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Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows

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ABSTRACT

Understanding the scale at which habitat influences species richness in terrestrial ecosystems is central to both ecology and conservation biology [Wettstein, W., Schmid, B., 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. Journal of Applied Ecology, 36, 363–373]. Community composition may be influenced by habitat variation at patch and/or landscape-scales depending on the body size, home range area, and dispersal distances of the focal taxa [Calder III, W.A., 1984. Size, function, and life history. Harvard University Press, Cambridge, MA; Haskell, J.P., Ritchie, M.E., Olff, H., 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418, 527–530; Thomas, C.D., 2000. Dispersal and extinction in fragmented landscapes. Proceedings of the Royal Society Biological Sciences Series B 267, 139–145], not merely their phylogenetic affinity. We investigated the importance of habitat variables at different scales on the richness and abundance of bumble bees both annually and seasonally in Sierran montane meadows over two years. We found that both patch and landscape factors influence the species richness and abundance of bumble bees and these factors have a seasonal component to their importance. The proportion of meadow in the surrounding habitat was the most consistent positive influence on both species richness and abundance across years. In the second year, 2003, patch factors, plant species richness and current livestock grazing also influenced bumblebee species richness; plant species richness was positively correlated and current livestock grazing was negatively correlated with bumble bee species richness. Bumble bee abundance was positively influenced by meadow wetness and proportion of meadow in the surrounding habitat in both years. These data suggest conservation of pollinators depends on conservation planning with attention to the quality and context of the landscape.

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1. Introduction

Understanding the scale at which habitat influences species richness in ecosystems is central to ecology (Wettstein and Schmid, 1999) as both patch and landscape factors may contribute to the diversity of resident taxa (Collinge et al., 2003; Fleishman et al., 2002; Graham and Blake, 2001; Lowe and Bolger, 2002; Noss, 1990; Soderstrom et al., 2001; Wettstein and Schmid, 1999). Patch-level factors include patch area and shape, natural and anthropogenic disturbances (e.g. flooding,

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fire, logging, and livestock grazing), vegetation structure and composition. Landscape-level factors include the type and quality of the surrounding matrix (e.g. urban, developed, undeveloped, agricultural, etc.), elevation, and isolation. Because anthropogenically mediated habitat changes are taking place at multiple scales, science must distinguish between patch and landscape threats in order to develop effective conservation strategies.

Community composition may be influenced by habitat variation from patch to landscape-scale depending on body size, home range area, and dispersal distance of the taxa of interest (Calder, 1984; Haskell et al., 2002; Thomas, 2000). In a recent review, Mazerolle and Villard (1999) conclude that for most invertebrate taxa, patch characteristics are better predictors of species richness and abundance than landscape characteristics whereas for vertebrates, both landscape and patch characteristics are important predictors of species richness and abundance. Although Mazerolle and Villard (1999) include an impressive number of both vertebrate and invertebrate studies in their review, they do not make an effort to separate taxa biologically. From a biological perspective, many of the invertebrates Mazerolle and Villard (1999) studied (ants, beetles, cockroaches and termites) are relatively sessile as adults, with small home ranges when compared to the movement of the reported vertebrates (mammals and birds). Because of this, it is not clear if the results of the study are a consequence of the biology of the species (i.e. mobility) or their phylogenetic affinity. Many different invertebrates (e.g. Hymenoptera, Lepidoptera, etc.) would match the scale of mobility of smaller vertebrates.

Bumble bee (*Bombus*) communities provide an excellent model for examining the relative importance of patch and landscape factors in a mobile invertebrate community. Though bumble bees forage over large distances (>2000 m) (Dramstad, 1996; Osborne et al., 1999; Saville et al., 1997; Kreyer et al., 2004), they exhibit high site fidelity as central place foragers (Heinrich, 1979; Inouye, 1978; Kreyer et al., 2004; Osborne et al., 1999; Osborne and Williams, 2001). Moreover, bumble bees exist in naturally patchy habitats like montane meadows (Bowers, 1985) and anthropogenically fragmented habitats like wildlands adjacent to agricultural fields (Backman and Tiainen, 2002; Dramstad and Fry, 1995; Goulson et al., 2002; Osborne and Williams, 2001). While patch factors such as temporal and spatial variation in floral resources are known to directly influence the abundance of individual bumble bee species (Steffan-Dewenter et al., 2002; Widmer and Schmid-Hempel, 1999), little is known about the importance of landscape variables for the maintenance of bumble bee communities with high species richness.

