

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)?

Quinn S. McFrederick*, Gretchen LeBuhn

San Francisco State University, Department of Biology, 1600 Holloway Avenue, San Francisco, CA 94132-1722, United States

ARTICLE INFO

Article history:

Received 10 November 2004

Received in revised form

4 November 2005

Accepted 8 November 2005

Available online 22 December 2005

Keywords:

Bombus

Urban parks

San Francisco

Matrix

Nest sites

ABSTRACT

Declines in bee populations have been documented in several parts of the world. Bees are dependent upon flowering plants for resources, and flowering plants often depend upon bees for pollination services. Bees can therefore serve as indicator species of habitat degradation due to these relationships with flowering plants. This study investigates how the bumble bee community in San Francisco has responded to urbanization and which urban park characteristics are important for the current community's structure. To answer these questions we sampled bumble bees, in 18 urban parks and two nearby wild parks. We estimated park characteristics and used multiple regression analysis to determine which characteristics predicted bumble bee abundance and species richness. Bumble bee abundance was positively associated with resource availability or proxies of resource availability; "natural area" (areas that contain remnant fragments that have been largely unchanged by human activity) in 2003 and nest site abundance and openness of the surrounding matrix in both 2003 and 2004. Bumble bee species richness was negatively associated with abundance of a dominant species, *Bombus vosnesenskii*, in 2004. The importance of the surrounding matrix suggests that these parks do not act as islands. Accordingly, area of park did not explain species richness, while abundance of the dominant competitor did. The species that was most influenced by competition, *Bombus sitkensis*, uses rodent holes as nest sites and is possibly excluded from nest sites by the early emerging *B. vosnesenskii*, another subterranean nester. The species least influenced by competition, *Bombus melanopygus*, is able to use both rodent holes and abandoned bird nests as nest sites.

© 2005 Elsevier Ltd. All rights reserved.

1. Introduction

Urbanization threatens species in one of two ways: direct replacement of habitat and removal of resources (Czech et al., 2000). In the United States alone, 2.2 million acres of farmland and open space are converted into urban areas every year (USDA, 2000). Often, the only open spaces left in urban areas are parks, which are fragments of what was once continuous habitat. These fragments are usually drastically altered, and become a new type of habitat. These new urban

habitats must function as recreational sites, open space and, increasingly, refuges for native species of plants and animals (Fernandez-Juricic and Jokimaki, 2001; Koh and Sodhi, 2004). As urban development continues, the role of refuge will become increasingly important for urban parks. To maximize the utility of parks as refuges, we need to know what characteristics of parks influence biodiversity.

Studies of insects in human modified fragmented habitats have focused on biogeographic processes, edge effects and the importance of the matrix surrounding the fragment.

* Corresponding author. Present address: University of Virginia, Department of Environmental Sciences, Clark Hall, 291 McCormick Road, P.O. Box 400123, Charlottesville, VA 22904-4123, United States. Tel.: +1 434 924 6846.

E-mail address: qsm5a@virginia.edu (Q.S. McFrederick).

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.11.004

The first study of insects in urban parks showed that urban parks can behave as islands of useable habitat surrounded by an inhospitable sea of development, in accord with the theory of island biogeography (Faeth and Kane, 1978). In this study, species richness of Diptera and Coleoptera was positively correlated with area of the park. Other studies confirm the importance of park size and distance from a source population for arthropods in urban habitat fragments (Bolger et al., 2000; reviewed in McIntyre, 2000; Zanette et al., 2005). The ratio of perimeter to area of a habitat patch can also influence the community assemblage of that patch (Tscharntke et al., 2002a). Edges create an ecological gradient of wind and light, changing the microclimate at the edge. Edge adapted species proliferate within patches with a high ratio of perimeter to area while non-edge adapted species decline, altering community dynamics and structure (Bolger et al., 2000). Patches with high perimeter to area ratios are devalued for conservation (Tscharntke et al., 2002b). Recent studies of insects in fragmented habitats have looked at landscape scales to help predict species assemblages (Tscharntke et al., 2002a). Proportion of surrounding seminatural habitats positively correlates with species richness of trap nesting bees, wasps and their natural enemies (Steffan-Dewenter, 2002) and solitary, wild bees at small spatial scales and honey bees at large spatial scales (Steffan-Dewenter et al., 2002), while diversity of surrounding matrix positively correlates with natural enemies (Steffan-Dewenter, 2003).

Urban park usage and maintenance changes the resources available to insects within parks. Soils are compacted and microclimates become less stable (Bradley, 1995). Urban parks lose native vegetation to landscaping and to invasive plants. The spread of invasive plants is often facilitated by anthropogenic disturbances, which are common in urban parks (Meekins and McCarthy, 2001). Fallen trees and brush piles removed from urban parks are no longer available as substrates for animals to utilize as nesting sites or predator refuges. Species persisting in urban parks must be able to utilize the resources found in this new type of habitat.

The nascent study of insect assemblages in urbanized landscapes does not yet provide clear predictions as to which insects can persist in urban areas, although several trends are becoming apparent. Insects with low dispersal capacity are less common in habitat fragments than insects with high dispersal capabilities (Thomas, 2000). Rare insects tend toward extinction in habitat fragments (Tscharntke et al., 2002b). Steffan-Dewenter and Tscharntke (2000) claim that habitat specialists are more susceptible to extinction in fragments than generalists. However, Shapiro (2002) found that some host-specific butterflies can thrive on alien, weedy plants that are related to their native host plant. Rickman and Connor (2003) found no difference between urban and agricultural communities of leaf mining moths on *Quercus agrifolia* Nee (Fagaceae). Connor et al. (2002) point out that insects in urban areas are at risk primarily due to loss of habitat, but that changes in habitat quality can result in either declines or increases in the abundances of insects, due to changes in the effectiveness of plant defenses or abundances of natural enemies.

The response of bees to urbanization is yet unclear. Bees forage on patches of floral resources that may be a considerable distance from their nest sites (Dramstad, 1996; Osborne

et al., 1999; Keyer et al., 2004). If nest sites and suitable floral resources are available and the distance between these two resources is not too great, bees should be able to persist in urban areas. Urban surveys of bees are few, and the few published studies usually have no historical records to compare to the current community. The number of species found can be high, but we do not know if this is a subset of the previous community. In Berlin, Germany, one-half of Germany's bee fauna was found within city limits (Cane, 2005). In Tucson, Arizona, cavity nesting bees were more abundant in urban fragments than in the outlying desert, probably because of the higher availability of nesting sites in the urban area (Cane, 2001). Seventy-four species of native bees were collected in gardens in Berkeley, CA (Frankie et al., 2002). This represents less than half the number of species collected in wild areas in nearby Napa and Sonoma Counties (G. LeBuhn, personal observation).

