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Permalink

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Journal

Environmental entomology, 46(6)

ISSN

0046-225X

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Publication Date

2017-12-01

DOI

10.1093/ee/nvx155

Peer reviewed

Pollinator Ecology and Management

Vegetation Management and Host Density Influence Bee–Parasite Interactions in Urban Gardens

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Subject Editor: Gloria DeGrandi-Hoffman

Received 17 April 2017; Editorial decision 28 August 2017

Abstract

Apocephalus borealis phorid flies, a parasitoid of bumble bees and yellow jacket wasps in North America, was recently reported as a novel parasitoid of the honey bee *Apis mellifera* Linnaeus (Hymenoptera: Apidae). Little is known about the ecology of this interaction, including phorid fecundity on bee hosts, whether phorid-bee parasitism is density dependent, and which local habitat and landscape features may correlate with changes in parasitism rates for either bumble or honey bees. We examined the impact of local and landscape drivers and host abundance on phorid parasitism of *A. mellifera* and the bumble bee *Bombus vosnesenskii* Radoszkowski (Hymenoptera: Apidae). We worked in 19 urban gardens along the North-Central Coast of California, where phorid parasitism of honey bees was first reported in 2012. We collected and incubated bees for phorid emergence, and surveyed local vegetation, ground cover, and floral characteristics as well as land cover types surrounding gardens. We found that phorid parasitism was higher on bumble bees than on honey bees, and phorids produced nearly twice as many pupae on individual bumble bee hosts than on honey bee hosts. Parasitism of both bumble and honey bees increased with abundance of honey bees in a site. Differences in landscape surroundings did not correlate with parasitism, but local factors related to bee resource provisioning (e.g., tree and shrub abundance) positively correlated with increased parasitism. This research thus helps to document and describe conditions that may have facilitated phorid fly host shift to honey bees and further elucidate how resource provisioning in urban gardens influences bee–parasite interactions.

Key words: *Apocephalus borealis*, California, urban agriculture, insect–parasite interaction, bee decline

Honey and bumble bee populations are declining in several regions, with negative implications for ecosystem services (Potts et al. 2010). In 2014–2015, commercial beekeepers lost 42.1% of managed honey bee (*Apis mellifera* Linnaeus [Hymenoptera: Apidae]) hives, an increase from the losses of 2013–2014 and the second highest annual loss to-date (USDA 2015). Bee decline is troublesome because bees are critical pollinators in many agricultural ecosystems, with 35% of global crops depending on pollination (Klein et al. 2007). With the mounting concern around honey bee losses, many have looked to wild and domesticated bee species (such as bumble bees, *Bombus* spp.) for insurance against pollination losses (Buchmann and Nabhan 2012). Domesticated bumble bees are widely used in commercial agriculture and for some crops are more efficient pollinators than honeybees (e.g., Stubbs and Drummond 2001, Li et al. 2006). However, bumble bee populations are also declining. In Europe, many bumble bee species have experienced range contractions and localized extinctions (Kosior et al. 2007, Goulson et al. 2008). In North America, formerly abundant and widespread bumble bee species have declined since the late 1990s, with some species presumed extinct (Williams and Osborne 2009, Grixti et al. 2009). There is also evidence of bumble

bee population decline and species richness loss in South America (Schmid-Hempel et al. 2014), China (Xie et al. 2008, Williams et al. 2009), and Japan (Matsumura et al. 2004, Inoue et al. 2008).

Bumble bee and honey bee decline can be attributed to an overlapping set of stressors including parasites, pathogens, and land-use change (Grixti et al. 2009, Potts et al. 2010, Goulson et al. 2015). Bees host a broad range of parasites and parasitoids that can negatively affect their populations. Several parasites (including *Nosema* spp., *Apicystis bombi*, and *Crithidia* spp.) are implicated in the decline of honey bees and commercial *Bombus terrestris* (Cameron et al. 2011, Graystock et al. 2013). While honey bee parasites have received attention for their role in colony loss (e.g., Cox-Foster et al. 2007, Nazzi et al. 2012), our knowledge of parasites and parasitoids for wild bee species is more limited. Nevertheless, information about honey bee parasites and parasitoids may be relevant to understanding wild bumble bee declines because many honey bee parasites such as *Nosema ceranae* (Graystock et al. 2013) infect both honey bees and bumble bees (Fürst et al. 2014, McMahon et al. 2015). Furthermore, infection by parasites and parasitoids has been shown to impact bumble bee foraging patterns, behavior, and physiology

(König and Schmid-Hempel 1995, Müller 1994, Schmid-Hempel and Schmid-Hempel 1998).

In addition, land-use change at local and landscape scales may negatively impact bee populations. Several qualitative syntheses suggest that agricultural intensification and habitat fragmentation negatively affect bee abundance and diversity (e.g., Ricketts et al. 2008, Winfree et al. 2009). This is because changes in urban cover, natural woodlands, or open space within a landscape, as well as changes in vegetation structure within a site, can alter the habitat and food resources available to bees with population-level impacts (Kremen et al. 2007). Interactions between land-use change and parasites and pathogens may be important for bee decline (Paxton et al. 2016, Botías et al. 2017). When landscape processes such as urbanization or conversion of natural habitat to intensive agriculture alter the availability of food and habitat resources of a host, there can be one of two outcomes for parasitism: dilution or amplification (Becker et al. 2015). Dilution may occur when land-use change increases the quality and quantity of food and habitat resources for a host, resulting in higher immunity or defense against parasitism. Amplification may occur if increase in resources in the landscape results in host aggregation, increasing parasite transmission between individuals (Becker et al. 2015). Resource mediated dilution has been observed in lace monitor reptiles for which increased access to urban waste improves nutrition and lowers parasite intensity (Jessop et al. 2012), in long-tailed macaques with higher access to nutrition and lower *Giardia* infection (Lane et al. 2011), and in other non-arthropod systems (Becker et al. 2015). Amplification due to resource provisioning has been observed for infection of Elk by *Brucella abortus* (Cross et al. 2007) and infection of white-tailed deer by *Mycobacterium bovis* (Miller et al. 2003). Yet, very little is known about how resource or habitat changes alter bee–parasite interactions.

