durrer, 1991; Charman *et al*., 2009; Colla & Dumesh, 2010). Similar seasonal patterns may occur in warmer subtropical regions (de la Hoz, 2006). The number or density of observed foragers generally increases from spring to summer, finally declining to zero in autumn (Bowers, 1986a; Schmid-Hempel & Durrer, 1991; Hirao *et al*., 2006; Gurel *et al*., 2008; Colla & Dumesh, 2010). There may sometimes be an early trough in bumble bee numbers following the emergence of the spring queens, when they have established nests and have eggs and larvae to look after, but before the first workers begin to forage (Teras, 1983).

Although apparent to any naturalist, this seasonal pattern of bumble bee abundance has rarely been quantified (Bowers, 1986a; Schmid-Hempel & Durrer, 1991; Gurel *et al*., 2008) As queens initially produce workers who take over the role of foraging and provide food to support further production of workers and subsequently new reproductives (Baer, 2003; de la Hoz, 2006), an exponential increase in overall bumble bee abundance over most of the season might be expected (Baer, 2003), unless floral resources are insufficient to support such numerical growth. The rate of this increase would presumably depend on the abundance of foraging bees at any point in time and their net rates of energy and protein return to their colonies. It would also be affected by any colony mortality (Goulson *et al*., 2010). An exponential decline at the end of the season might be similarly expected, as floral resources dwindle and bees die off. However, neither this nor any other possible dynamical process has so far been evaluated.

Bumble bee species differ in when they emerge from their overwinter sites and initiate colonies (Richards, 1978; Bowers, 1985; Goodwin, 1995; Bertsch *et al*., 2004; Goulson *et al*., 2005; Hatfield & LeBuhn, 2007; Williams *et al*., 2009a), when they reach peak abundance (Lack, 1982; Teras, 1985b; Bowers, 1986a; Prys-Jones & Corbet, 1991; Goodwin, 1995), and how long they continue to forage (Prys-Jones & Corbet, 1991; Goodwin, 1995). Some species may, on average, initiate colonies 2–3 weeks before other species (Richards, 1978; Bowers, 1985; Bertsch *et al*., 2004) and some species continue foraging for distinctly longer periods than other species (Goodwin, 1995; Goulson *et al*., 2005). It seems likely that such interspecific differences will reflect differences in foraging profitability for pollen and/or nectar, but so far this possibility has not apparently been evaluated.

Seasonal patterns in the abundance of bumble bee foragers may also affect plant visitation and pollination (Yumoto, 1988; Cane & Payne, 1993; Thompson & Hunt, 1999). Because different plant species have their own seasonal patterns of flowering, some may be visited primarily by spring queens while others are visited mostly by workers or males (Pleasants, 1980; Macior, 1994). Some early-flowering plant species may be visited infrequently by bumble bees while later-flowering species receive higher flower visitation (Kwak & Bergman, 1996), and some long-flowering plant species may receive flower visitation that varies significantly over the season in terms of bee species and rate of visitation (Thomson, 1982; Cane & Payne, 1993). Pollination rates will depend on the match between the phenologies of plant flowering and abundance of bumble bee flower visitors (Yumoto, 1988; Kwak & Bergman, 1996), and the output of crop pollination may be similarly affected (Ruben Palma *et al*., 2005; Wermuth & Dupont, 2010).

Daily and seasonal patterns of bumble bee activity and abundance may vary geographically, especially with latitude and elevation (Gurel *et al*., 2008; Colla & Dumesh, 2010), with the driving factors being weather parameters such as temperature or floral parameters such as nectar production, both of which may vary geographically. In snowy regions, snowmelt, bee activity, and the onset of flowering may occur later at higher elevations (Inouye & Wielgolaski, 2003). Geographic variation in the plant species present and their flowering phenologies may explain other geographic variation in bumble bee phenology (Gurel *et al*., 2008). Comparisons of bumble bee activity and abundance between regions that differ in elevation may therefore need to be temporally adjusted (Williams *et al*., 2009a). If, for example, the season for bumble bees and the flowers they visit began later in one elevational zone than in another, offsetting seasonal peaks of abundance, then comparisons between the two regions should be adjusted for this phenological difference. The same may apply to comparisons of regions that differ in latitude and comparisons across smaller spatial scales may similarly require temporal adjustment because of spatial variation in phenological patterns

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(Wermuth & Dupont, 2010). Such an adjustment could be achieved by either transforming absolute dates to dates relative to when peak abundances occurred or by adopting the observed peak abundance as the variable of interest (Wermuth & Dupont, 2010). Comparisons in bumble bee abundance between different years may similarly require adjustment to reflect differences in the timing of events such as snowmelt and the onset of flowering.