Our study uses bumble bee communities to address this gap in our understanding by investigating the importance of habitat variables at different scales on the richness and abundance on a group of mobile invertebrates. Because of their size and mobility, we expect that this group of species will likely be influenced by both patch and landscape factors. To determine the properties of meadows that contribute to the species richness and abundance of bumble bees, we delineated six patch attributes: floral species richness, proportion of perennial plant species, meadow area, meadow wetness, and grazing regime. We also investigated two landscape level attributes: elevation of each meadow and proportion of the surrounding matrix (2 km from the edge of the meadow) that is meadow habitat.

2. Methods

2.1. Study site

We studied bumble bee communities during the summers of 2002 and 2003 at 20 meadow sites of the Tahoe National Forest, north and east of Truckee, in Nevada and Sierra Counties, California (Fig. 1). Meadows of the Sierra Nevada are geomorphically determined open basins (Whitney, 1979) with characteristic vegetation. The Sierra Nevada receives most precipitation in the form of snow and Sierra meadows are moistened by runoff from snowmelt, springs, streams and rivers. In our study area, meadow locations ranged from 1750 m to 2300 m in elevation and meadows size from 3.5 to 75 ha. The meadows were surrounded by mixed conifer and white fir forest, consisting mostly of lodgepole pine (*Pinus contortus*), Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*) (Franklin and Fites-Kaufmann, 1996; Sawyer and Keeler-Wolf, 1995). Study meadows are situated in several different hydrologic drainage basins: Davies Creek; Little Truckee River; Prosser Creek; and Sagehen Creek.

2.2. Study species

The bumble bee community in our study consisted of 12 species of *Bombus*. Eleven were non-parasitic bumble bees: *Bombus bifarius* Cresson, *B. californicus* F. Smith, *B. centralis* Cresson, *B. flavifrons* Cresson, *B. fervidus* (Fabricius), *B. mixtus* Cresson, *B. nevadensis* Cresson, *B. occidentalis* Greene, *B. rufocinctus* Cresson Kirby, *B. vosnesenskii* Radoszkowski, *and B. vandykei* (Frison) and one was a cuckoo (parasitic) bumble bee, *B. insularis* (F. Smith). Each species has a characteristic timing of emergence and senescence. Some species emerge as the snow melts, others appear later in the season.

2.3. Bumble bee richness and abundance

To explore the differences in bumble bee richness and abundance across meadows, we selected 20 meadows that varied in elevation, moisture and size (Table 1). In 2002, we sampled each meadow four times from June 10 to August 15 during hours when bumble bees are most active (10:00–16:00). We sampled in four 90 min time blocks: 10–11:30, 11:30–13:00, 13–14:30 and 14:30–16:00 to ensure evenness of sampling effort. Throughout the course of the season, each meadow was sampled once in each time block. In 2003, we sampled each meadow three times from June 6 to August 12. We sampled meadows between the hours of 10:00 and 16:00 PDT. Because we sampled three times during this year, we divided a day into three 120 min time blocks (10:00–12:00, 12:00–14:00 and 14:00–16:00) and throughout the summer sampled each meadow in each time block.

Within each meadow, we selected three points for sampling bumble bees. We used a modified point count method to survey bumble bees (Carvell, 2002). Throughout both years,