Urban gardens provide a unique environment to study how land use change and parasitism influence bees. Urban spaces are characterized by increases in impervious cover, structural simplification of vegetation, and a heterogeneous mosaic of land-use (Marzluff and Ewing 2001, Thompson et al. 2003). However, local and landscape features of urban gardens provide habitat and food resources for biodiversity, supporting pollinator populations and other beneficial insects (Goddard et al. 2010). Across multiple studies, floral abundance and richness in urban gardens promotes higher bee diversity (Tommasi et al. 2004, Wojcik et al. 2008, Pardee and Philpott 2014, Quistberg et al. 2016). In a review of urban bee ecology, Hernandez et al. (2009) found a negative correlation between bee species and urban development, although the effect of landscape variation can differ across scales (Pardee and Philpott 2014, Quistberg et al. 2016). These local and landscape characteristics of urban gardens may also impact insect–parasite and insect–parasitoid interactions. Urbanization-mediated resource shifts may result in changes to parasite and host geographic ranges and population densities, potentially leading to the emergence of key parasites and parasitoids, altered behavior for hosts, parasites, and parasitoids, and potentially higher infection rates (Bradley and Altizer 2007, Keesing et al. 2010, Becker et al. 2015). If urbanization results in biodiversity losses, shifts in species composition may also influence parasitism.

Here, we investigate parasitism of bees by *Apocephalus borealis* (Diptera: Phoridae), a phorid fly native to North America (Brown 1993). *A. borealis* phorids can reduce bee worker lifespan by up to 70% in the native host, the bumble bee (*Bombus* spp.) (Otterstatter et al. 2002). It is also a native parasitoid of the yellow jacket wasp (*Vespa* spp.) (Ennik 1973). Phorids in the genus *Apocephalus* are called ‘decapitating flies’ and commonly have host associations with ant species (Brown 1997). Recently, researchers documented

A. borealis phorids parasitizing honey bees (*A. mellifera*), a novel host–parasitoid interaction (Core et al. 2012). Phorid-infected honey bees are described as ‘zombie bees’ because they may show hive abandonment behavior at night. Multiple phorid larvae develop from each bee host, feeding on thoracic flight muscle (Ennik 1973). Larvae then emerge to pupate, although this has only been observed in vitro (Core et al. 2012). The dispersal range of *A. borealis* is unknown, although phorid in the genus *Pseudacteon* have been shown to disperse 650 m away from hosts (Morrison et al. 1999). Research on phorid parasitism of honey bees and bumble bees is limited to a few studies examining prevalence and mortality rates in bees (e.g., Core et al. 2012, Otterstatter et al. 2002) and an on-going citizen science project (zombeewatch.org) examining the distribution of phorid parasites in bees across the United States.

One of the unknowns about phorid–bee interactions is whether honey bees are a native host previously undiscovered for *A. borealis* or whether *A. borealis* phorid flies have recently extended their host range to include honey bees. Understanding host choice is important because changes in host size for other arthropod parasites influences behavioral, morphological, and life history traits of the parasitoid (Messina 2004). Another unknown about this system is whether parasitism is spatially density dependent. While it is commonly assumed that parasitism rate and host density are positively correlated, this is not always the case because of limits to parasitoid ability to search for and handle hosts (Walde and Murdoch 1988). Understanding the ecology of this novel parasitoid–host system is important for diagnosing what factors mediate parasitism rates in vulnerable bee populations.

In this study, we examined bee–phorid interactions in an array of urban gardens that differ in bee abundance, local habitat conditions, and landscape surroundings. We examined if bee abundance influences parasitism by the phorid fly. We also asked if parasitized honey bees are host to a greater number of phorid pupae than bumble bees. To determine if resource provisioning influences parasitism rates, we examined the influences of local vegetation change and landscape-level land-cover change on parasitism of *A. mellifera* and *B. vosnesenskii* by phorid parasitoids. For some phorid–host interactions (e.g., with ant hosts), effects on hosts may differ with land-use change (e.g., agricultural management) (Pardee and Philpott 2011, De la Mora et al. 2015), but little is known about how land-use change may alter bee–phorid interactions, specifically. We asked, 1) Does the number of pupae emerging from *A. mellifera* and *B. vosnesenskii* individuals differ? 2) How do parasitism rates of *A. mellifera* and *B. vosnesenskii* differ depending on the abundance of honey bees and bumble bees within garden sites? 3) Which local and landscape level factors influence parasitism rates in honey bees and bumble bees? We expected more pupae in *B. vosnesenskii* hosts because they are large-bodied bees, and a native host of the phorid. We expected more phorid infection in sites with more honey bees and bumble bees because phorids and other parasitoids often exhibit density dependence with hosts (e.g., Philpott et al. 2009). Finally, we expected lower phorid parasitism in sites with higher local vegetative diversity and lower urban landscape cover due to potential nutrition benefits to bees and subsequent dilution effects.

Materials and Methods

Characterization of the Study Sites

Between June and October 2014, we examined local and landscape characteristics of 19 urban gardens, ranging in size from 444 m² to 15,525 m², each separated by 2 km, across three counties (Monterey,

Fig. 1. Map of urban garden field sites in along the central coast of California. Each dot represents an urban garden field site in which there was no parasitism, parasitism of *A. mellifera* bees, or parasitism of *B. vosnesenskii*.

Santa Clara, and Santa Cruz) in the California central coast (Fig. 1). We measured local habitat characteristics (e.g., vegetation and ground cover) five times within a 20 × 20 m plot placed at the center of each garden. We measured canopy cover with a convex spherical densitometer at the center of the plot, and 10 m to the N, S, E, and W. We counted and identified all trees and shrubs and noted the number of individuals in flower. In each plot, we randomly selected four 1 × 1 m plots within which we identified all herbaceous plants (except grasses) to morphospecies, measured the height of the tallest non-woody vegetation, counted flowers, and assessed percent ground cover from bare soil, grass, herbaceous plants, leaf litter, rocks, and mulch. In a 100 × 100 m plot surrounding each garden, we counted all trees and quantified percent area with concrete and buildings, mulch, lawn, woody vegetation, weedy or non-woody vegetation, and bare ground. For analysis, values were averaged across the five sample dates. We also estimated the total garden size. Overall, we measured 21 local habitat variables (Table 1).