Several studies have shown that some species of bumble bees (*Bombus* Latreille) are able to persist in anthropogenic habitats (Klemm, 1996; Goulson et al., 2002; Goulson, 2003). The minimum requirements for bumble bees to survive are nest sites, nest building materials such as rodent fur and grasses and flowers from which they can collect pollen and nectar (Westrich, 1996). Bumble bees nest either in the ground, often in abandoned rodent burrows, or above ground, in tall grasses or abandoned birds nests (Thorp et al., 1983; Kearns and Thomson, 2001). Gardens may benefit some bumble bee species, providing a variety and continuity of floral resources (Comba et al., 1999a,b; Goulson, 2003). However, not all ornamental flowers provide resources for insects. Comba et al. (1999a) showed that less modified cultivars tended to have higher insect visitation and greater resource yield than more modified cultivars. Therefore, the composition of the garden may influence its usefulness to bumble bees. Recent studies have shown that bumble bees routinely forage around 200–300 m from their nests, but have been recorded up to 2 km from their nests (Osborne et al., 1999; Keyer et al., 2004). This suggests that bumble bees can use floral resources disconnected from their nest sites, as long as they are willing or able to traverse the intervening habitats. If these intervening habitats are difficult to traverse bumble bees may be limited to local resources. A matrix that is hostile to dispersal has been shown to hinder movement between patches in plant-hoppers and butterflies (Ricketts, 2001; Baum et al., 2004).

To understand the influence of park characteristics on bumble bee abundance and species richness, we asked four questions: (1) Is the current bumble bee community a subset of the historical community? (2) Which park characteristics are important for the current community's structure? (3) How does the urban community compare to communities found in larger and wilder nearby parks? and (4) Can urban parks be designed to act as refuges for pollinators?

2. Methods

2.1. Study area

We conducted this study in 18 urban parks inside San Francisco city limits (Fig. 1). To determine if there are fewer species and lower abundance of bumble bees in urban parks in

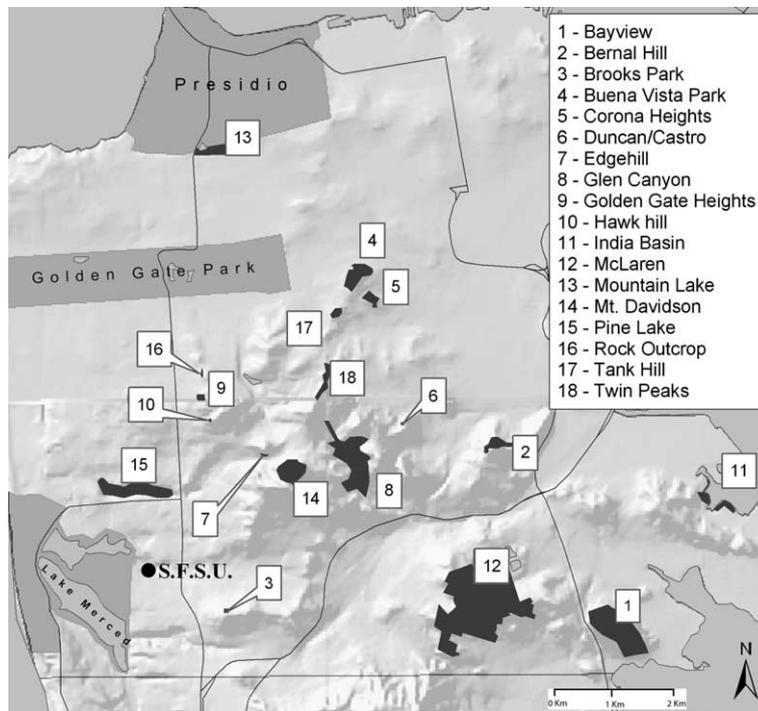


Fig. 1 – Map of San Francisco and the 18 urban parks included in this study.

comparison to larger, wilder parks, we also sampled two parks outside of San Francisco: San Bruno and Sweeny Ridge. The urban parks we worked in are designated significant natural resource areas by the Recreation and Park Department of San Francisco. Significant natural resource areas (hereafter called “natural areas”) are defined as parks that contain remnant fragments that have been largely unchanged by human activity (EIP Associates, 2002). Natural areas are often dominated by non-native plant species, so the designation describes areas that are undeveloped, rather than pristine habitats. The urban parks contain diverse habitats, from north franciscan coastal scrub dominated by *Baccharis pilularis* DC (Asteraceae), *Toxicodendron diversilobum* Torrey and *A. Gray* (Anacardiaceae), *Rubus ursinus* Cham. And Schldl. (Rosaceae) and *Artemisia californica* Less (Asteraceae), to annual and perennial grasslands dominated by exotics such as *Lolium multiflorum* Lam. (Poaceae) and *Avena fatua* L. (Poaceae) and natives such as *Nasella pulchra* A. Hitchc. (Poaceae). Many of the parks also contain developed or landscaped areas, including sports fields, dog runs and community gardens. Eucalyptus forest covers parts of many of the parks. The parks have varying amounts of natural area, from 3.6% to 87.9% of the park area. The area of the parks varies tremendously, from 0.32 ha to 158.64 ha (EIP Associates, 2002).

To select parks for this study, we assigned numbers to the parks and used a random number generator to select 18 of the 32 parks in San Francisco that are classified as natural areas (Appendix 1).

2.2. Study organisms

California bumble bees are annual, primitively eusocial insects. Worldwide, all bumble bees, except for *Bombus consobri-*

nus Dahlbom, forage from a wide variety of flowers (Lavery and Plowright, 1988) and may be able to find suitable floral resources in urban areas (Westrich, 1996). There are, however, differences among bumble bee species in their preferred host plants (Inouye, 1978; Ranta and Vepsäläinen, 1981). The species recorded in this study all nest underground, although *B. melanopygus* Cresson also nests in abandoned bird nests (Thorp et al., 1983; Kearns and Thomson, 2001). Bumble bees are central place foragers, meaning that they return from foraging trips to their nest sites and are, therefore, constrained in the distance of their foraging bouts. There is significant annual variation in bee communities, making detection of community change difficult (Williams et al., 2001). For this reason we conducted our study over two seasons.

There are museum specimens of nine species of bumble bees that have been collected in the city of San Francisco; *Bombus bifarius* (“nearcticus” populations) Cresson, *Bombus californicus* F. Smith, *Bombus caliginosus* Frison, *Bombus melanopygus* (“edwardsii” populations) Cresson, *Bombus rufocinctus* Cresson, *Bombus sitkensis* Nylander, *Bombus occidentalis* (“nigroscutatus” populations) Greene, *Bombus vosnesenskii* Radoszkowski and *Bombus (Psithyrus) insularis* F. Smith (Thorp et al., 1983). Twelve species of bumble bees have been recorded in the greater Bay Area (Thorp et al., 1983).