In 1974, Pyke (1982) surveyed several species of bumble bee along elevational transects in the West Elk Mountains of Colorado, U.S.A. Those intensive surveys of fixed routes spanned times of day ranging from about 9 am to 5 pm, across almost an entire flowering season extending from 22 June to 8 September 1974, and across elevations ranging from 2693 to 3760 m, and they included records of host plants (Pyke, 1982). In analysing the results of these surveys, Pyke (1982) focused on the elevational ranges of different bee species, but did not examine phenological patterns. Here, we reanalyse the data collected during these surveys (Pyke, 1982) looking for effects of *time of day*, *date*, and *elevation* on observed activity levels of bumble bees, and of *date* and *elevation* on flowering. These analyses provide basic information about important pollinating insects, and permit future investigations of elevational shifts over time to be properly adjusted for phenological effects in survey data. They also provide a basis for comparing these survey data with data from identical contemporary surveys, thus potentially documenting shifts over more than 30 years – perhaps driven by climate change.

Materials and methods

Transects, sites, and survey methods

Surveys of bumble bees and flowers were carried out between 22 June and 8 September 1974 at sites along road and walking transects in the vicinity of the Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado (for further details see Pyke, 1982). Roadside sites consisted of areas of about 50 m radius around fixed points alongside roads. Sites that were along walking transects consisted of the areas that were within about 25 m of regular but sometimes unmarked foot-trails and within elevational ranges that were generally 151.5 m (i.e. 500 ft; Pyke 1982). The elevation for each site is taken as the elevation at its centre, and sites are considered within elevational regions based on intervals of 151.5 m (i.e. 500 ft; see below). The sites ranged in elevation from about 2693 m to about 3760 m (for further details, see Pyke, 1982).

During visits to these sites, one of us (G.H. Pyke) plus up to two assistants surveyed the area as uniformly as possible recording the caste and species for each observed bumble bee, as well as what the bee was doing at the time (e.g. visiting flowers, nest searching) and, if it was visiting flowers, the identity of the plant (usually to species, occasionally to genus). These surveys were carried out opportunistically with respect to time of day and lasted about 42 min on average or about 1.3 person-hours (for further details see Pyke, 1982).

The number of plant species that are flowering within a site, besides being a direct measure of floral resource diversity, may also be a rough measure of the level of floral resources available to bumble bees at that time (Hines & Hendrix, 2005; Hegland & Boeke, 2006; Ebeling *et al*., 2008). The seasonal pattern in number of flowering plant species may therefore reflect the seasonal pattern in floral resources available to bumble bees and be correlated with the seasonal pattern in bumble bee abundance. We therefore use the number of recorded plant species in flower as an independent variable in our analyses.

Pyke (1982) identified some of the bumble bees that he observed as *Bombus kirbyellus* Smith. However, most authors consider this species to be synonymous with *Bombus balteatus* Dahlbom and adopt the latter name (e.g. Thorp *et al*., 1983; Williams, 1998), and we do likewise here.

Twelve bumble bee species were recorded in the study area, with the seven most commonly recorded species accounting for about 96% of all bumble bees recorded (Pyke, 1982). Bumble bees were recorded visiting flowers of a total of about 100 plant species but only about 30 plant species accounted for 90% of all such observations (Pyke, 1982).

Analyses

Statistical analyses were carried out using Forward Stepwise Linear General Model, as provided by the computer software SYSTAT v11 (Wilkinson, 1990), with the *number of bees recorded per person-hour* as the dependent variable. This variable was not transformed, although it has a right-skewed and non-normal frequency distribution, because a log transformation did not improve 'normality'. 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, etc) and *elevational region*, divided into intervals of 500 ft (i.e. region 1 is 8500–9000 ft or 2576–2727 m; region 2 is 9000–9500 ft or 2727–2879 m, etc.). Because the dependent variable was not normally distributed and analyses involved approximately five distinct statistical tests, a Bonferroni correction was made to set the probability threshold adopted for significance at 0.01 (i.e. 0.05/5).

In some cases the results of an analysis indicated appropriate directions for further analysis. For example, the observations that relatively few queens were recorded, male abundance may not have peaked before the study ended, and many workers were recorded, with seasonal rise and fall in worker abundance, indicated that consideration of how various factors affect bumble bee phenology should focus on just the workers. This and other examples are explained in the results section below.

Results

Temporal and spatial variation in surveys and bumble bees recorded per hour

The timing of the survey visits to sites was affected by both site elevation and time period during the summer. Average time of the day of surveys increased both with increasing elevational region and time during the season (forward stepwise GLM, $r^2 = 0.05$, Ps = 0.009 and 0.002 respectively).