At the landscape scale, we classified land cover types within 2 km buffers surrounding each garden with data from the 2011 National Land Cover Database (NLCD, 30 m resolution) (Homer et al. 2015). We selected 2 km buffers as most bees forage within 2 km from a nesting site (Kremen et al. 2004). While honey bees have a large maximum foraging distance, foraging distance varies as a function of landscape context (Steffan-Dewenter and Kuhn 2003) and mean

foraging distances for honey bees have been reported at approximately 1 (Waddington et al. 1994, Beekman and Ratnieks 2000, Schneider and Hall 1997) and 2.3 km (Visscher and Seeley 1982). *B. vosnesenskii* has a predicted maximum foraging distance of 2.1 km (Greenleaf and Kremen 2006), and some fly parasitoids in the family Phoridae are known to disperse under 1 km (Morrison et al. 1999). We created four land-use categories: 1) natural habitat (deciduous [NLCD number 41], evergreen [42], and mixed forests [43], dwarf scrub [51], shrub/scrub [52], and grassland/herbaceous [71]), 2) open (lawn grass, parks, and golf courses [21]), 3) urban (low [22], medium [23], and high intensity developed land [24]), and 4) agriculture (pasture/hay [81] and cultivated crop [82]). Other land cover types covered <5% of the total area and were not included. We assessed land cover with spatial statistics tools in ArcGIS v. 10.1.

Bee Collection and Parasitism Assessment

We collected bees (*B. vosnesenskii* and *A. mellifera*) at each site and incubated bees in the lab to assess phorid emergence. We netted bees along walking transects in 20 × 20 m plots (and within 20 m of plots) for 30 min every 3 wk between mid-June and early-October 2014, for a total of six sampling periods. Bees were captured alive, placed in individual rearing containers, and observed for pupae to determine parasitism. Bees were held at in terrariums under heat lamps between

Table 1. Results of Pearson's correlations showing groups of explanatory variables, variables selected for GLM analysis, and variables correlated ($P < 0.01$) with selected variables ($n = 19$).

Group	Selected variables	Correlated variable ($P < 0.01$)	Correlation coefficient	Direction of Correlation
Ground cover (20 × 20 m plots)	Grass	NA	NA	NA
	Litter	NA	NA	NA
Ground cover (100 × 100 m plots)	Concrete and buildings	Weedy, non-woody vegetation	0.684	-
		Mulch	0.561	-
	Lawn	NA	NA	NA
	Bare	NA	NA	NA
	No. trees and shrubs (20 × 20 m plot)	Canopy cover	0.919	+
Tree and shrub characteristics		No. tree and shrub species (20 × 20 m plot)	0.793	+
		No. trees and shrubs in flower (20 × 20 m plot)	0.83	+
		No. trees and shrubs (100 × 100 m plot)	0.597	+
		Woody cover (100 × 100 m plot)	0.632	+
Landscape characteristics	Natural 2 km	Urban 2 km	0.912	-
		Open 2 km	0.777	-
Non-grouped characteristics	Agriculture 2 km	NA	NA	NA
	No. of flowers	NA	NA	NA
	Height of tallest vegetation	NA	NA	NA
	Herbaceous plant richness (crops, weeds, ornamentals)	NA	NA	NA
	Garden size	NA	NA	NA

72 and 74°F and monitored daily for 10 d for phorid emergence. We recorded number of pupae that emerged from each infected bee.

Data Analysis

Because many explanatory variables measured may be correlated, we divided most variables into four biologically relevant groups (ground cover in 20 × 20 m plots, ground cover in 100 × 100 m plots, tree and shrub characteristics, and landscape characteristics) and ran Pearson's correlations to identify correlated ($P < 0.01$) variables within groups. We selected variables that were correlated with the largest number of other variables in that group for subsequent analysis (Table 1). Four variables (number of flowers, height of tallest vegetation, herbaceous plant richness, and garden size) were not put into any group, and were also included. In all, we included 10 local vegetation variables and two landscape variables for subsequent analyses.

In order to examine differences in the number of pupae emerging from honey bees and bumble bees, we compared the mean number of pupae per parasitized individual with t -tests assuming unequal variance in Excel. In order to examine density dependence of phorid infection, we fit linear models using the `lm` function in R. To examine the relationship between sampling period and phorid infection, we fit a generalized linear mixed model of infection rates with site as a random effect and sampling period as a fixed effect using the `glmer` function using the `lme4` package in R. Because the data were not normally distributed, we used the `cbind` function, a binomial error distribution, and logit link (Warton and Hui 2011). For the local and landscape features, we did not include sampling period in our model because changes over the summer in vegetation at the field sites did not change drastically.

We used generalized linear models (GLMs) with the `glm` function in R (Team RC 2014) to examine relationships between bee abundance (*A. mellifera* and *B. vosnesenskii* abundance) in selected site variables (local variables, landscape variables) and the percent of *A. mellifera* and *B. vosnesenskii* infected by *A. borealis* phorids at each site. When the percent of individual individuals of each bee was averaged across time periods, the data were normally distributed. We tested all combinations of the 14 selected variables with the 'glmulti' package (Calcagno and de Mazancourt 2010) and selected the top model based on the AICc values. For models where the AICc for top models was within 2 points of the next best model, we ran model averages with the MuMIn package (Barton 2012). For both *A. mellifera* and *B. vosnesenskii*, the best models shared the same significant predictors as model averages, and thus we report output from best models only. Dependent and predictor variables were normally distributed, so we used a Gaussian error structure for GLMs, and report AICc values, and P -values. To determine the goodness-of-fit of the best models, we calculated a pseudo- R^2 value as [(null deviance – residual deviance)/null deviance] (Dobson and Barnett 2008). All residuals from best models conformed to the conditions of normality as checked with QQ-Plots and Shapiro–Wilk tests.