2.3. Sampling methods – bumble bee abundance and species richness

To estimate species richness and abundance, we censused bumble bees in 10 randomly placed 10-m diameter plots in each park. This sampling method allowed us to detect foraging workers and queens as well as mate searching males and nest searching queens, providing a complete representation

of the bumble bee community. Other studies of bumble bee communities have used similar random sampling techniques (Bowers, 1985a; Carvell, 2002). To place plots in the parks, we generated coordinates of the center of the plots using a random number generator. To control for climate, we sampled between the hours of 10 AM and 4 PM on days when the temperature was above 18 °C, cloud cover was less than 50% and wind speed was less than 24 km/h. We sampled the plots for 5 min each by netting every bee encountered within the plot, for a total of 50 min of sampling per park per sampling day. We identified the bees to species and caste, and then released them. Bumble bees immediately leave the area after being netted and released, so recapture of a specimen during a sampling period was not an issue. We identified and recorded the species of flower when bees were found on flowers. We took all samples in April–July 2003 and February–July 2004.

In 2003, we sampled each park once in early summer, once in middle summer and once in late summer. In 2004, we sampled in spring and early, middle and late summer. We changed the sampling schedule in 2004 in hopes of detecting species that might emerge early, and were not detected in 2003.

2.4. Sampling methods – park characteristics

To measure the availability of floral resources, we measured abundance of flowering plants in each park. We visually estimated abundance of flowers in each plot at the same time we sampled for bumble bees. We used a logarithmic scale to estimate flower abundance, i.e. 0, 1, 10, 100, 1000, 10,000 flowers per plot. We used existing plant lists compiled by the Natural Areas Program of the Recreation and Park Department of San Francisco for species richness of plants in each park.

To measure the availability of possible bumble bee nest sites, we sampled each park for rodent holes in the summer of 2003. We placed 15 20-m by 1-m transects in each park. We used the center of the existing bumble bee plots for 10 transects, and we randomly laid five new points. We used a random number generator to generate compass headings and placed the transects in the direction of the heading. We then searched each transect for rodent burrows. To obtain an estimate of nest site availability per park, we summed the total number of burrows found from all 15 transects.

To estimate the amount of the surrounding urban matrix that was open space (openness of the surrounding matrix), we analyzed a 1-km buffer surrounding each park. We analyzed aerial photos of one foot per pixel resolution (http://gis-pubweb.sfgov.org/website/sfshare/index.htm#login_10/28/03) using ArcView 3.1 software. We measured and recorded the proportion of the perimeter that was not paved or built on, for example, yards and empty lots. Openness of the surrounding matrix provided a measure of the proportion of land that may provide either nesting or floral resources to bumble bees. To estimate the edge to area ratio, we used the same aerial photos and ArcView to measure the amount of edge and area of each park. We measured the distance of each park to the nearest possible source population using the nearest features extension in ArcView (Jenness, 2004), which calculates the shortest straight line between two features. We considered the three largest parks (larger than 400 ha) within or adjacent to San Francisco (San Bruno Mountain, the Presidio National

Recreation Area and Golden Gate Park) as possible source populations. We measured the mean elevation and edge to area ratio of each park from these same aerial photos.

We used existing classifications of proportion of each park that is natural area and number of habitats within each park (EIP Associates, 2002). The age of each park was provided by the Recreation and Park Department and by a history of San Francisco (Benet, 1966).

2.5. Data analysis

To model which park characteristics influence bumble bee community structure, we analyzed the data using least squares multiple linear regressions. The dependent variables conformed to a normal distribution, or were square root transformed to conform to a normal distribution (Zar, 1999). We used the natural log transformation on natural area and number of rodent holes to achieve linearity between the independent variables and natural area and number of rodent holes. We used forward regression (p to enter the model < 0.05) to build the models. All analyses were done in SPSS (ver. 11.0.1, 2001). We built models for each year, with species richness and abundance as the dependent variables. We entered park area, age, mean elevation, habitat heterogeneity, edge to area ratio, distance to a possible source population, proportion of the surrounding area that is open space, proportion of park that is designated natural resource area, floral abundance, floral species richness, number of rodent holes, and abundance of a dominant bumble bee species as possible explanatory variables. To determine if bees respond to total size of natural area rather than proportion of the park that is natural area, we redid the analyses with size of the natural area in each park as an independent variable. The results were virtually identical; therefore, we report only the analyses with proportion of park that is natural area. For each model, we examined the residuals and tested the variables for multicollinearity and found there were no problems. We also examined the percentage difference between the coefficient of determination and the adjusted coefficient of determination. No difference was greater than 10%, which suggests we have an appropriate number of observations for our number of variables (Sokal and Rohlf, 2000).

To visualize the degree of influence each predictor variable had on the dependent variables, we plotted significant predictor variables against the dependent variables, fit least squares regressions lines and calculated the slope of each line. To examine the effect of a dominant bumble bee species on the rest of the community, we performed logistic regressions of the abundance of the dominant competitor on the presence or absence of every other bee species (Zar, 1999). We used logistic regressions because the non dominant species were not present in all parks and were in low abundance (Appendix 1). We analyzed the data using SPSS (ver. 11.0.1, 2001). A few of the parks included in this study are within bumble bee flight range of each other, as measured by Keyer et al. (2004). Therefore, to check for spatial autocorrelation in the samples, we calculated Sorensen's similarity index ($S = 2C/(A + B)$), where A and B are the number of species in the two parks being compared and C is the number of species the two parks have in common, for each pair of parks (Sklenar and Jorgensen,

1999). We also calculated the distances between pairs of parks and assembled matrices for both similarity and distance. We then used a Mantel test, in which we created a probability distribution by randomly permuting the matrices 10,000 times (Sokal and Rohlf, 2000). We tested for spatial autocorrelation in species richness data in both 2003 and 2004 with the program Mantel for Windows version 1.16 (Cavalcanti, 2005).

3. Results

3.1. Bumble bee distribution

Altogether, we sampled 1660 bumble bees in 2003 and 2183 in 2004 (Appendix 2). We used the same sampling methods in both years, but included an extra sampling round in 2004. This means that our overall abundances from 2004 are greater than 2003. We hoped to detect additional species with added sampling effort. In both years, however, we found the same four species in San Francisco: *B. vosnesenskii*, *B. melanopygus*, *B. californicus* and *B. sitkensis*. We pooled the number of bees sampled in each park each year to compare abundances between parks. Bumble bee abundance in 2003 ranged from a

low of 15 to a high of 183 per park. In 2004, bumble bee abundance ranged from a low of 17 to a high of 238. In 2003, bumble bee species richness ranged from one species per park to four species per park, while in 2004 bumble bee species richness ranged from one species per park to three species per park. *B. vosnesenskii* was by far the most common bee (3665 specimens), and occurred in every park in both years of the study. On San Bruno Mountain, we found three of the four species present in San Francisco and *B. caliginosus*. We sampled 122 individuals on San Bruno Mountain. On Sweeny Ridge, we found 155 *B. vosnesenskii* (Appendix 2).