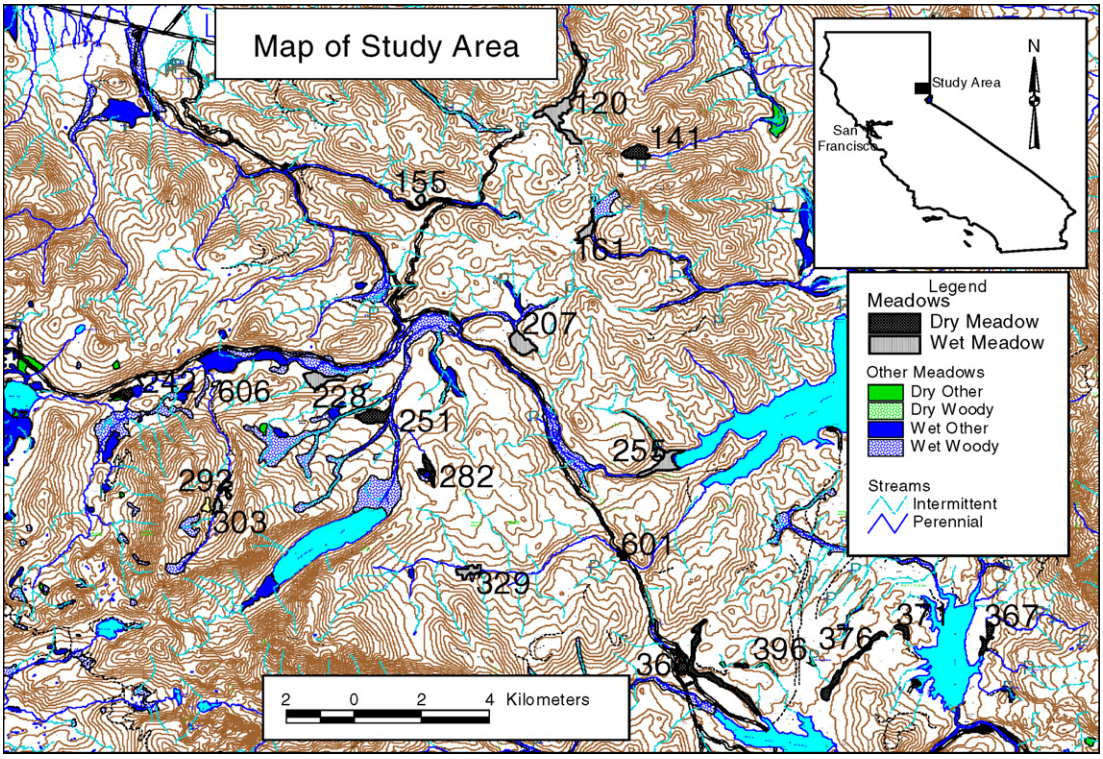

Fig. 1 – Map of study area.

Table 1 – Characteristics of the research meadows

Meadow number	Elevation (m)	Area (m^2)	Bumble bee species richness		Plant species richness	Wetness index	Grazing in 2002	Grazing in 2003
			2002	2003				
606	2004	5310	9	9	26	0.40	1	1
396	1799	34,772	2	3	20	0.33	3	1
155	1863	56,344	6	7	45	0.67	1	1
292	2327	66,995	6	7	34	0.93	1	1
303	2351	75,095	6	5	27	0.88	1	1
371	1727	87,127	1	3	8	0.00	1	1
251	2017	124,870	5	5	31	0.83	1	2
329	1975	143,359	6	5	29	0.71	1	1
367	1723	146,153	2	5	57	0.43	3	1
282	2120	158,739	2	6	17	0.83	2	2
242	1992	160,674	11	10	37	0.38	2	1
141	2226	215,683	5	4	43	0.44	2	2
601	1872	250,000	3	5	11	1.00	1	1
255	1816	305,864	3	6	70	0.54	2	1
228	1981	329,798	8	7	68	0.64	2	2
376	1755	334,903	1	4	48	0.22	3	1
161	2055	500,208	3	6	115	0.22	2	2
366	1795	700,840	6	6	71	0.46	3	1
120	1973	793,285	6	5	113	0.50	2	2
207	1925	1,190,143	9	8	89	0.33	3	3

Meadows are sorted by size. Grazing is coded as un-grazed meadows = 1, cattle-grazed meadows = 2 and sheep-grazed meadows = 3.

the same investigator conducted all samples. Around each point, we established a circular plot with a 20 m radius. On each date we visited a meadow, we sampled each plot within the meadow for 15 min. When we sighted a bumble bee, we either identified the bee to species level in flight, or captured the bee in an insect net and identified the bee to species. When we captured bees in a net, we stopped time during the identification period. We collected bees that we could not identify in the field and identified them in the laboratory. R.W. Thorp (University of California, Davis) verified identifications. If the bee was on a flower, we recorded the plant species visited; otherwise, we scored the bee as in flight.

2.4. Patch scale factors

2.4.1. Meadow area and area to perimeter ratio

We calculated meadow size and perimeter to area ratio using Environmental Systems Research Institute's ArcView GIS (1999) software and meadow elevation using TOPO! (2000). In 2003, we ground-truthed USFS meadow layers to confirm and correct our estimates of meadow size and shape. We corrected the maps to reflect current meadow configurations.

2.4.2. Composition of floral resources

In 2002, we sampled the flowering plant community in each meadow using .25 m × 20 m quadrats. We conducted a preliminary study that suggested that this size and shape increased the number of species detected and reduced variance among samples when compared to $1 \times 1\ m^2$ square quadrats (unpublished data). To standardize sampling across meadows, we scaled the number of quadrats used based on meadow area. The number of quadrats sampled in a single meadow ranged from one to 25. We randomized location and orientation of quadrats. Additionally, to quantify resources available and document flowering plant phenology, we established a permanent 1 × 1 m plot at each point count which we sampled upon each visit to a meadow.