Results

Phorids were more likely to parasitize bumble bees and bumble bees supported higher pupae loads. Of the 1819 *A. mellifera* individuals we collected, 30 were parasitized. Of the 290 *B. vosnesenskii* individuals we collected, 17 were parasitized. Across all garden sites, an average of $0.77\% \pm 0.33$ (SE) *A. mellifera* and $4.53\% \pm 1.99$ *B. vosnesenskii* individuals were parasitized. Of all urban garden

Table 2. The mean and standard deviation of infection rate for each species by garden site

Garden	County	Honey bee		Bumble bee	
		Mean (%)	SD	Mean (%)	SD
Garden 1	Santa Cruz	1.866	3.188	0.000	0.000
Garden 2	Santa Cruz	1.111	2.485	0.000	0.000
Garden 3	Santa Cruz	4.505	3.184	26.111	37.536
Garden 4	Santa Cruz	3.687	5.200	7.176	13.712
Garden 5	Santa Cruz	1.754	3.923	19.444	36.536
Garden 6	Santa Cruz	4.627	4.402	19.697	36.521
Garden 7	Santa Cruz	0.000	0.000	0.000	0.000
Garden 8	Santa Cruz	0.000	0.000	0.000	0.000
Garden 9	Monterey	2.924	3.269	2.778	6.211
Garden 10	Monterey	0.000	0.000	0.000	0.000
Garden 11	Monterey	0.000	0.000	0.000	0.000
Garden 12	Monterey	0.000	0.000	0.000	0.000
Garden 13	Monterey	0.000	0.000	0.000	0.000
Garden 14	Monterey	0.000	0.000	0.000	0.000
Garden 15	Santa Clara	0.000	0.000	0.000	0.000
Garden 16	Santa Clara	0.000	0.000	0.000	0.000
Garden 17	Santa Clara	0.000	0.000	0.000	0.000
Garden 18	Santa Clara	0.000	0.000	0.000	0.000
Garden 19	Santa Clara	0.000	0.000	0.000	0.000

Garden sites are numbered 1–19 to maintain confidentiality.

sites sampled, 37% contained parasitized honey bees and 21% contained parasitized bumble bees. Infected bees were found in coastal sites in Monterey and Santa Cruz county, but not present in inland sites in Santa Clara County (Fig. 1; Table 2). When site was taken into account as a random factor, however, sampling period had no impact on infection rates for honey bees ($z = 1.46$, $P = 0.14$) and bumble bees ($z = -0.271$, $P = 0.79$). There were nearly twice as many pupae per bumble bee (7.26 ± 0.87 SE) than per honey bee (4.23 ± 0.46 SE) in the parasitized individuals collected ($t = 3.076$, $P = 0.0046$).

Phorid parasitism in both *A. mellifera* ($P = 0.00081$) and *B. vosnesenskii* ($P = 0.012$) increased with the abundance of *A. mellifera* in a site. In contrast, phorid parasitism did not differ with increasing *B. vosnesenskii* abundance for either *A. mellifera* or *B. vosnesenskii* ($P < 0.05$).

Parasitism of both species of bees responded to local, but not landscape variables. The model that best predicted *A. mellifera* parasitism included garden size, the number of trees and shrubs, the percent lawn within a 100×100 m plot, the average percent of bare soil in 20×20 m plots, and the average abundance of *B. vosnesenskii* collected per sampling period (AICc = 35.86, df = 18, pseudo- $R^2 = 0.945$). Parasitism of *A. mellifera* was higher in gardens with more trees and shrubs ($P < 0.0001$) in larger gardens ($P < 0.0001$), with more lawn ($P = 0.005$), in gardens with less bare soil ($P = 0.004$), and in gardens with lower *B. vosnesenskii* abundance ($P = 0.001$) (Fig. 2). The model that best predicted *B. vosnesenskii* parasitism included the number of trees and shrubs and percent of bare soil in 20×20 m plots (AICc = 128.265, df = 18, pseudo- $R^2 = 0.604$). *B. vosnesenskii* parasitism was higher in gardens with more trees and shrubs ($P = 0.006$) and in gardens with less bare soil ($P = 0.011$) (Fig. 3).

Discussion

Core et al. (2012) hypothesize that parasitism by *A. borealis* phorids in honey bees reflects a recent host shift from their native host, the bumble bee. Possible reasons for a host shift include a benefit to phorid fitness due to increased parasitism success with a new host

or increased abundance of an alternative host. To examine if phorids experience increased parasitism success with host choice, we compared the mean number of pupae emerging from bumble bees and honey bees and found that the mean number of pupae emerging from each infected bumble bee (7.26 ± 0.87 SE) was significantly higher (by nearly twice) than the number of pupae emerging from each honey bee (4.23 ± 0.46 SE). Our finding that bumble bees are host to more fly progeny is consistent with previously published studies: Otterstatter et al. (2002) found an average of 6.57 fly larvae per female bumble bee and Core et al. (2012) found an average of 4.8 fly larvae in honey bee females. Honey bee bodies may be hospitable to fewer phorid pupae because they are smaller than bumble bee bodies, suggesting a loss to phorid fitness and implying that there may be other reasons for a host shift to honey bees. In this study, honey bees out-numbered bumble bees in our field collection by approximately 6:1. Even though phorids produce less offspring in honey bee hosts, a phorid facing a multitude of available honey bee hosts may counter a reduction to fitness by parasitizing more honey bees in her lifetime than bumble bees. Infecting two honey bees would, on average, produce more phorid offspring than a single bee. Future experiments determining how many honey bee hosts a single phorid female parasitizes in her lifetime may help explain why phorids infect honey bees. Another important question is whether honey bees and bumble bees are only parasitized by one phorid or by multiple phorids, as this can impact the fitness tradeoff between host availability and pupal load per bee.