3.2. Bumble bee abundance

Two factors associated with bumble bee abundance in both 2003 and 2004, while three other factors were significant in only one year (Table 1). Bee communities are inherently variable, which may account for the inconsistency in the variables that were significant in one year only (Williams et al., 2001). For 2003, three variables explained a significant amount of variation in bumble bee abundance ($F_{3,17} = 12.082$, $p = 0.000$, $r^2 = 0.721$): proportion of the park that is natural area (Fig. 2),

Table 1 – Results of multiple linear regressions of bumble bee abundance and species richness with slope and significance of independent variables

Model	Variable	Beta	t	p
2003 abundance	Natural area	0.529	3.497	0.004
	Matrix	0.472	3.249	0.006
	Rodent holes	0.382	2.464	0.027
2003 species richness	Elevation	-0.539	-7.562	0.021
2004 abundance	Park age	-0.248	-1.502	0.157
	Matrix	0.395	2.176	0.049
	Rodent holes	0.533	3.301	0.006
	Elevation	0.0283	1.810	0.093
2004 species richness	Vosnesenskii abundance	-0.628	-3.229	0.005

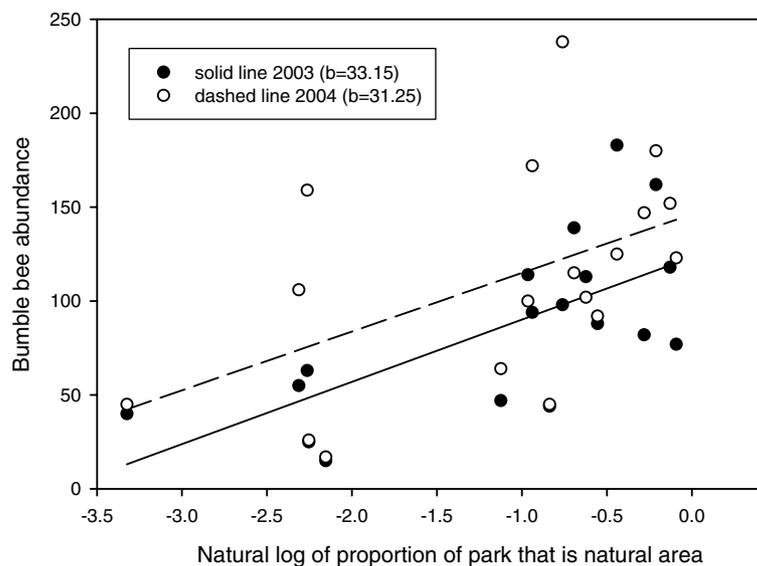


Fig. 2 – Simple linear regression of bumble bee abundance and natural log of the proportion of park that is natural area.

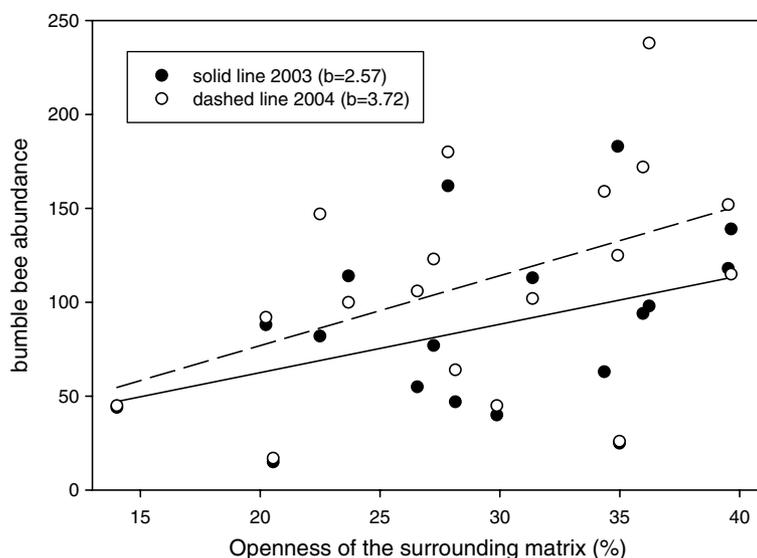


Fig. 3 – Simple linear regression of abundance of bumble bees and proportion of the surrounding matrix that is open space.

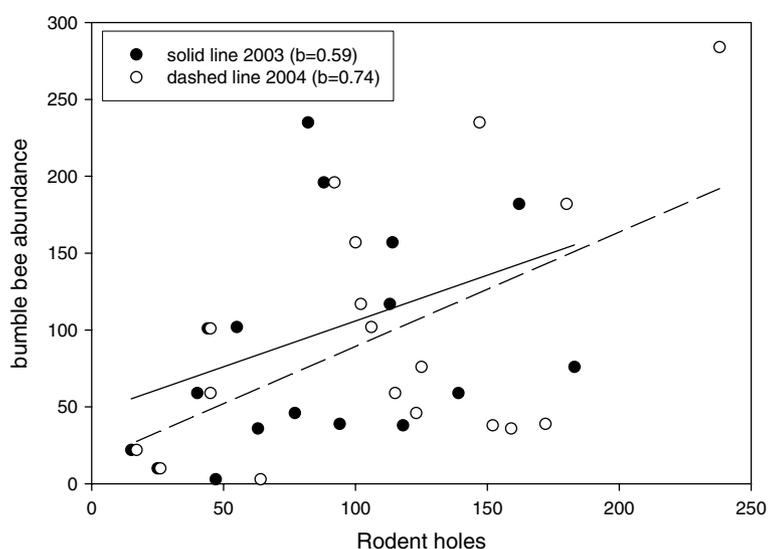


Fig. 4 – Simple linear regression of abundance of bumble bees and number of rodent holes.

openness of the surrounding matrix (Fig. 3) and number of rodent holes (Fig. 4). Bumble bee abundance positively associated with each of these variables. In 2004, abundance of bumble bees was again positively associated with number of rodent holes and openness of the surrounding matrix, but also positively associated with park elevation and negatively associated with park age ($F_{4,17} = 9.615$, $p = 0.001$, $r^2 = 0.670$). The regression lines for the plots of the openness of the surrounding matrix and rodent holes versus bumble bee abundance (Figs. 3 and 4) have slightly steeper slopes in 2004 than 2003.