After ground truthing and digitizing the study area in ArcView, we determined we had used incorrect meadow areas for three of our meadows. Because we based vegetation sampling on the size of the meadow, these three meadows were undersampled for vegetation. After confirming the similarity between estimates of plant species richness between 2002 and 2003 (see below), we re-sampled these three meadows for plant species richness.

In June 2003, we re-sampled five quadrats from 2002 in a meadow that had been improperly sampled to test for differences in plant species richness and abundance between years. We conducted a paired sample t-test to test for differences. From our analysis it was apparent that while plant species richness was similar between years that there were significant differences in plant abundance ($t = 3.416$, $p = 0.027$, df = 4). Because there were significant differences in plant abundance between years, we could not correct our 2002 samples for abundance. Therefore, we only used plant species richness in our analyses.

A previous study showed a trend that bumble bees prefer perennial plants (Fussell and Corbet, 1992). To test if the proportion of perennial plants affected bumble bee species richness and/or abundance in our system, we calculated the proportion of the species in the meadow that are perennials.

2.4.3. Meadow wetness index

We created a meadow wetness index using wet and dry meadow species categories established by Weixelman et al. (1999) for plant species associated with meadow habitats in the eastern Sierra. We identified 30 plant species indicative of wet meadows and 27 plant species indicative of dry meadows. We calculated the moisture metric by dividing the number of wet meadow species found in the meadow by the total number of wet and dry meadow plant species found in the meadow. The meadow wetness index ranged between zero and one (0 = dry, 1 = wet). Since most indicator species are perennial and our earlier analysis of differences in species richness between years showed no significant differences, there should be little difference in the wet meadow index between years.

2.4.4. Livestock grazing

During the summer of 2002, cattle grazed seven of our study meadows and sheep grazed five. In 2003, cattle grazed seven meadows and sheep grazed one meadow. We used our grazing data as an ordinal variable in our regression analysis. Because sheep grazing resulted in a greater loss of floral biomass than cattle grazing (Hodgson et al., 1991, pers. obs.), we assigned un-grazed meadows a 1, cattle-grazed meadows a 2 and sheep-grazed a 3. We used current year's livestock grazing in our analysis of 2002 bumble bee data and both current and previous year's livestock grazing regime in our analysis of 2003 bumble bee data. We were unable to obtain accurate historical grazing data prior to 2002.

2.5. Landscape scale factors

2.5.1. Proportion of the surrounding matrix that is meadow habitat

In most montane regions, meadows can occur singly or as part of a meadow complex. To determine the proportion of the surrounding matrix that was meadow habitat, we identified a 2 km buffer around the edge of each study meadow using a meadow layer from the Tahoe National Forest, USFS, and ArcView. We calculated the proportion of the 2 km buffer that was meadow habitat (not including the area of the focal meadow) using Patch Analyst 2.2 (Carr, 2002).

2.5.2. Elevation

We calculated elevations using TOPO! (2000).

2.6. Data analysis

For each year, we constructed multiple linear regression models to determine the best predictors of bumble bee species richness. To normalize the data, we square root transformed bumble bee species richness and bumble bee abundance and natural log transformed meadow area. We constructed different multiple linear regression models to determine the fewest number of variables that explained the largest proportion of the variance for each year. Ultimately, we chose either forward or backward (p to enter the model <0.05 and p to remove >0.10) multiple regression models, depending on which model provided the most rigorous analysis. We analyzed the data using SPSS 11.5 (SPSS, 2002).

To confirm that our sample sizes were adequate, we used the SPECRICH program which computes the total number of species from empirical species abundance distribution data based on methods described by Burnham and Overton (1979) and Hines, 1996. In general, our actual species richnesses were not different than the estimated values. However, for four meadows in 2002, the species richness estimator estimated more species than there are species of bumblebees known from the Sierra Nevada. Because of this, we chose to evaluate actual species richness values rather than estimates. These actual values may be less than the true number of species found in each meadow.

Additionally, for 2002, we analyzed grazing data with a repeated measures analysis of variance (ANOVA) to investigate the effects of grazing on bumble bee abundance. Meadows were our subjects, time was the within subject (repeated measures) effect and grazing regime (none, sheep, or cattle) was our between subjects comparison. Since sheep only grazed one meadow in 2003, the ANOVA was uninformative and we do not report it here.

3. Results

In 2002, we counted 1758 individuals of 12 bumble bee species. In 2003, we counted 2692 individuals of 12 bumble bee species. Voucher specimens of the bumble bees are stored at the California Academy of Sciences and at San Francisco State University (SFSU).

3.1. *Plant species richness*

We observed 195 different flowering plant species. Plant species richness per meadow varied dramatically from 113 to 8 flowering plant species. Voucher specimens of the plant species are stored at SFSU.