With declines of bumble bee populations reported in North America (Cameron et al. 2011), a possible explanation for a host shift to honey bees may be a loss of access to bumble bee hosts. Indeed, we were able to collect more honey bees than bumble bees during field collections, and more likely to find honey bees infected with phorids than bumble bees infected with phorids. As the six sampling periods progressed, we caught fewer bumble bees. When we stopped finding bumble bees, we saw a slight increase in the percent of honey bees parasitized by phorids (Fig. 4). Otterstatter et al. (2002) and Core et al. (2012) previously found that phorid infection of bees increased between May and August. However, we did not

Fig. 2. Relationships between significant factors in generalized linear models and parasitism of honey bees by *A. borealis* (A–E). Each dot represents an urban garden field sites. Lines show the best fit, and gray area reflects confidence bands of the generalized linear models.

Fig. 3. Relationships between significant factors in generalized linear models and parasitism of bumble bees by *A. borealis* (A and B). Each dot represents an urban garden field sites. Lines show the best fit, and gray area reflects confidence bands of the generalized linear models.

find a significant impact of season on infection, possibly because we found so few bumble bees at the end of our sampling season or because our collection period started 30 d later than previous studies. In addition to sampling period, another driver of phorid infection might be temperature and climate. We did not find infected bees from the very high-temperature inland sites in Santa Clara. When infected bees were present, they were found in sites along the cooler Monterey and Santa Cruz coastal region (Fig. 1). And previously studied *A. borealis* phorids were also found in coastal regions or near bodies of water (Core et al. 2012, Otterstatter et al. 2002).

Phorid flies in urban settings respond to population-level changes in host abundance: we found that increased abundance of honey bees, but not bumble bees, correlated with higher parasitism of both honey bees and bumble bees. One possible explanation may be that

honey bees may be easier to locate or parasitize than bumble bees, but little is known about host location in bee–phorid interactions, as Phoridae is one of the least studied groups of Dipterans (Brown 2004). Previous studies have also noted that density dependence may be temporally or spatially scale dependent (Philpott et al. 2009). In this study, we found that phorid parasitism is density dependent at the garden scale – but interestingly only for abundance of the domesticated, non-native host (*A. mellifera*). The abundance of the non-native honey bee may contribute to bumble bee infection and decline. Even if honey bees are infected with phorids, their numbers are often re-established by beekeepers, keeping the honey bee population high even in the face of increased levels of parasitism. Indeed, beekeeping is highly popular and practiced widely in our region of study, both by commercial and backyard beekeepers. Because of this,

Fig. 4. Seasonal changes across 2014 in (A) the average percent of total captures from urban gardens that were honey bees or bumble bees, and (B) the average percent of honey bees and bumble bees captured at each site that were parasitized by phorid flies.

bumble bees might continue to encounter large numbers of phorid parasitoids even as their availability as a host declines. Overall, more research is required to determine when and why *A. borealis* phorids began to shift bee hosts, under which conditions parasitism of honey bees and bumble bees is more likely, and what the impacts might be to native bumble bee populations. This is important because parasitoids can mediate the composition and dynamics of communities (Feender 2002).

We found that differences in parasitism of both *A. mellifera* and *B. vosnesenskii* were driven by local features of urban gardens, not landscape factors. The local variables that correlate with parasitism, tree and shrub abundance, bare soil, lawn, and garden size, may directly or indirectly benefit phorids in some way. These factors, however, are also indicators of resource availability for bees. Trees and shrubs include flowering species that provide pollen and nectar for food, larger gardens may provide more habitat than smaller gardens, and bare ground has been associated with increases in ground-nesting bee populations (Potts et al. 2005, Quistberg et al. 2016). Even the amount of lawns in a given area has been shown to be an important food source for bees due to the presence of flowering weeds (Larson et al. 2014). Garden size was a positive indicator of parasitism for only *A. mellifera*. Garden size may be an important indicator of resource availability for *A. mellifera* because honey bees have been said to forage across long distances, up to 20 km, but their foraging is influenced by resource availability (Steffan-Dewenter and Kuhn 2003). For a honey bee foraging across long distances, larger gardens may host more resources and, therefore, attract more visitation than smaller gardens. Comparatively, *B. vosnesenskii* have recorded foraging distances of 0.8 – 2.8 km (Jha and Kremen 2013), suggesting that those bees collected for study are somewhat more

likely to have nested locally and that garden size may not be as critical an indicator as resource availability. If local habitat features are responsible for parasitism increases through indirect impacts to bees, then our results support the idea that resource provisioning results in amplification of parasitism. As larger resource-rich urban gardens with more food and habitat attract more bees, this may result in increased contact rates between hosts and phorid parasites. Another interesting finding was that, in modeling the combined influence of vegetation and bee diversity on parasitism, the average abundance of *B. vosnesenskii* individuals in a garden was a negative predictor of the number of infected *A. mellifera* individuals. This may have to do with competitive interactions between bumble bees and honey bees for resources, phorid host preferences, or point to complicated relationships between vegetative resources, bee community composition, and parasitism.

We initially expected that habitats with high floral diversity would provide resources for bees, conferring immunological or physiological defense against phorid parasitism. In lab experiments, bees fed poly-floral pollen diets showed higher expression of immune-related genes and lower mortality when challenged by *Nosema* parasites than bees fed mono-floral diets (Di Pasquale et al. 2013). Further, chemical constituents of pollen and honey up-regulate select detoxification and antimicrobial peptide genes related to immunity (Mao et al. 2013). However, we did not find any influence (either positive or negative) of floral abundance on parasitism rates. One explanation may be that honey bees and bumble bees are simply not able to overcome phorid infection through immunological defense, regardless of resource availability. Additionally, because phorid adults also consume pollen and nectar diets (Nicolson 2007) and because increased food provisioning has been shown to promote phorid longevity (Wäckers 2001), any immunity or nutritional benefits conferred to the bee may be obscured by increased resource availability for phorids. Whether or not resource availability dilutes parasitism may thus be a function of the availability of preferred floral resources for phorid parasitoids, a factor that is still virtually unknown for many phorids (Wäckers and Fadamiro 2005).