3.3. Bumble bee species richness

The factors that associated with species richness of bumble bees differed between 2003 and 2004 (Table 1). In 2003, mean park elevation negatively associated with bumble bee species richness ($F_{1,17} = 6.524$, $p = 0.021$, $r^2 = 0.291$). In 2004, abundance

of *B. vosnesenskii* negatively associated with bumble bee species richness (Fig. 5) ($F_{1,17} = 10.425$, $p = 0.005$, $r^2 = 0.395$). In both years of the study, the presence of one species, *B. sitkensis* is negatively associated with the abundance of *B. vosnesenskii* (Cox and Snell $r^2 = 0.439$ and 0.560 , Table 1). The slope of the regression line between abundance of *B. vosnesenskii* and species richness is steeper in 2004 than 2003 (Fig. 5). The data did not show significant autocorrelation in 2003 ($r = 0.139$, $p = 0.8661$) or 2004 ($r = -0.155$, $p = 0.0787$).

4. Discussion

4.1. Is the current bumble bee community a subset of the historical community?

Bumble bees are disappearing from the city of San Francisco. Though we were unable to determine the sampling effort that

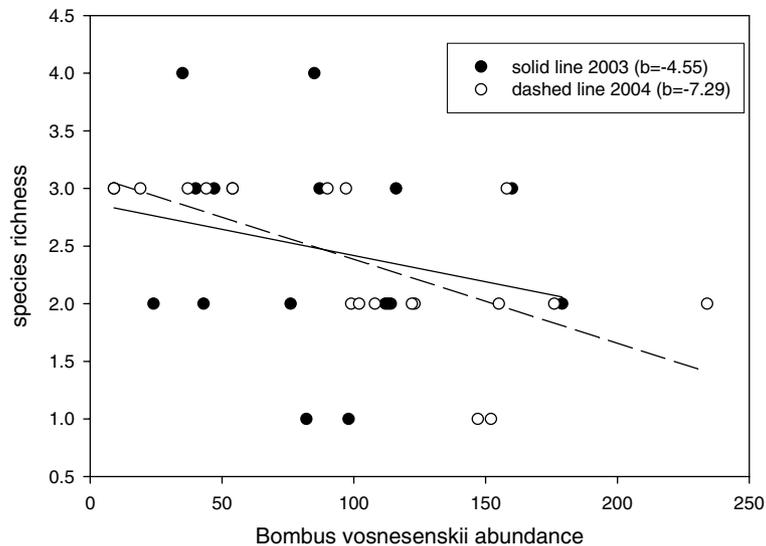


Fig. 5 – Simple linear regression of species richness of bumble bees and abundance of *Bombus vosnesenskii*.

went into the historical collections of *Bombus* in San Francisco, we detected less than half of the species represented in museums from collections conducted in San Francisco. We recorded bumble bees seen outside our plot before, during and after our sampling period and never saw a species not detected in a plot. In addition, none of our volunteer observers from within the city detected any of the absent species. We detected one of the missing species, *B. caliginosus*, on nearby San Bruno Mountain. Another missing species, *B. occidentalis*, was once common in San Francisco but recently suffered a population crash extending from California to southern British Columbia, possibly from the introduction of a protozoan disease from commercial *B. occidentalis* colonies (Thorp et al., 2003). The other three species; *B. rufocinctus*, *B. bifarius* and *B. (Psithyrus) insularis* have intact populations in other parts of California, but *B. rufocinctus* has not been reported in the Bay Area in recent years (R. Thorp, personal communication).

As predicted by recent studies of insect community assemblages (Tscharntke et al., 2002b), bumble bee species that are less represented in collections, and therefore less common, such as *B. caliginosus*, *B. rufocinctus*, and *B. bifarius*

(Thorp et al., 1983), are missing from San Francisco. Because these bumble bees are less common, they may be more difficult to detect. To estimate the likelihood of our sampling methods detecting these rare species, we obtained records of San Francisco collections from the California Academy of Sciences Department of Entomology and records of collections compiled by Dr. Robbin Thorp. We then compared the number of specimens of each species from each collection to our collection, to determine if we were able to detect the less common species (Table 2). Based on this comparison, we are confident that we should have detected *B. bifarius*, *B. caliginosus*, and *B. occidentalis* had they been present.

4.2. Which factors affect bumble bee abundance and species richness?

Area of the parks, distance to the nearest source population, and perimeter to area ratio did not predict bumble bee community structure in San Francisco's urban parks. Openness of the surrounding matrix positively associated with abundance of bumble bees, which suggests that the matrix

Table 2 – A comparison of records from San Francisco and two sites contiguous with San Francisco (San Bruno Mountain and Daly City) from Dr. Robbin Thorp and San Francisco collections from the California Academy of Sciences to records of San Francisco collections from this study

Bumble bee species	Previous records from San Francisco and surrounding area (from Thorp)	Previous records from San Francisco (from Cal. Academy)	Our San Francisco collections
<i>Bombus insularis</i>	64	0	0
<i>Bombus rufocinctus</i>	150	1	0
<i>Bombus californicus</i>	44	2	27
<i>Bombus caliginosus</i>	16	3	0
<i>Bombus bifarius</i>	9	9	0
<i>Bombus sitkensis</i>	23	14	37
<i>Bombus melanopygus edwardsii</i>	22	19	105
<i>Bombus occidentalis</i>	259	105	0
<i>Bombus vosnesenskii</i>	192	129	3665

provides resources that bumble bees can utilize or is traversable for bumble bees. The importance of the surrounding matrix suggests why area and distance to the nearest source population were not significant predictors. The parks do not represent islands surrounded by an inhospitable urban sea to the species persisting in San Francisco. The lack of any effect of perimeter to area ratio showed that bumble bees are neither edge adapted nor negatively affected by edge habitats or competitors that are edge adapted.

4.3. Bumble bee abundance

Bumble bee abundance was positively associated with the number of rodent holes and the openness of the surrounding matrix in both 2003 and 2004 (Table 1), and the association was stronger in 2004 than in 2003. The number of rodent holes represents the available nest resources available to ground nesting bumble bees. Parks with fewer rodent holes had fewer bumble bees, which suggests that bumble bees are nest site limited, as reported in a previous study (Richards, 1978). The openness of the surrounding matrix suggests that bumble bees are either able to find resources in the surrounding neighborhoods, as has been found in studies of bumble bees in gardens (Comba et al., 1999a; Comba et al., 1999b), or are able to more easily transit through neighborhoods with more open space. During this project, we received reports from the public of bumble bees using flowers in their yards and several reports of bumble bees nesting in backyards. This shows that the surrounding matrix does provide resources for bumble bees. It is not surprising that the proportion of park that is natural area had a positive relationship with bumble bee abundance, as this factor reflects the amount of the park that is not developed (Fig. 2). Parks with more natural area should offer more nest sites and floral resources than parks with less natural area, as has been found with field margins in agricultural settings (Carvell et al., 2004; Pywell et al., 2005). Interestingly, percentage of the park that is natural area was significant only in 2003. In 2004 the resources available in the surrounding matrix may have been more important.