3.2. *Bumble bee species richness*

There was a difference between years in the influence of patch and landscape factors on species richness of bumble bees. In 2002, only the landscape factor, percent surrounding meadow habitat, significantly contributed to bumble bee species richness (for the whole model: $F = 5.63$, df = 1,18, $p = 0.029$, $r^2 = 0.24$, individual p-values are reported in Table 2). Meadows with a larger proportion of the surrounding habitat consisting of meadow habitat had a greater number of bumble bee species in them. In 2003, percent of the surrounding habitat that is meadow, current year livestock grazing and plant species richness emerged as the best predictors of bumble bee species richness (for the whole model: $F = 4.79$, df = 3,16, $p = 0.014$, $r^2 = 0.47$, individual p-values are reported in Table 2). Increased intensity of livestock grazing was negatively associated with bumble bee species richness (Table 2). Percent of surrounding habitat that is meadow and plant species diversity were positively associated with bumble bee species richness (Table 2).

3.3. *Bumble bee abundance*

Patch and landscape level factors influenced bumble bee abundance in both years. In both years, the same factors were important in the models of abundance: the percent of the surrounding habitat that is meadow and meadow wetness (for the whole model: 2002: $F = 9.76$, df = 2,17, $p = 0.002$, $r^2 = 0.48$ and 2003: $F = 15.65$, df = 2,17, $p < 0.0001$, $r^2 = 0.65$, individual variables are reported in Table 2). Both these variables positively influenced abundance (Table 2).

3.4. *Livestock grazing*

Livestock grazing significantly influenced the temporal change in bumble bee abundance over the course of 2002 (time × grazing, $F = 2.889$, df = 6,51, $p = 0.017$). There was no significant effect of time alone ($F = 0.346$, df = 3, $p = 0.792$) or grazing alone ($F = 1.547$, df = 2,17, $p = 0.241$). Average bumble bee abundance in ungrazed meadows increased throughout the season (Fig. 2a). Average bumble bee abundance in cattle grazed meadows remained fairly constant throughout the season (Fig. 2a). Average bumble bee abundance in sheep grazed meadows declined as the season progressed (Fig. 2a). While the trend in sheep grazed meadows was similar in 2003, sheep grazed only one meadow so a similar analysis was uninformative (Fig. 2b). The trend for cattle grazed meadow in 2003 was the opposite of what we observed in 2002. In fact, at the end of the season, bumble bee abundance was higher in meadows that had been grazed by cattle than bumble bee abundance in ungrazed and sheep grazed meadows.

3.5. *Floral resources*

To determine if there was a relationship between floral resource availability, meadow wetness and season, we constructed a linear regression model comparing the total abundance of flowers available in the meadow (as determined from the 1 × 1 m plots from 2002, see Section 2) to the meadow wetness index. We constructed one model for the early season (first visit of the season) and one model for the late season (last visit of the season). A significant negative relationship between meadow wetness and floral resources was detected early in the season, whereas this relationship was reversed late in the season (Fig. 3). This suggests that wetter

Table 2 – The effect of individual variables in the multiple regression models built to explain bumble bee species richness and abundance (p-values reflect the individual variables contribution to the whole model)

Year	Model	Variable	β	t	p-Values
2002	Richness	Percent meadow	0.488	2.372	0.029
	Abundance	Percent meadow	0.447	2.667	0.016
		Meadow wetness	0.509	3.036	0.007
2003	Richness	Plant species richness	0.613	2.774	0.014
		Percent meadow	0.641	3.278	0.005
		2003 Grazing	−0.489	−2.169	0.045
	Abundance	Meadow wetness	0.713	4.890	0.001
		Percent meadow	0.274	1.877	0.078

Only variables that significantly contributed to the final model were included.