Because phorid parasitism is density dependent in this system, possible increases to bee richness and abundance due to changes to resources may amplify phorid detection of bee hosts or increase contact rates between infected bees. Ultimately, deciphering the relationship between local and landscape features and epidemiology of parasitic infections is complex: beyond resource provisioning, landscape can exert direct influences on host or parasite growth, through indirect impacts to host and parasite physiology and behavior, through alterations to host community structure, and more (Kilpatrick and Altizer 2010). Further studies, including both laboratory and field observation research, are needed to tease apart the complex interactions between resource provisioning and parasitism. The first step may be to learn more about *A. borealis* ecology. By understanding phorid habitat, food, and microclimate preferences, how and where they locate and parasitize bees, we may elucidate how phorid–bee interactions are impacted by resource availability, bee diversity, and landscape context.

Acknowledgments

P. Bichier and M. Otoshi participated in logistics and field data collection. J. Hafernik and C. Quock provided guidance for rearing and handling phorids and phorid-infected bees. K. Ennis provided assistance with statistics. Thanks to J. Velzy and greenhouse staff at the University of California, Santa Cruz for support with insect rearing equipment. Special thanks to the community

gardens for allowing us to conduct research: Aptos Community Garden; Beach Flats Community Garden; Berryessa Community Garden; Center for Agroecology and Sustainable Food Systems; Chinatown Community Garden; Coyote Creek Community Garden; El Jardín at Emma Prusch Park; The Forge at Santa Clara University; Giving Garden at Faith Lutheran Church; Homeless Garden Project; La Colina Community Garden; Laguna Seca Community Garden; The Live Oak Grange; MEarth at Carmel Valley Middle School; Mi Jardín Verde at All Saints' Episcopal Church; Our Green Thumb Garden at Monterey Institute for International Studies; Salinas Community Garden at St George's Episcopal Church; Trescony Community Garden. Funding for this project was provided by University of California, Santa Cruz New Faculty Research Grant to S. M. P., Ruth and Alfred Heller Chair in Agroecology and University of California, Santa Cruz general funds. Funding for materials and supplies was provided to H. C. from the Ruth and Alfred Heller Graduate Student Research Grant. Funding was provided by the Committee on Research Faculty Research Grant from UCSC to S. M. P. in 2014.

References Cited

- Barton, K. 2012. Package 'MuMIn': model selection and model average based on information criteria (AICc and alike). CRAN R Project. <http://www.R-project.org/> (accessed 1 September 2017).
- Becker, D. J., D. G. Streicker, and S. Altizer. 2015. Linking anthropogenic resources to wildlife-pathogen dynamics: a review and meta-analysis. *Ecol. Lett.* 18: 483–495.
- Beekman, M., and F. L. W. Ratnieks. 2000. Long-range foraging by the honey-bee, *Apis mellifera*. *Functional Ecol.* 14: 490–496.
- Botías, C., A. David, E. M. Hill, and D. Goulson. 2017. Quantifying exposure of wild bees to mixtures of agrochemicals in agricultural and urban landscapes. *Environ. Poll.* 222: 73–82.
- Bradley, C. A., and S. Altizer. 2007. Urbanization and the ecology of wildlife diseases. *Trends Ecol. Evol.* 22: 95–102.
- Brown, B. V. 1993. Taxonomy and preliminary phylogeny of the parasitic genus *Apocephalus*, subgenus *Mesophora* (Diptera: Phoridae). *Sys. Entom.* 18:191–230.
- Brown, B. V. 1997. Revision of the *Apocephalus attophilus*-group of ant-decapitating flies (Diptera: Phoridae). *Contrib. Sci.* 468: 1–60.
- Brown, B. V. 2004. Revision of the subgenus *Udamochiras* of *Melaloncha* bee-killing flies (Diptera: Phoridae: Metopininae). *Zool. J. Linn. Soc.* 140: 1–42.
- Buchmann, S. L., and G. P. Nabhan. 2012. The forgotten pollinators. Island Press, Washington, DC.
- Calcagno, V., and C. de Mazancourt. 2010. glmulti: an R Package for easy automated model selection with (generalized) linear models. *J. Statistical Softw.* 34: doi:10.18637/jss.v034.i12.
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proc. Natl Acad. Sci.* 108: 662–667.