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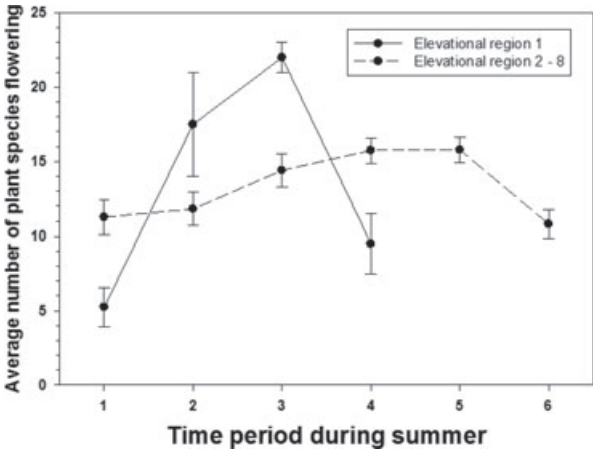

Fig. 2. Average number of plant species in flower per survey vs. time period during the summer, separately for elevational regions 1 and 2–8. Vertical lines represent ±1 SE.

The interaction between elevational region and summer time period was not significant (forward stepwise GLM, $P = 0.03$). We shall therefore consider elevational region and summer time period in subsequent analysis.

The number of bumble bees recorded per hour increased, as expected, with increasing time period (Fig. 1; forward stepwise GLM, $r^2 = 0.15$, $P < 0.005$). It was not, however, significantly affected by elevational region or time of day (forward stepwise GLM, Ps $= 0.17$ and 0.17 respectively). Interactions between time period and the other two variables were not significant (forward stepwise GLM, Ps > 0.1).

Temporal and spatial variation in number of recorded plant species

For elevational region 1 (i.e. 2576–2727 m), flowering peaked in July and by the end of August sites within this region had almost no flowering plants and surveys of them had ceased (Fig. 2).

Excluding the lowest elevational region (i.e. region 1), the average number of plant species recorded per survey was higher during August, with a broad peak during this month, than either earlier or later (Fig. 2) and was not affected by the kind of transect (i.e. walking vs. road) nor by elevational region. For the road transects, which included five elevational regions, elevational region was not significant (forward stepwise GLM, $P = 0.23$), but both the time period during the summer (i.e. period) and period^2 were significant (forward stepwise GLM, Ps < 0.0001). Also interactions between region and either period or period^2 were not significant (forward stepwise GLM, Ps > 0.08). For the walking transects, which included six elevational regions, period and period^2 were both significant (forward stepwise GLM, $P = 0.01$ and 0.005 respectively) while elevational region and interactions were not (forward stepwise GLM, Ps > 0.05). When road and walking transects were considered together period and period^2 continued to be significant (GLM, Ps $= 0.000$) but the difference between walking and road transects was not significant (GLM, $P = 0.48$). The consistently significant effect of period^2 indicates that, in all cases, the relationships with time period reached peaks during the summer (Fig. 2).

Bumble bee phenology

As described below, we found differences in phenology among the different castes and the areas of different elevation, but no differences among bumble bee species. Because of these differences, we shall, in subsequent analyses, focus on workers and use different time periods to compare different elevations.

Bumble bee phenology, for all species combined, generally showed the patterns expected following colony development. For queens and workers, there was an initial period when numbers recorded per person-hour were low, followed by a period of exponential growth in numbers to a peak, and then an exponential decline in numbers (Fig. 3). Sampling stopped before male numbers declined, and they showed only the increasing phase and not a decreasing one (Fig. 3). However, at the beginning of autumn, when recorded male abundance was greatest and 'fall queens' would have been mating and searching for winter hibernacula, queens were rarely recorded (Fig. 3). There were successive periods when first queens, then workers and finally males, were the most abundant in terms of bees recorded per person hour (Fig. 3). Peak numbers of bees recorded per hour increased from queens to workers to males (Fig. 3). Because queens were recorded in relatively low numbers and males perhaps had not reached peak abundance when the study ended, we shall use workers to consider how phenology may vary with other factors such as elevational region and bumble bee species.

Worker bumble bees, for all species combined, showed the expected shift towards later time periods with increasing elevation, but the analyses were affected by significant interactions (Fig. 4). There were significant interactions between region and powers of time period up to four when all eight elevational regions were considered together and the dependent variable

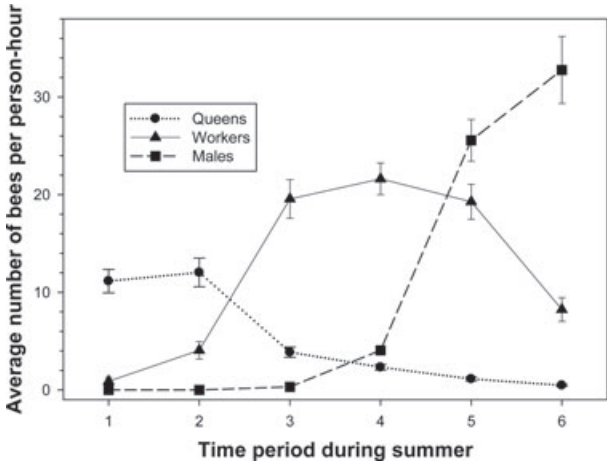

Fig. 3. Average numbers of bumble bee queens, workers, and males vs. time period during the summer. Vertical lines represent ±1 SE.