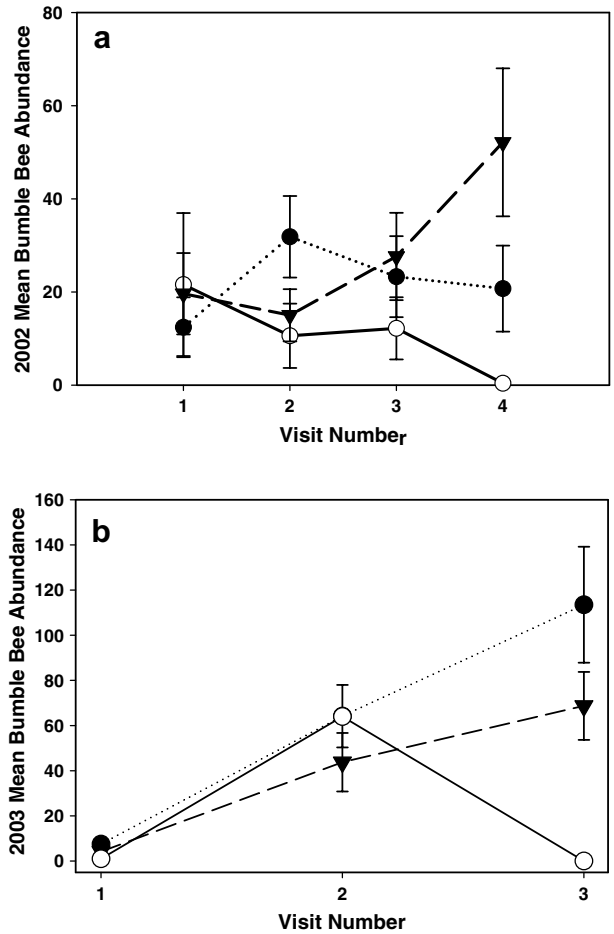

Fig. 2 – Effects of sheep and cattle grazing on bumble bee abundance across the season in (a) 2002 and (b) 2003. Triangles (▼) represent sequential surveys in ungrazed meadows (*n* = 8 in 2002 and 12 in 2003); Closed circles (●) represent sequential surveys in cattle grazed meadows (*n* = 7 in 2002 and 2003); Open circles (○) represent sheep grazed meadows (*n* = 5 in 2002 and 1 in 2003). Error bars display means ± 1.0 SE.

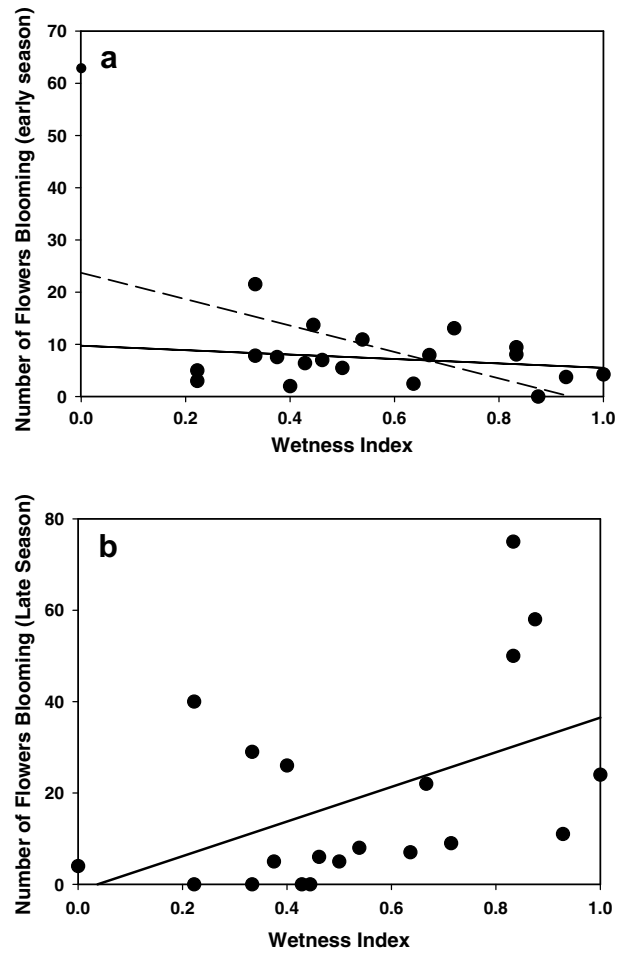

Fig. 3 – Relationship between meadow wetness and the number of flowers in bloom during (a) the early flowering season (b) and the late flowering season. We measured phenology at each bumble bee sampling location in three 1 × 1 m plots per meadow. The two trend lines in a represent the data analysis with (dashed line) and without (solid line) a possible outlier. Note that the dependent variable, the number of flowers in bloom for the early flowering season, has been square root transformed for normality.

meadows had fewer floral resources available early in the season ($F = 8.867$, df = 1,18, $r^2 = 0.330$, $p = 0.008$, Fig. 3a), and more floral resources available later in the season when compared to dryer meadows (Fig. 3). This trend was significant in both the early and late season ($F = 5.047$, df = 1,18, $r^2 = 0.219$, $p = 0.037$, Fig. 3b).