- Core, A., C. Runckel, J. Ivers, C. Quock, T. Siapno, S. DeNault, B. Brown, J. DeRisi, C. Smith, and J. Hafernik. 2012. A new threat to honey bees, the parasitic phorid fly *Apocephalus borealis*. *PLoS One* 7: e29639.
- Cox-Foster, D. L., S. Conlan, E. C. Holmes, G. Palacios, J. D. Evans, N. A. Moran, P. L. Quan, T. Briese, M. Hornig, D. M. Geiser, et al. 2007. A metagenomic survey of microbes in honey bee colony collapse disorder. *Science* 318: 283–287.
- Cross, P. C., W. H. Edwards, B. M. Scurlock, E. J. Maichak, and J. D. Rogerson. 2007. Effects of management and climate on elk brucellosis in the Greater Yellowstone ecosystem. *Ecol. Appl.* 17: 957–964.
- De la Mora, A., G. Pérez-Lachaud, J. P. Lachaud, and S. M. Philpott. 2015. Local and landscape drivers of ant parasitism in a coffee landscape. *Environ. Entomol.* 44: 939–950.
- Di Pasquale, G., M. Salignon, Y. Le Conte, L. P. Belzunces, A. Decourtye, A. Kretschmar, S. Suchail, J. L. Brunet, and C. Alaux. 2013. Influence of pollen nutrition on honey bee health: do pollen quality and diversity matter? *PLoS One* 5: e72016.
- Dobson, A. J., and A. Barnett. 2008. An introduction to generalized linear models. CRC press.
- Ennik, F. 1973. *Apocephalus borealis* Brues parasitic upon *Vespa* spp. (Diptera: Phoridae; Hymenoptera: Vespidae). *Panpac Entomol.*
- Feener, Jr. D. H. 2002. Is the assembly of ant communities mediated by parasitoids? *Oikos* 90: 79–88.
- Fürst, M. A., D. P. McMahon, J. L. Osborne, R. J. Paxton, and M. J. F. Brown. 2014. Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature* 506: 364–366.
- Graystock, P., K. Yates, S. E. Evison, B. Darvill, D. Goulson, and W. O. Hughes. 2013. Emerging dangers: deadly effects of an emergent parasite in a new pollinator host. *J. Invert. Pathol.* 114: 114–119.
- Greenleaf, S. S., and C. Kremen. 2006. Wild bee species increase tomato production and response differently to surrounding land use in Northern California. *Bio. Conserv.* 133: 81–87.
- Grixti, J. C., L. T. Wong, S. A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biol. Conserv.* 142: 75–84.
- Goddard, M. A., A. J. Dougill, and T. G. Benton. 2010. Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol. Evol.* 25: 90–98.
- Goulson, D., G. C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. *Ann. Rev. Entomol.* 53: 191–208.
- Goulson, D., E. Nicholls, C. Botías, and E. L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347: 1255957.
- Hernandez, J. L., G. W. Frankie, and R. W. Thorp. 2009. Ecology of urban bees: a review of current knowledge and directions for future study. *Cities Environ.* 2: 3.
- Homer, C. G., J. A. Dewitz, and L. Yang, et al. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States – representing a decade of land cover change information. *Photogramm. Eng. Remote Sensing* 81: 345–354.
- Inoue, M. N., J. Yokoyama, and I. Washitani. 2008. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). *J. Insect Conserv.* 12: 135–146.
- Jessop, T. S., P. Smitsen, F. Scheelings, and T. Dempster. 2012. Demographic and phenotypic effects of human mediated trophic subsidy on a large Australian lizard (*Varanus varius*): meal ticket or last supper? *PLoS One* 7: e34069.
- Jha, S., and C. Kremen. 2013. Resource diversity and landscape-level homogeneity drive native bee foraging. *PNAS* 110: 555–558.
- Keesing, F., L. K. Belden, P. Daszak, A. Dobson, C. D. Harvell, R. D. Holt, P. Hudson, A. Jolles, K. E. Jones, C. E. Mitchell, et al. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468: 647–652.
- Kilpatrick, A. M., and S. Altizer. 2010. Disease ecology. *Nat. Edu. Knowl.* 1: 13.
- Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B: Biol. Sci.* 274: 303–313.
- König, C., and P. Schmid-Hempel. 1995. Foraging activity and immunocompetence in workers of the bumble bee, *Bombus terrestris* L. *Proc. Bio. Sci.* 225: 227.
- Kosior, A., W. Celary, P. Olejniczak, J. Fijał, W. Krol, W. Solarz, and P. Plonka. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. *Oryx* 41: 79–88.
- Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* 10: 299–314.
- Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.* 7: 1109–1119.
- Larson, J. L., A. J. Kesheimer, and D. A. Potter. 2014. Pollinator assemblages on dandelions and white clover in urban and suburban lawns. *J. Insect Conserv.* 18: 863–873.