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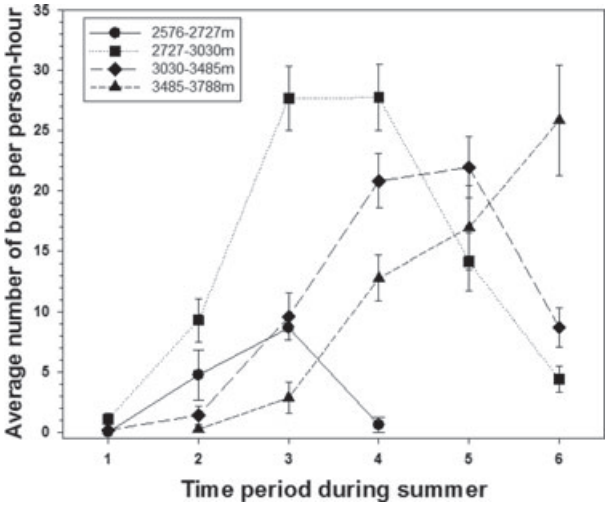

Fig. 4. Average numbers of bumble bee workers recorded per person-hour vs. time period for different elevational regions. Vertical lines represent ±1 SE.

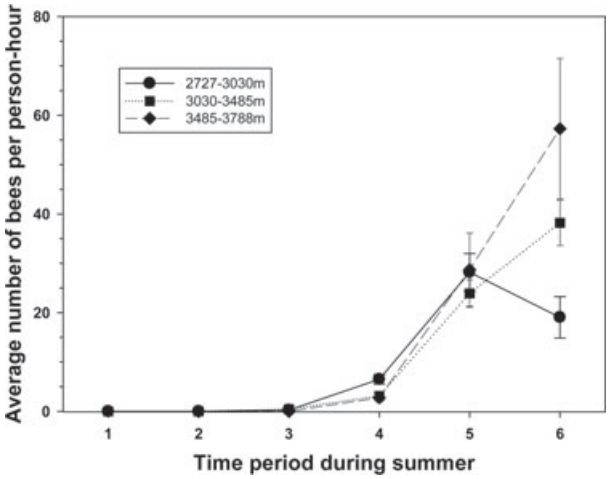

Fig. 5. Average numbers of bumble bee males recorded per person-hour vs. time period for different elevational regions. Results for the lowest elevational region (i.e. 2576–2727 m) are not shown because the recording rates for males were very low in this region (e.g. rate = 1.2 bees per person hour in period 2; otherwise = 0). Vertical lines represent ±1 SE.

was number of bumble bees recorded per person-hour (forward stepwise GLM, Ps < 0.01). However, the signs of these interactions indicated that the general relationship between bumble bee numbers and time period tended to shift towards later time periods, and in particular the time when peak numbers occurred became later in the season, with increasing elevational region (Fig. 4). Furthermore, when these elevational regions were combined into four new elevational ranges (see Fig. 4) and each of these was analysed separately, the effect of elevational region (within each range) was not significant and the interactions were no longer significant (forward stepwise GLM, Ps > 0.3). For all of these four elevational ranges except the highest one, there was a significant negative effect of period^2, indicating peaks in numbers at some points in time (Fig. 4, forward stepwise GLM, one-tailed test; 2576–2727 m: $P = 0.01$; 2727–3030 m: $P = 0.002$; 3030–3485 m: $P < 0.001$). For the two intermediate elevational ranges, there were also significant effects of period^4, indicating that there were also two troughs in numbers (Fig. 4, forward stepwise GLM, one-tailed test; 2727–3030 m: $P < 0.001$; 3030–3485 m: $P < 0.001$).

These results influenced subsequent analysis in terms of bumble bee worker abundance in relation to bumble bee species and elevational region, and comparing the phenologies of different bumble bee species. To consider the numbers of worker bumble bees in relation to bumble bee species and elevational region, we used the two time periods for each elevational region when worker numbers per person-hour were greatest (i.e. region 2576–2727 m, periods 2 and 3; two regions between 2727 and 3030 m, periods 3 and 4; three regions between 3030 and 3485 m, periods 4 and 5; two regions between 3485 and 3788 m, periods 5 and 6; see Fig. 4). In order to compare the phenologies of different bumble bee species, we separately considered the numbers of workers recorded per person-hour within the two intermediate elevational ranges (Fig. 4).