4. Discussion

We found that patch and landscape habitat characteristics are important predictors of species richness and abundance for bumble bee communities. For these bumble bees, a landscape factor, proportion of surrounding habitat that is meadow, was the most consistent factor influencing annual bumble bee species richness in both years (Table 2). One explanation for the dissimilarity between our results and the results from other systems (Collinge et al., 2003; Mazerolle and Villard, 1999) may be the mobility of bumble bees. Bumble bees are known to fly long distances to retrieve floral resources (Dramstad, 1996; Kreyer et al., 2004; Osborne et al., 1999). Therefore, surrounding habitat may be more important to the maintenance of bumble bees and other mobile invertebrates than it is to many of the species considered in other studies (butterflies, ants, beetles, cockroaches and termites) (Collinge et al., 2003; Mazerolle and Villard, 1999).

A high proportion of surrounding habitat that is meadow may buffer the focal meadow in two ways. First, because of the mobility of bumble bees, a higher proportion of surrounding meadow habitat that is meadow should decrease the probability of individual species extirpation from a meadow as there is the possibility of colonization or recolonization through queen dispersal from adjacent meadows between years (cf. Kodric-Brown and Brown, 1979). Second, meadows that are embedded in a landscape with a high density of surrounding meadows may support more species because such a

landscape may provide varied habitats, differences in wetness, and flowering phenology, thus increasing the probability that individuals will encounter flowering plants throughout the season. Moreover, the reduced distance of travel for forage may increase bumble bee reproductive success (Heinrich, 1979). Whether this result is due to the greater availability of habitat or the specific configuration of the habitat remains untested. Nevertheless, meadow complexes that provide a variety of habitat types, with floral resources available continuously throughout the breeding season, are likely to support more diverse and abundant bumble bee communities than single meadows that have a burst of floral resources that quickly disappear as the flowering season progresses.

High quality meadows might occur in groups, which would lead to species rich meadows having a high proportion of meadow surrounding the focal meadow. In our data, the six most species rich meadows were distant from each other and did not cluster in a way that would indicate that there was a relationship between high quality and a high proportion of meadow in the matrix.

4.1. *Bumble bee richness*

Surprisingly, we did not find meadow size to be an important factor in determining the species richness of bumble bee communities. This is contrary to most species–area relationships that have been investigated (Preston, 1962; Rosenzweig, 1995; Williamson, 1989). One reason meadow area may not show up as a significant contributer to species richness is that if meadow complexes are indeed supporting bumble bee communities and bumble bees are moving between meadows, a single meadow may not be appropriate scale to consider the species–area relationship. If we delineate the habitat as a meadow complex, or meadows within a certain distance of a focal meadow, large meadow complexes will likely support more species than smaller meadow complexes. Another possibility is that the quality of habitat is much more important than patch size (Fred and Brommer, 2003; Schultz and Crone, 2005). Many of our larger meadows are large expanses of sagebrush, with a paucity of floral resources, particularly in the late season. The high quality habitat of a medium or small meadow could easily equal or exceed the high quality area of a large meadow. The effects of within meadow habitat diversity on species richness and abundance is an interesting question that is beyond the scope of our study.

Livestock grazing had a significant negative impact on annual bumble bee species richness in 2003. Livestock grazing has differing impacts on flora and fauna based on the type, habitat, intensity, timing and length of livestock grazing (Gibson et al., 1992). Our results agree with previous studies of livestock grazing on bees that suggest increased intensity of livestock grazing negatively affects the species richness of bees (Carvell, 2002; Morris, 1967; Sugden, 1985; Vazquez and Simberloff, 2003). We were surprised that the previous year's grazing did not influence bumble bee species richness. Since we saw no bumble bees in sheep grazed meadows after grazing occurred, and grazing happened prior to bumble bee reproduction in 2002, we expected to see a decrease in species richness in 2003. Most grazed meadows retained the same number of species in 2003 although, often, species composition changed. This suggests that these meadows may be acting as metacommunities and that forests do not serve as significant barriers to early season dispersal. However, isolated sheep-grazed meadows (e.g. far upper elevations) might be especially vulnerable to grazing if they are too far away from source populations to be 'rescued'.

The data from 2003 show that meadows with high plant species richness harbored communities more rich in bumble bee species compared with meadows that have a lower richness of flowering plants. This result, consistent with the findings of many different authors (e.g. Heinrich, 1976; Inouye, 1978; Kells and Goulson, 2003; Pyke, 1982; Ranta and Lundberg, 1980, 1981; Ranta et al., 1981), suggests that the availability of varied floral resources are important for species rich bumble bee communities at the local level.