4.4. Bumble bee species richness

Annual bumble bee species richness was predicted by different factors in different years (Table 1). In 2004, but not 2003, abundance of *B. vosnesenskii* negatively associated with bumble bee species richness (Fig. 5). While not a test of competition, this finding suggests that competition may be influencing community structure, and that *B. vosnesenskii* is the dominant competitor. The importance of interspecific competition in bumble bee community structure has been reported in other studies (Bowers, 1985b; Soltz, 1987). The differences in the 2 years may be explained by higher abundance of *B. vosnesenskii* in 2004. If we equalize sampling effort to include the same months in each year, we sampled 1573 *B. vosnesenskii* in 2003 and 1959 *B. vosnesenskii* in 2004. If we assume that abundance of all castes is correlated with abundance of starting queens in each year, our data would indicate that there were more founding queens present in 2004. Large numbers of

queens means that competition for nest sites in spring 2004 should have been higher than in spring 2003. If nest sites are a limiting resource for bumble bees, as suggested by the relationship between nest sites and bumble bee abundance, *B. vosnesenskii*, which emerges early in the season (Thorp et al., 1983; Q. McFrederick, personal observation), may monopolize nest sites early. In both years, *B. vosnesenskii* was negatively associated with abundance of one species, *B. sitkensis* (Table 1). If we again equalize sampling effort to include only the same months in both years, there was a loss of *B. sitkensis* abundance (18 in 2003 to 12 in 2004) and parks where *B. sitkensis* was recorded (six in 2003 to five in 2004).

The second most abundant bee in both years of the study, *B. melanopygus*, did not negatively associate with *B. vosnesenskii* abundance. The presence or absence of a specific floral resource may be more important than abundance of *B. vosnesenskii* in explaining abundance of *B. melanopygus*. *B. melanopygus* was recorded on *Ceanothus thrysiflorus* Eschsch. (Rhamnaceae) 23 times, which was 42% of the flower visitation records for *B. melanopygus*. In every plot that was sampled with flowering *C. thrysiflorus*, and on every mature, flowering *C. thrysiflorus* that was casually encountered outside of the plots, we detected *B. melanopygus*. The relationship between this floral resource and *B. melanopygus* merits further study. *B. melanopygus* is known to nest in both rodent holes and abandoned bird nests (Thorp et al., 1983), and may be able to avoid nest site competition with *B. vosnesenskii* by using bird nests. *B. californicus* was found in such low numbers ($n = 27$) that we were unable to detect important factors for this species.

4.5. How does the urban community compare to the community from wilder parks?

We did not sample enough wild parks ($n = 2$) to conduct statistical tests on the differences between urban and wilder parks, but the data makes for interesting comparisons. The urban parks had higher mean abundances of bees than the two wilder parks in both 2003 and 2004, although the difference was greater in 2003 (Table 3). This difference could be due to the concentration of resources and, therefore, bees in urban parks, or because the surrounding urban matrix offers resources to bumble bees. Backyard gardens can be important floral resources to bumble bees, so it is possible that bumble bees are truly more abundant in urban parks than in nearby, wilder parks (Comba et al., 1999a; Comba et al., 1999b; Goulson et al., 2002). In a Mediterranean climate such as San Francisco, gardens can provide resources in the dry summer that would be sparser in wilder areas. It is likely that the

Table 3 – Comparison of bumble bee abundance and species richness of bumble bees in urban parks to nearby large, wilder parks (San Bruno Mountain and Sweeny Ridge)

Year	San Bruno	Sweeny Ridge	Urban parks
2003 abundance	47	56	Mean of 86.5
2003 sp. richness	3 species	1 species	1–3 species/park
2004 abundance	75	99	Mean of 107
2004 sp. richness	4 species	1 species	1–4 species/park

proportion of the matrix surrounding the parks that is open space was a significant predictor of bumble bee abundance in part due to greater floral resources found in less densely developed neighborhoods.

Urban parks were as diverse as the nearby wilder parks, which suggests that the decline in bumble bee diversity may not be limited to densely urban areas, but includes nearby, wilder areas. Surveys conducted by Dr. Robbin Thorp on San Bruno Mountain in 1960 and 2001 show a loss of three *Bombus* species and a decline in abundance of a fourth species (R. Thorp, personal communication), which provides support for this claim. Wilder parks were as dominated by *B. vosnesenskii* as urban parks (Table 3). The two wilder parks are larger than any of the city parks, but are still within the urban envelope, though not as densely urban as San Francisco. It is possible that the effects of urbanization reach into these large parks. Samples from Napa and Sonoma counties, which are adjacent to San Francisco but less developed, are not as dominated by *B. vosnesenskii* (LeBuhn, personal observation), which suggests that there may be a threshold of urbanization that must be crossed to bring about the dominance of *B. vosnesenskii*.

4.6. Can urban parks be designed to act as refuges for pollinators?

If land-use managers are interested only in increasing abundance of bumble bees, parks with high proportion of natural area and many rodent holes situated in neighborhoods with greater amounts of open space will make the best refuges. Most managers, however, will be concerned with maximizing the species richness of the bumble bee community, both for maintenance of diversity and bumble bee pollination services for habitat restoration efforts. Be-

cause of the dominance of *B. vosnesenskii*, refuges designed to maximize species richness may have to minimize the possible negative impact of *B. vosnesenskii* on *B. sitkensis* and provide plants attractive to *B. melanopygus*. The best refuges for the bumble bee community may need to have middle range values of the factors that influence abundance in order to mitigate the possible competitive effect of *B. vosnesenskii*: openness of the surrounding matrix, proportion natural area and number of rodent holes. They will also provide plants attractive to *B. melanopygus*, *B. sitkensis* and *B. californicus*. This should maximize the species richness of the bumble bee communities.

Rosenzweig (2001) proposed that, to slow the loss of biodiversity, conservation biologists should look at anthropogenic habitats and identify ways that these habitats can be modified to be useful to the organisms that occurred there before development. He calls this approach reconciliation ecology. One of the main ideas behind reconciliation ecology is that we can return organisms to their native ranges without removing humans from the landscape. This idea can be neatly applied to the parks in San Francisco, and this project is the first step in showing how parks can be designed to provide refuges for pollinators. The next step is to identify the factors that are important to the extirpated species.

Acknowledgements

We thanks: E. Connor, J. Hafernik, T. Roulston, E. Julier, J. Cleaves, E. Rentz, and R. Thorp. We also thank Ben and Dolores McFrederick for support; the Natural Areas Program, for data and support and all of the backyard bumble bee monitors. In addition, we thank J. Chaves, S. Chess, C. Fenter, M. Reynolds, S. Simono, E. Swinney and four anonymous reviewers for comments on earlier drafts.