Male bumble bees similarly showed the expected shift towards later time periods with increasing elevation (Fig. 5; forward stepwise GLM). However, the effect of elevation was less for males than for workers, and, as previously noted (Pyke, 1982), very few males were recorded in the lowest elevational region (Fig. 5). In subsequent analyses of numbers of male bumble bees, we shall use time period 4 for the region 2576–2727 m and periods 5 and 6 for all other regions (Fig. 5).

There were no apparent differences in phenology in terms of workers among the different bumble bee species (Figs 6–8). For the bumble bee species that were commonly recorded within the two elevational regions between 2727 and 3030 m (i.e. *B. appositus* Cresson, *B. bifarius* Cresson, *B. flavifrons* Cresson and *B. occidentalis* Greene) and with bees recorded per person-hour as the dependent variable, there were significant effects of time period and period^3 (forward stepwise GLM, Ps < 0.001), consistent with the observed phenologies (Fig. 6), and significant differences amongst the bumble bee species (forward stepwise GLM, $P < 0.001$), but no significant interactions between bumble bee species and either time period or period^3 (forward stepwise GLM, Ps $>$ 0.04). The same was true for the two commonly recorded bumble bee species (i.e. *B. flavifrons* and *B. balteatus*) within the three elevational regions between 3030 and 3485 m (Fig. 7). In the case of the two highest elevational regions between 3485 and 3788 m and the three bumble bee species that were commonly recorded within this elevational range (i.e. *B. frigidus* Smith, *B. balteatus*, and *B. sylvicola* Kirby), the number of workers recorded per hour increased with increasing time period (Fig. 8, forward stepwise GLM, $P <$ 0.001), but was not significantly affected by bumble bee species or interaction between bumble bee species and time period (forward stepwise GLM, Ps > 0.3).

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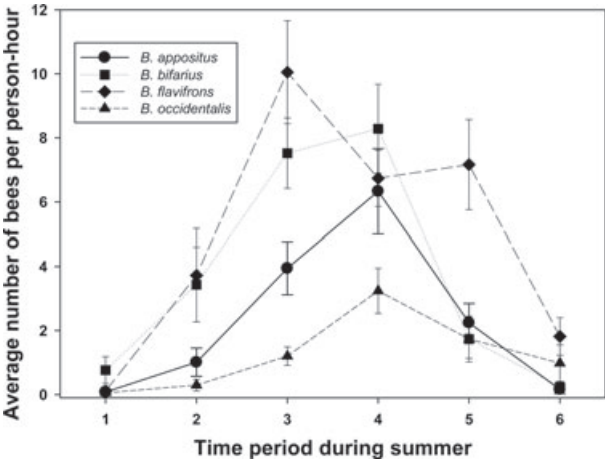

Fig. 6. Average numbers of worker bumble bees recorded per person-hour within the elevational regions between 2727 and 3030 m vs. time period for the four bumble bee species commonly recorded within these elevational regions. Vertical lines represent ±1 SE.

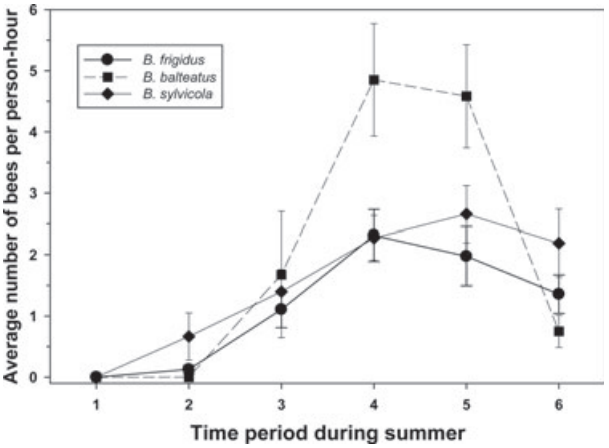

Fig. 8. Average numbers of worker bumble bees recorded per person-hour within the elevational regions between 3485 and 3788 m vs. time period for the three bumble bee species commonly recorded within these elevational regions. Vertical lines represent ±1 SE.

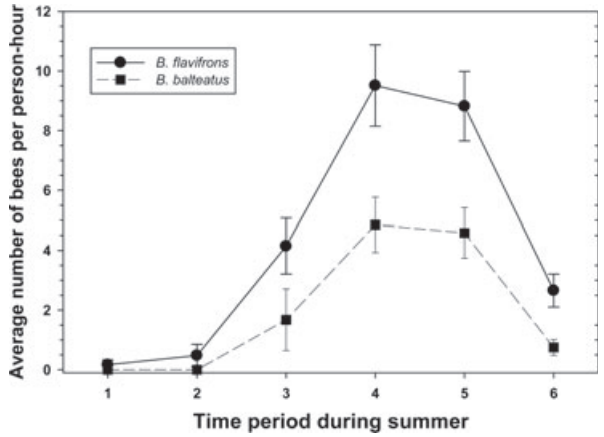

Fig. 7. Average numbers of worker bumble bees recorded per person-hour within the elevational regions between 3030 and 3485 m vs. time period for the two bumble bee species (*Bombus flavifrons* and *B. kirbyellus*) commonly recorded within these elevational regions. Vertical lines represent ±1 SE.