4.2. *Bumble bee abundance*

Livestock grazing had a significant negative impact on late season abundance in 2002, but was not a factor in 2003 abundance. In 2002, five meadows were grazed by sheep and seven by cattle. In 2003, sheep grazed one meadow and cattle grazed the same seven meadows. In 2002, sheep had a particularly strong effect on bumble bee abundance. In all meadows grazed by sheep in 2002 and 2003, we did not detect any bumble bees after sheep were present in the meadow (Fig. 2). Sheep remove nearly all available floral resources and create vegetation gaps (Andersen and Calov, 1996; Bastrenta, 1991; Bullock et al., 1994a,b, 1995; Morris, 1967; Sugden, 1985; Tiver and Andrew, 1997). Therefore, the fact that grazing was an important factor in 2002, but not in 2003, may be explained by the fact that sheep only grazed one meadow in 2003; therefore, grazing intensity was less in 2003 than in 2002.

The effects of sheep grazing on bumble bee populations are particularly significant because of the timing during which it occurred. All sheep grazing occurred between mid and late season sampling dates (late July/early August 2002). By late July and early August, floral resources are declining. The end of the season is particularly important for bumble bee colonies because this is when colonies produce reproductive members of the colony. This final cohort of offspring determines the fitness of a colony. Because sheep remove nearly all floral resources from a meadow (Hodgson et al., 1991), bumble bees likely have a more difficult time finding rewarding flowers in sheep-grazed meadows than in un-grazed meadows.

In 2003, we did not find an effect of the previous year's grazing regime. Since bumblebees can disperse several kilometers between seasons (Darvill et al., 2006; Goulson, 2003), local extirpation by heavy grazing in one meadow may not affect bee abundance the following year.

The matrix surrounding a meadow is also important to annual bumble bee abundance (Table 2). In addition to increasing the potential resources usable by bees from the focal meadow, a meadow with a higher proportion of meadow surrounding the focal meadow may provide floral resources for bumble bees nesting in other meadows when the host meadow habitats experience a paucity of resources. However, Bowers (1985) found that there was no movement of bees between montane meadows in Utah. As such, further study is needed to determine if the higher abundance we observed in focal meadows

with a higher proportion of meadow in the surrounding habitat may be due to foragers coming from different meadows or indicative of higher abundance of resident bees.

Meadows with a higher meadow wetness index had a greater abundance of bumble bees than meadows with a lower wetness index. We suspect that meadow moisture may be closely tied to floral resource availability. For example, if we examine the relationship between the wetness index and the seasonal abundance of flowers in bloom (the sum of flowers in bud and flowers open), we find that meadows with a higher wetness index have a greater reliability and abundance of late season floral resources (Fig. 3). Interestingly, in the early summer, meadows with a higher wetness index have fewer floral resources, but by late summer, those same meadows have more floral resources than meadows with a smaller wetness index (Fig. 3). Since larger colonies produce more queens (Goulson et al., 2002) and the size of the colony at the transition to producing reproductive bees depends on resource availability (Beekman et al., 1998), the availability of late season resources may increase bumble bee fitness. Higher bumble bee abundances observed in meadows with a higher wetness index may be because individual bumble bee colonies are larger or because colony density is greater. It is difficult to distinguish between the two because bumble bee nests are difficult to locate in the field (Kells and Goulson, 2003). However, it is a critical distinction because if meadows with a higher wetness index host larger bumble bee colonies, those colonies will have higher fitness (Goulson et al., 2002).

Our results show that conservation of mobile organisms like pollinators will depend on conservation planning that pays attention to both landscape and patch quality variables. Meadow complexes which provide a heterogeneous landscape with patches of locally abundant floral resources continuously throughout the breeding season will likely support diverse bumble bee communities. Since landscape and patch factors contribute to both species richness and abundance of bumble bees, our study independently confirms that for invertebrate taxa, protecting clusters of habitat is a more effective conservation strategy than preserving islands of habitat (Mangel and Tier, 1994; Rivard et al., 2000). These results are in contrast to recent publications regarding species richness and abundance of invertebrates in different landscapes, as influenced by patch and landscape characteristics (Collinge et al., 2003; Mazerolle and Villard, 1999). These studies reported that for the majority of invertebrate taxa, patch characteristics were better predictors of species richness and abundance than landscape characteristics. One explanation for this dissimilarity may be the mobility of bumble bees. Bumble bees are known to fly long distances to retrieve floral resources (Dramstad, 1996; Kreyer et al., 2004; Osborne et al., 1999). Therefore, bumble bees may see clustered patches of meadows as continuous foraging habitat instead of inaccessible islands. Understanding how patch and landscape factors affect abundance and richness of both invertebrate and vertebrate communities is critical to their long-term persistence and management.

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