Appendix 1. San Francisco Parks included in this study and coordinates for each park

Park	Size of park (ha)	Size of natural area (ha)	% Park that is natural area	Park coordinates
Bayview	45.97	17.52	38.1	37°42'54", 122°23'35"
Hawk hill	2.83	1.82	64.3	37°44'48", 122°28'04"
McLaren	158.64	68.63	43.3	37°43'05", 122°25'10"
Mt. Davidson	17.81	16.23	91.2	37°44'19", 122°27'19"
Twin Peaks	26.06	19.67	75.5	37°45'09", 122°26'51"
Glen Canyon	41.93	24.08	57.4	37°44'27", 122°27'19"
Bernal Hill	12.91	10.44	80.9	37°44'35", 122°24'50"
Brooks Park	1.86	0.73	39.1	37°43'02", 122°28'00"
Buena Vista Park	15.05	4.9	32.5	37°46'06", 122°26'30"
Corona Heights	7.41	3.97	53.6	37°45'53", 122°26'18"
Duncan/Castro	0.32	0.16	50	37°44'45", 122°26'00"
Golden Gate Heights	3.12	0.32	10.4	37°44'59", 122°28'10"
India Basin	6.92	0.69	9.9	37°44'06", 122°22'32"
Pine Lake	29.54	3.44	11.6	37°44'10", 122°28'54"
Rock Outcrop	1.21	0.57	46.7	37°45'16", 122°28'16"
Tank Hill	1.34	1.17	87.9	37°45'34", 122°26'52"
Edgehill	4.61	0.49	10.5	37°44'31", 122°27'34"
Mountain Lake	5.58	0.2	3.6	37°47'13", 122°28'12"

Appendix 2. Abundance of each species found per park in 2003 and 2004

Year	Californicus		Caliginosus		Melanopygus		Sitkensis		Vosnesensk II		Grand total	
	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004
			Park									
Bayview		1	1	2					113	97	114	100
Bernal Heights	1		1	4					160	176	162	180
Brooks Park	5	7	2	7					87	158	94	172
Buena Vista			5	9			2	1	40	54	47	64
Corona Heights	1			3					112	99	113	102
Duncan Castro			25	7					114	108	139	115
Edgehill				1			1	6	24	19	25	26
Glen Park	1	1	1	1			1		85	90	88	92
Golden Gate Heights			1	2			8	2	54	155	63	159
Hawk Hill			4	1				1	179	123	183	125
India Basin	1	4	7						47	102	55	106
McLaren		1	1	1					43	44	44	46
Mountain Lake	1		2	7			2	1	35	37	40	45
Mt. Davidson			1					1	76	122	77	123
Pine Lake			2	1			4	7	9	9	15	17
Rock Outcrop				4					98	234	98	238
San Bruno	1	1		1	3	6			43	67	47	75
Sweeny Ridge									56	99	56	99
Tank Hill	1		1						116	152	118	152
Twin Peaks									82	147	82	147
Grand total	12	15	54	51	3	6	18	19	1573	2092	1660	2183

REFERENCES

- Baum, K.A., Haynes, K.J., Dillemoth, F.P., Cronin, J.T., 2004. The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* 85, 2671–2676.
- Benet, J., 1966. *A Guide to San Francisco and The Bay Region*. Random House, New York.
- Bolger, D.T., Suarez, A.V., Crooks, K.R., Morrison, S.A., Case, T.J., 2000. Arthropods in urban habitat fragments in southern California: Area, age, and edge effects. *Ecological Applications* 10, 1230–1248.
- Bowers, M.A., 1985a. Bumble bee colonization, extinction and reproduction in subalpine meadows in northeastern Utah. *Ecology* 66, 914–927.
- Bowers, M.A., 1985b. Experimental analyses of competition between two species of bumble bees (Hymenoptera: Apidae). *Oecologia* 67, 224–230.
- Bradley, G., 1995. *Urban Forest Landscapes: Integrating Multidisciplinary Perspectives*. University of Washington Press, Seattle.
- Cane, J.H., 2001. Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* 5. Art. No. 3.
- Cane, J., 2005. Bees needs challenged by urbanization. In: Johnson, A.J., Klemens, M.W. (Eds.), *Nature in Fragments: The Legacy of Sprawl*. Columbia University Press, New York.
- Cavalcanti, M.J., 2005. Mantel for Windows version 1.18. Available from: <<http://life.bio.sunysb.edu/morph/soft-mult.html>>.
- Carvell, C., 2002. Habitat use and conservation of bumble bees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation* 103, 33–49.
- Carvell, C., Meek, W.R., Pywell, R.F., Nwadowski, M., 2004. The response of foraging bumblebees to successional change in newly created arable field margins. *Biological Conservation* 118, 327–339.
- Comba, L., Corbet, S.A., Barron, A., Bird, A., Collinge, S., Miyazaki, N., Powell, M., 1999a. Garden flowers: insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany* 83, 73–86.
- Comba, L., Corbet, S., Hunt, L., Warren, B., 1999b. Flowers, nectars and insect visits: Evaluating British plant species for pollinator friendly gardens. *Annals of Botany* 83, 369–383.
- Connor, E.F., Hafernik, J., Levy, J., Moore, V.L., Rickman, J.K., 2002. Insect conservation in an urban biodiversity hotspot: the San Francisco Bay Area. *Journal of Insect Conservation* 6, 247–259.
- Czech, B., Krausman, P.R., Devers, P.K., 2000. Economic associations among causes of species endangerment in the United States. *Bioscience* 50, 593–601.
- Dramstad, W.E., 1996. Do bumble bees (Hymenoptera: Apidae) really forage close to their nests? *Journal of Insect Behavior* 9, 163–182.
- EIP Associates, 2002. *Significant Natural Resource Areas Management Plan*. E.I.P. Associates, San Francisco.
- Faeth, S.H., Kane, T.C., 1978. Urban Biogeography: city parks as islands for Diptera and Coleoptera. *Oecologia* 32, 127–133.
- Fernandez-Juricic, E., Jokimaki, J., 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity and Conservation* 10, 2023–2043.
- Frankie, G., Thorp, R.W., Schindler, M.H., Ertter, B., Przybylski, M., 2002. Bees in Berkeley? *Fremontia* 30, 41–49.
- Goulson, D., Hughes, W.O.H., Derwent, L.C., Stout, J.C., 2002. Colony growth of the bumble bee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia* 130, 267–273.