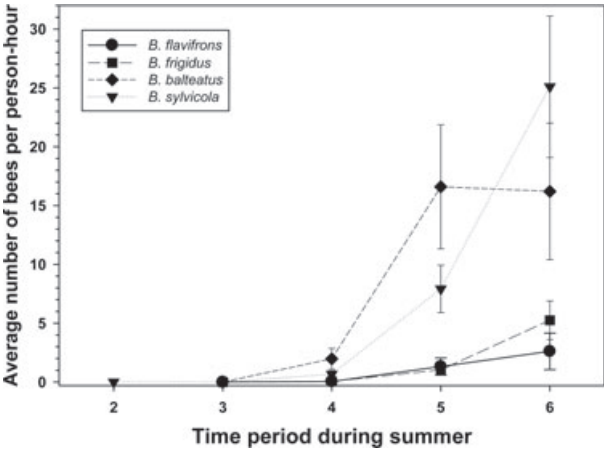

Fig. 9. Average number of male bumble bees per person hour at sites over 3485 m vs. time period during the summer for different bumble bee species. Vertical lines represent ±1 SE.

There were, however, significant differences among the bumble bee species in terms of phenology of males. For the two highest elevational regions between 3485 and 3788 m, males of *B. balteatus* reached peak recording level per person hour during the last half of August (i.e. time period 5), whereas *B. sylvicola* and *B. frigidus* did not reach peak recording levels until the first half of September, and *B. flavifrons* was in between (Fig. 9; forward stepwise GLM; interaction between bumble bee species and time period not significant when just *B. sylvicola* and *B. frigidus* are considered, $P = 0.1$; otherwise such interactions were significant, $P < 0.001$). For the two elevational regions between 2727 and 3030 m, which were the lowest such regions where reasonable numbers of males were recorded, *B. appositus*, *B. bifarius*, and *B. flavifrons* all reached peak recording levels during the last 2 weeks of August, whereas *B. frigidus* and *B. occidentalis* did not reach such levels until the first half of September (Fig. 10; forward stepwise GLM; interaction between bumble bee species and time period not significant when just the former group of species was considered and when just the latter group was considered, Ps > 0.03; otherwise such interactions significant, $P < 0.001$). For the intermediate elevational regions between 3030 and 3485 m, those bumble bee species that also occurred commonly at higher elevations but not lower elevations (i.e. *B. balteatus* and *B. sylvicola*) exhibited seasonal patterns consistent with these higher elevations (e.g. *B. sylvicola* did not reach peak recording levels until the first half of September), those species additionally common only at lower elevations (i.e. *B. appositus*, *B. bifarius*, and *B. occidentalis*) exhibited seasonal patterns consistent with these lower elevations, and those species that were reasonably common at both high and lower elevations either exhibited either the same seasonal

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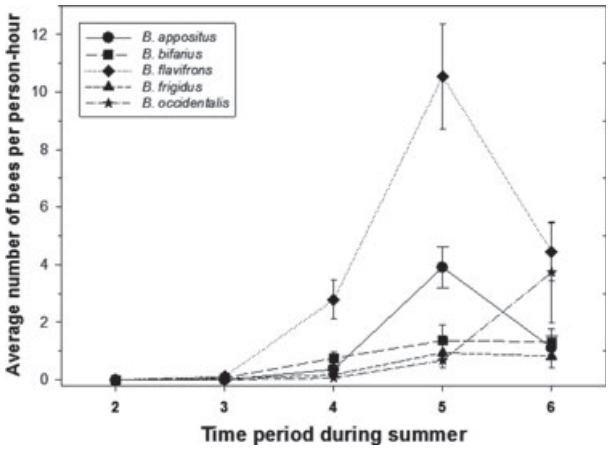

Fig. 10. Average number of male bumble bees per person hour at sites between 2727 and 3030 m elevation vs. time period during the summer for different bumble bee species. Vertical lines represent ±1 SE.

pattern throughout the elevational range (i.e. *B. frigidus*) or a pattern intermediate between the higher and lower elevational regions (i.e. *B. flavifrons*).