- Lane, K. E., C. Holley, H. Hollocher, and A. Fuentes. 2011. The anthropogenic environment lessens the intensity and prevalence of gastrointestinal parasites in Balinese long-tailed macaques (*Macaca fascicularis*). *Primates* 52: 117–128.
- Li, J., W. Peng, J. Wu, J. An, Z. Guo, Y. Tong, and J. Huang. 2006. Strawberry pollination by *Bombus lucorum* and *Apis mellifera* in greenhouses. *Acta Entomologica Sinica* 49: 342.
- Mao, W., M. A. Schuler, and M. R. Berenbaum. 2013. Honey constituents up-regulate detoxification and immunity genes in the western honey bee *Apis mellifera*. *Proc. Natl Acad. Sci.* 110: 8842–8846.
- Marzluff, J. M., and K. Ewing. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restor. Ecol.* 9: 280–292.
- Matsumura, C., J. Yokoyama, and I. Washitani. 2004. Invasion status and potential ecological impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in Southern Hokkaido. *Glob. Environ. Res.* 8.1: 51–66.
- McMahon, D. P., M. A. Fürst, J. Caspar, P. Theodorou, M. J. F. Brown, and R. J. Paxton. 2015. A sting in the spit: widespread cross-infection of multiple RNA viruses across wild and managed bees. *J. Anim. Ecol.* 84: 615–624.
- Messina, F. J. 2004. Predictable modification of body size and competitive ability following a host shift by a seed beetle. *Evolution* 58: 2788–2797.
- Miller, R., J. B. Kaneene, S. D. Fitzgerald, and S. M. Schmitt. 2003. Evaluation of the influence of supplemental feeding of white-tailed deer (*Odocoileus virginianus*) on the prevalence of bovine tuberculosis in the Michigan wild deer population. *J. Wildl. Dis.* 39: 84–95.
- Morrison, L. W., E. A. Kawazoe, R. Guerra, and L. E. Gilbert. 1999. Phenology and dispersal in the *Pseudacteon* flies (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* 92: 198–207.
- Müller, C. B. 1994. Parasitoid induced digging behaviour in bumblebee workers. *Anim. Behav.* 48: 961–966.
- Nazzi, F., S. P. Brown, D. Annoscia, F. Del Piccolo, G. Di Prisco, P. Varricchio, G. Della Vedova, F. Cattonaro, E. Caprio, and F. Pennacchio. 2012. Synergistic parasite–pathogen interactions mediated by host immunity can drive the collapse of honeybee colonies. *PLoS Pathog.* 8: e1002735.
- Nicolson, S. W. 2007. Nectar consumers, pp. 289–342. *In* S. W. Nicolson, M. Nepi, and E. Pacini (eds.), *Nectaries and nectar*. Springer, The Netherlands.
- Otterstatter, M. C., T. L. Whidden, and R. E. Owen. 2002. Contrasting frequencies of parasitism and host mortality among phorid and conopid parasitoids of bumble-bees. *Ecol. Entomol.* 27.2: 229–237.
- Pardee, G. L., and S. M. Philpott. 2011. Cascading indirect effects in a coffee agroecosystem: effects of parasitic phorid flies on ants and the coffee berry borer in a high-shade and low-shade habitat. *Environ. Entomol.* 8: 581–588.
- Pardee, G. L., and S. M. Philpott. 2014. Native plants are the bee's knees: local and landscape predictors of bee richness and abundance in backyard gardens. *Urban Ecosyst.* 17: 641–659.
- Philpott, S. M., I. Perfecto, J. Vandermeer, and S. Uno. 2009. Spatial scale and density dependence in a host parasitoid system: an arboreal ant, *Azteca instabilis*, and its *Pseudacteon* phorid parasitoid. *Environ. Entomol.* 38: 790–796.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweige, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25: 345–353.
- Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Wilmer. 2005. Role of nesting resources in organizing diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.* 30: 78–85.
- Quistberg, R. D., P. Bichier, and S. M. Philpott. 2016. Landscape and local correlates of bee abundance and species richness in urban gardens. *Environ. Entomol.* 45: 592–601.
- Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanskii, B. Gemmill-Herren, S. S. Greenleaf, A. M. Klein, M. M. Mayfield, et al. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* 11: 499–515.
- Schmid-Hempel, R., M. Eckhardt, D. Goulson, D. Heinzmann, C. Lange, S. Plischuk, L. R. Escudero, R. Salathé, J. J. Scriven, and P. Schmid-Hempel. 2014. The invasion of southern South America by imported bumblebees and associated parasites. *J. Anim. Eco.* 83: 823–837.
- Schmid-Hempel, P., and R. Schmid-Hempel. 1998. Parasitic flies (Conopidae, Diptera) may be important stress factors for the ergonomics of their bumblebee hosts. *Ecol. Entomol.* 13: 469–472.
- Schneider, S. S., and H. G. Hall. 1997. Diet selection and foraging distances of African and European-African hybrid honey bee colonies in Costa Rica. *Insect Soc.* 44: 171–187.
- Singh, R., A. L. Levitt, E. G. Rajotte, E. C. Holmes, N. Ostiguy, W. I. Lipkin, A. L. Toth, and D. L. Cox-Foster. 2010. RNA viruses in hymenopteran pollinators: evidence of inter-taxa virus transmission via pollen and potential impact on non-*Apis hymenopteran* species. *PLoS One* 5: e14357.
- Steffan-Dewenter, I., and A. Kuhn. 2003. Honeybee foraging in differentially structured landscapes. *Proc. R. Soc. Lond. Ser. B. Biol. Sci.* 270: 569–575.
- Stubbs, C. S., and F. A. Drummond. 2001. *Bombus impatiens* (Hymenoptera: Apidae): an alternative to *Apis mellifera* (Hymenoptera: Apidae) for low-bush blueberry pollination. *J. Econ. Entomol.* 94: 609–616.
- Team RC. R Development Core Team. 2014. R: a language and environment for statistical computing. 2010. <http://www.R-project.org/> (accessed 1 September 2017).
- Theodorou, P., R. Radzevičiūtė, J. Settle, O. Schweiger, T. E. Murray, and R. J. Paxton. 2016. Pollination services enhanced with urbanization despite increasing pollinator parasitism. *Proc. R. Soc. B.* 283: 20160561.
- Thompson, K., K. C. Austin, R. M. Smith, P. H. Warren, P. G. Angold, and K. J. Gaston. 2003. Urban domestic gardens: putting small-scale plant diversity in context. *J. Veg. Sci.* 14: 71–8.
- Tommasi, D., A. Miro, H. A. Higo, and M. L. Winston. 2004. Bee diversity and abundance in an urban setting. *Can. Entomol.* 136: 851–869.
- USDA. United States Department of Agriculture. Agricultural Research Service. 2015. Bee survey: lower winter losses, higher summer losses, increased total annual losses. Cited 13 May 2015. <http://ars.usda.gov/is/pr/2015/150513.htm> (accessed 1 September 2017).
- Visscher, P. K., and T. D. Seeley. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63: 1790–1801.
- Wäckers, F. L. 2001. A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *J. Insect Phys.* 47: 1077–1084.
- Wäckers, F. L., and H. Fadamiro. 2005. The vegetarian side of carnivores: use of non-prey food by parasitoids and predators. *Sel. Food Suppl. Conserv. Bio. Control.*
- Waddington, K. D., P. K. Visscher, T. J. Herbert, and M. Raveret Richter. 1994. Comparisons of forager distributions from matched honey bee colonies in suburban environments. *Behav. Ecol. Sociobiol.* 35: 423–429.
- Walde, S. J., and W. W. Murdoch. 1988. Spatial density dependence in parasitoids. *Ann. Rev. Entomol.* 33: 441–466.
- Warton, D. I., and F. K. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92: 3–10.
- Wickham, J. D., and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States – representing a decade of land cover change information. *Photogramm. Eng. Remote Sens.* 81: 345–354.
- Williams, P. H., and J. L. Osborne. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie* 40: 367–387.
- Williams, P., Y. Tang, J. Yao, and S. Cameron. 2009. The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini). *Syst. and Biodivers.* 7: 101–189.
- Winfree, R., R. Aguilar, D. P. Vázquez, G. LeBuhn, and M. A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90: 2068–2076.
- Wojcik, V. A., G. W. Frankie, R. W. Thorp, and J. L. Hernandez. 2008. Seasonality in bees and their floral resource plants at a constructed urban bee habitat in Berkeley, California. *J. Kansas Entomol. Soc.* 81: 15–28.
- Xie, Z., P. H. Williams, and Y. Tang. 2008. The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *J. Insect Conserv.* 12: 695–703.