- Goulson, D., 2003. *Bumblebees: Their Behaviour and Ecology*. Oxford University Press, New York.
- Inouye, D.W., 1978. Resource partitioning in bumble bees: experimental studies of foraging behavior. *Ecology* 59, 672–678.
- Jenness, J., 2004. Nearest features (nearfeat.avx) extension for ArcView 3.x, v. 3.7. Jenness Enterprises. Available from: http://www.jennessent.com/arcview/nearest_features.htm.
- Kearns, C.A., Thomson, J.D., 2001. *The Natural History of Bumble bees: A Sourcebook for Investigations*. University Press of Colorado, Boulder.
- Keyer, D., Oed, A., Walther-Hellwig, K., Frankl, R., 2004. Are forests potential landscape barriers for foraging bumble bees? landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascorum* (Hymenoptera, Apidae). *Biological Conservation* 116, 111–118.
- Klemm, N., 1996. Man-made bee habitats in the anthropogenous landscape of central Europe: substitutes for threatened or destroyed riverine habitats? In: Matheson, A., Buchmann, S.L., O'Toole, C., Westrich, P., Williams, I.H. (Eds.), *The Conservation of Bees*. Academic Press, London, UK.
- Koh, L.P., Sodhi, N.S., 2004. Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecological Applications* 14, 1695–1708.
- Laverty, T.M., Plowright, A.C., 1988. Flower handling by bumblebees a comparison of specialists and generalists. *Animal Behaviour* 36, 733–740.
- McIntyre, N.E., 2000. Ecology of urban arthropods; a review and call to action. *Annals of the Entomological Society of America* 93, 825–835.
- Meekins, J.F., McCarthy, B.C., 2001. Effect of environmental variation on the invasive success of a nonindigenous forest herb. *Ecological Applications* 11, 1336–1348.
- Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 36, 519–533.
- Pywell, R., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 121, 479–494.
- Ranta, E., Vepsäläinen, K., 1981. Why are there so many species? Spatiotemporal heterogeneity and northern bumblebee communities. *Oikos* 36, 28–34.
- Richards, K.W., 1978. Nest site selection by bumble bees (Hymenoptera: Apidae) in Southern Alberta Canada. *Canadian Entomologist* 110, 301–318.
- Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158, 87–100.
- Rickman, J.K., Connor, E.F., 2003. The effect of urbanization of the quality of remnant habitats for leaf-mining Lepidoptera on *Quercus agrifolia*. *Ecography* 26, 777–787.
- Rosenzweig, M.L., 2001. Loss of speciation rate will impoverish future diversity. *Proceedings of the National Academy of Sciences of the United States of America* 98, 1504–1510.
- Shapiro, A.M., 2002. The California urban butterfly fauna is dependent on alien plants. *Diversity and Distributions* 8, 31–40.
- Sklenar, P., Jorgensen, P.M., 1999. Distribution of páramo plants in Ecuador. *Journal of Biogeography* 26, 681–691.
- Sokal, R.R., Rohlf, F.J., 2000. *Biometry: the Principles and Practice of Statistics in Biological Research*. Freeman, New York.
- Soltz, R.L., 1987. Interspecific competition and resource specialization between bumble bees. *Southwestern Naturalist* 31, 39–52.
- Steffan-Dewenter, I., Tschardt, T., 2000. Butterfly community structure in fragmented habitats. *Ecology Letters* 3, 449–456.
- Steffan-Dewenter, I., 2002. Landscape context affects trap-nesting bees, wasps and their natural enemies. *Ecological Entomology* 27, 631–637.
- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tschardt, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Steffan-Dewenter, I., 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology* 17, 1036–1044.
- Thomas, C.D., 2000. Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London* 267, 139–145.
- Thorp, R.W., Horning, D.S., Dunning, L.L., 1983. *Bumble bees and Cuckoo Bumble bees of California*. University of California Press, Berkeley.
- Thorp, R.W., Schroeder, P.C., Ferguson, C.S., 2003. Bumble bees: boisterous pollinators of native California flowers. *Fremontia* 30, 26–31 [Jul/Oct 2002 distributed May 2003].
- Tschardt, T., Steffan-Dewenter, I., Kruess, A., Thies, C., 2002a. Contribution of small habitat fragment to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications* 12, 354–363.
- Tschardt, T., Steffan-Dewenter, I., Kruess, A., Thies, C., 2002b. Characteristics of insect populations on habitat fragments, a mini review. *Ecological Research* 17, 229–239.
- USDA, 2000. *Natural Resources Inventory Summary Report*, USDA.
- Westrich, P., 1996. Habitat requirements of central European bees and the problems of partial habitats. In: Matheson, A., Buchmann, S., O'Toole, C., Westrich, P., Williams, I.H. (Eds.), *The Conservation of Bees*. Academic Press, London, pp. 2–16.
- Williams, N.M., Minckley, R.L., Silveira, F.A., 2001. Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology* 5, Art. No.-7.
- Zanette, L.R.S., Martins, R.P., Ribeiro, S.P., 2005. Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape and Urban Planning* 71, 105–121.
- Zar, J.H., 1999. *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, New Jersey.

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Corrigendum

Corrigendum to “Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)?” [Biol. Conserv. 129 (2006) 372–382]

Quinn S. McFrederick *, Gretchen LeBuhn

San Francisco State University, Department of Biology, 1600 Holloway Avenue, San Francisco, CA 94132-1722, United States

In the May 2006 issue of *Biological Conservation*, the article entitled “Are Urban Parks Refuges for Bumble Bees *Bombus* spp. (Hymenoptera: Apidae)?,” by McFrederick and LeBuhn (129: 372–382), includes two errors. In Fig. 4, the data are plotted on the wrong axes. See the corrected Fig. 4 below. The interpretation of Fig. 4 in the text holds, as the strength of the asso-

ciations between bumble bee abundance and rodent holes are similar in the uncorrected and corrected graphs. In appendix two the column headings include the following errors: the column titled *Caliginosus* is *Melanopygus*, the column titled *Melanopygus* is *Caliginosus* and the column titled *Vosnesenskii* is *Vosnesenskii*. The authors apologize for these errors.

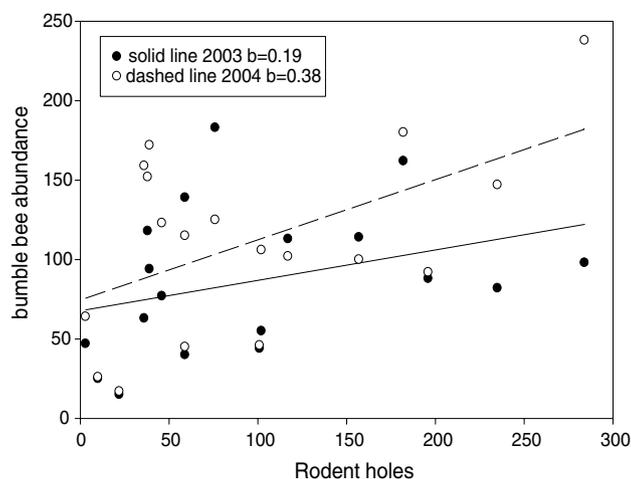


Fig. 4 – Simple linear regression of abundance of bumble bees and number of rodent holes.

DOI of original article: 10.1016/j.biocon.2005.11.004.

PII of original article: S0006-3207(05)00481-7.

* Corresponding author: Tel.: +1 434 924 6846.

E-mail address: qsm5a@virginia.edu (Q.S. McFrederick).

0006-3207/\$ - see front matter © 2006 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2006.05.014