Discussion

Diel patterns of bumble bee activity

That we found no significant diel patterns in bumble bee activity during our surveys was convenient because it meant that could omit such patterns from subsequent analyses However, this observation still warrants explanation as many factors could be involved, and the reasons for either observing or failing to observe a diel pattern of bumble bee activity are unclear. Rainfall could be a factor with moderate to heavy rain limiting bumblebees' ability to fly. Temperature, wind, and solar radiation could also be factors with cold or windy conditions and lack of sunshine similarly limiting the ability of bumblebees to fly (Lack, 1982; Bowers, 1986a; Young & Owen, 1989; Bergman *et al*., 1996), although bumblebees have well know capabilities of warming their flight muscles and remaining airborne at quite cold temperatures (Prys-Jones & Corbet, 1991; Heinrich, 1993). The overriding factor could be foraging energetics with net energetic return while foraging being a function of both the energetic gains, as influenced by the volumes and concentrations of floral nectar, and the energetic costs, as influenced by rain, wind, and temperature (Wright, 1988; Young & Owen, 1989; Potts *et al*., 2001). It has been suggested, in particular, that individual bees may forage optimally with regard their colony as a whole, deciding whether or not to forage on the basis of their expected resource returns to the colony from so doing (Stelzer *et al*., 2010), but no test of this hypothesis has apparently been carried out. In addition, it may be difficult to separate any effects of nectar properties (e.g. volume, concentration) from weather parameters, such as temperature and humidity, if such weather parameters affect the nectar properties (Young & Owen, 1989). Of course, it is also possible that foraging profitability in terms of pollen, as source of protein, is also important. Further research in this area is clearly needed.

Plant and bumble bee phenology and numbers

As the summer flowering season progressed, the bumble bees showed the expected phenological changes with abundance increasing and a turnover from spring queens to workers and then to males and fall queens (Baer, 2003). As obvious as this is, it has apparently been documented in only a few studies (Prys-Jones & Corbet, 1991; Schmid-Hempel & Durrer, 1991; Heinrich, 2004; Colla & Dumesh, 2010) and so far has not been the subject of quantitative investigation. Such quantitative investigations should help us to understand the population dynamics of bumble bees. However, as we observed in this study, it has often been noted that fall queens are relatively rarely observed in comparison with spring queens (Alford, 1975; Schmid-Hempel & Durrer, 1991; Williams, 1991; Goulson, 2003; Colla & Dumesh, 2010). Fall queens apparently do little foraging before entering hibernation, while spring queens need to forage extensively before their first workers eclose (Prys-Jones & Corbet, 1991; Schmid-Hempel & Durrer, 1991; Baer, 2003).

Although phenological differences have been observed in and near our study area in terms of when the spring queens of different bumble bee species emerge from hibernation, there were no apparent phenological differences during our study in terms of workers. In the spring (i.e. late May to early June) we have always observed queens of *B. bifarius* flying around and searching for potential nest sites before we have seen *B. appositus* queens doing likewise, without any apparent differences in how often early queens of these two species were observed (D.W. Inouye and J.D. Thomson, pers. obs.). This suggests that, on average, *B. bifarius* colonies become established earlier during the flowering season than those of *B. appositus*. However, the present study indicates that such a phenological difference had either disappeared or become insignificant by the time when most workers were produced.

That the average number of species of plants used by bumble bees first increased and then decreased during the summer is not surprising and agrees with many other observations. For example, the average number of flowering plant species in small permanent plots within our study area shows a similar seasonal pattern (Aldridge *et al*., 2011).

That the average number of bumble bees recorded per person-hour peaked later in the summer than the average numbers of flowering plant species used by these bees is consistent with the known population dynamics of bumble bee colonies and with the number of simultaneously flowering plant species being a measure of resource availability to the bumble bees. Bumble bee colonies grow exponentially for a period after establishment, because the queen forages to provision her first brood each of which ultimately forages to support the next brood and so on (Baer, 2003; Fig. 1). However bumble bee colonies must eventually decline if suitable flower resources decline to zero, as happens at the end of the summer in our study area (Fig. 2; few plants in flower by late September or

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time period 7 and no plants in flower by early October or time period 8 – Aldridge *et al*., 2011). Because it generally takes new workers and males about 4–5 weeks from egg laying to emergence (Alford, 1975; Baer, 2003), there should be a lag of about 4–5 weeks between the time when floral resources begin to decline and the time when bumble bee numbers go into decline. Because bumble bee numbers declined rapidly after early September or time period 6 (D.W. Inouye and J.D. Thomson, pers. obs.), our observed time lag was about 4–5 weeks (Figs 1 and 2), as expected.

Our observations in terms of maximum numbers of worker and male bumble bees recorded per unit time suggest that male abundances or densities probably reached levels at least as high as, and probably greater than, for workers. During periods of time ranging from about 1 h to 1 day, typically about 30–50% of worker bumble bees leave their colony and forage, while the remainder remain within the colony as 'house bees' (Brian, 1952; Alford, 1975; Cartar, 1992; O'Donnell *et al*., 2000). However, in our study area, foraging workers spend less than 10% of their time in their colonies and not foraging (G. H. Pyke, unpublished). Combining these two factors suggests that worker bumble bees observed foraging during our surveys would constitute only about one quarter to one half of the total number of workers. On the other hand, male bumble bees take about 2 weeks after eclosion to reach maturity (Baer, 2003), but then generally leave their colonies never to return (Prys-Jones & Corbet, 1991; Schmid-Hempel & Durrer, 1991; Kearns & Thomson, 2001). Hence a significant proportion of males will, at any point in time, still be living in their colonies. In addition, males that have left their colony spend most of their time seeking mates rather than foraging at flowers (Williams, 1991), and hence, at a particular point in time, most such males would be seeking mates rather than foraging at flowers. Hence the overall proportion of males that are foraging at flowers rather than being still in their colonies or seeking mates is probably low. Integrating these considerations with the results shown in Fig. 3 suggests that male abundance was at least as great as, and probably greater than, worker abundance. That bumble bee colonies generally produce numbers of males that are similar to or higher than the number of workers (Hannan *et al*., 1997; Yeninar & Kaftanoglu, 1997; Baer, 2003; Pelletier & McNeil, 2003) is consistent with this.

The observed phenological shifts in numbers of recorded workers and males towards later in the season with increasing elevation were also expected. With increasing elevation, snowmelt and the onset of the flowering season both occur later (Blionis *et al*., 2001; Clow, 2010), and this should shift bumble bee phenology towards later in the year (see fig. 302 in Williams *et al*., 2009b). This means that it is necessary to adjust for these phenological shifts when comparing locations with different elevations. However, we are not aware of other studies that indicate or adjust to such phenological shifts with changing elevation.

Differences in seasonal phenology among different bumble bee species have been reported (Teras, 1976; Prys-Jones & Corbet, 1991; Goodwin, 1992; Goodwin, 1995; Williams *et al*., 2009b). However, the different castes have rarely been considered separately (Prys-Jones & Corbet, 1991; Goodwin, 1995; Neumeyer & Moretti, 2005), bumble bee phenologies have seldom been expressed quantitatively (Lack, 1982; Prys-Jones & Corbet, 1991), and bumble bee phenologies have not previously been analysed statistically. Such phenological differences among bumble bee species would be expected, since many bumble bee species complete their 'summer' life-cycle (i.e. spring queens to fall queens) in about 9–13 weeks (Goodwin, 1995) and flowering seasons often last 20 weeks or more (Pojar, 1974; Lack, 1982; Prys-Jones & Corbet, 1991; Goodwin, 1995). The flowering season in the present study was about 20 weeks long (i.e. about 16 weeks shown in Fig. 2 plus 2 weeks at either end) and we found differences in phenology among different bumble bee species. Similarly, phenological differences between different bumble bee species have been found in Europe where the flowering season extends over about 8 months (Prys-Jones & Corbet, 1991). However, no such differences in bumble bee phenology have been reported in situations where the flowering season lasts only about 10 weeks (Bauer, 1983). Of course, there may also be phenological differences between different habitats (e.g. woodland vs. open field) corresponding to different flowering seasons in these different habitats (Colla & Dumesh, 2010).

That the various patterns we have considered have varied among the different bumble bee castes is presumably a reflection of how circumstances change through the summer season. The apparent paucity of male production within the lowest elevation region may be due to the lack of flowering within that region toward the end of the summer (Fig. 2). Bumble bee colonies may simply run out of flowers within easy commuting distance (Williams, 1991) and not have sufficient nearby floral resources to produce males. Similarly, a particular bumble bee species may be favoured by floral resources available at one time but not by those available at another time. Hence the relative abundances of different bumble bee species may change through time and from one caste to another.

The present study, based on 1974 survey data, provides not only an increased understanding of certain aspects of bumble bee biology, but also helps to set the stage for considerations of possible effects on bumble bees of climate change since 1974. We can, for example, compare the results of our 1974 surveys and repetitions carried out in 2007, and evaluate any observed changes over the intervening 33-year period in light of observed climatic changes over the same period. We can also compare any observed changes in flowering phenology between our 1974 and 2007 surveys with observations of plants carried out in nearby fixed plots over the same period (Aldridge *et al*., 2011). In this way, the existence of historical survey data presents opportunities to examine how the changing environment may influence bumble bee communities. We have archived our survey data from both 1974 and 2007, and hope this will encourage others to do the same with their historic data, carry out comparisons between their historic and more recently collected data, and use our data again in the future to see how bumble bees and their floral resources continue to change.

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Future research

There is a need for further research on diurnal patterns of bumblebee activity, seasonal patterns of bumblebee abundance, and how these patterns are affected by elevation and latitude. As explained above, such patterns have been little documented, especially quantitatively, and so far have been little explained. Understanding such patterns should significantly contribute to our knowledge of pollination systems and to application of this knowledge to crop pollination.

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