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Wild bee niche preferences and diversity changes in urban Bavaria

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Preface

Statutory declaration

Erklärung

Diese Dissertation wurde im Sinne von §12 der Promotionsordnung von Prof. Dr. Susanne S. Renner betreut. Ich erkläre hiermit, dass die Dissertation nicht einer anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

Eidesstattliche Erklärung

Ich versichere hiermit an Eides statt, dass die vorgelegte Dissertation von mir selbstständig und ohne unerlaubte Hilfe angefertigt wurde.

Michaela Hofmann, 18. Dezember 2019
(Unterschrift)

1. Gutachter: Prof. Dr. Susanne S. Renner
2. Gutachter: Prof. Dr. Gerhard Haszprunar

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Note

In this thesis, I present the results from my doctoral research, carried out in Munich from February 2017 to November 2019 under the guidance of Prof. Dr. Susanne S. Renner. My thesis resulted in eight manuscripts, presented in chapters 2-9, of which four have been published (chapters 2, 3, 7, 9), one is in print (chapter 8), one is accepted (chapter 6) and two are in review (chapters 4 and 5). I also gave five invited talks and wrote four invited articles as listed below. Writing and discussion involved collaboration with S. S. Renner (all chapters but chapter 8), with input from A. Fleischmann in chapters 3 and 5. Chapter 8 was written in collaboration with A. Fleischmann. The analyses in chapter 2 were conducted by C. M. Zohner, and for the analyses in chapter 4 I received help from the Statistical Consulting Unit (StaBLab) of the University of Munich (LMU). Matthias Schindler led the writing of chapter 9 for which I contributed all information on *Nomada flavoguttata*, including SEMs and field observations.

Michaela M. Hofmann	Prof. Susanne S. Renner
(Signature)	(Signature)

List of publications

Peer-reviewed journal articles

Hofmann, M. M., Fleischmann, A., and Renner, S. S. (2018). Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. *Oecologia* 187: 701-706.

Hofmann, M. M., and Renner, S. S. (2018). Bee species recorded between 1992 and 2017 from green roofs in Asia, Europe, and North America, with key characteristics and open research questions. *Apidologie* 49: 307-313.

Schindler, M., Hofmann, M. M., Wittmann, D., and Renner, S. S. (2018). Courtship behaviour in the genus Nomada – antennal grabbing and possible transfer of male secretions. *Journal of Hymenoptera Research* 65: 47-59.

Hofmann, M. M., Zohner, C. M., and Renner, S. S. (2019). Narrow habitat breadth and late-summer emergence increase extinction vulnerability in Central European bees. *Proceedings of the Royal Society B* 286: 20190316.

Hofmann, M. M., and Fleischmann, A. (2019). A photo-based assessment of wild bees in a filled-up gravel pit in Riem, Munich – with a species list of bees found in Central European gravel pits. (*Spixiana*, in print).

Hofmann, M. M., Fleischmann, A., and Renner, S. S. Empirical foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, using individual tagging. (submitted at 27 Nov. 2019, *Ecosphere*).

Hofmann, M. M., and Renner, S. S. Bee species persistence and increase in urban protected sites between 1990 and 2018. (submitted at 17 Nov. 2019, *Journal of Insect Conservation*).

Hofmann, M. M., and Renner, S. S. One-year-old flower strips already support a quarter of a city´s bee species. (accepted 15 Dez. 2019, *Journal of Hympenoptera Research*).

Invited articles

Hofmann, M. M. (2016). Dialog der Bienen – Wie Bienenvölker einen neuen Wohnort auswählen. *Fatum* 5: 80-83.

Hofmann, M. M. (2017). Hoch hinaus – Wildbienen auf Gründächern. *Gebäude-Grün* 2: 25-29.

Hofmann, M. M., and Fleischmann, A. (2019). Über das schwierige Leben der Wildbienen in Stadt und Land. *Jahrbuch des Vereins zum Schutz der Bergwelt* 84: 239-248.

Hofmann, M. M., and Renner, S. S. (2019). Bye, bye Biene – Welche ökologischen Eigenschaften machen Wildbienen zu bedrohten Arten? *Gesellschaft für Biologische Systematik Newsletter* 36: 28-31.

Invited talks

Hofmann, M. M. Der Botanische Garten und die Blühstreifen des LBV. Vortrag für die Bayerische Botanische Gesellschaft e.V., 17 Oct. 2017

Hofmann, M. M. Wer summt denn da? Bienenvielfalt in München. Vortragsreihe des Landesbundes für Vogelschutz, 27 Jan. 2018

Hofmann, M. M. Wildbienen auf den LBV-Blühstreifen in München. Vortragsreihe des Landesbundes für Vogelschutz, 11 Mar. 2019.

Hofmann, M. M. Wildbienen auf Gründächern. bdla-Fachseminar „Artenschutz in der Stadt!“, Bund deutscher Landschaftsarchitekten, 11 Apr. 2019

Hofmann, M. M. Wildbienen in München: wo sie leben und was sie brauchen. Vortrag für Green City e.V., 16 Dez. 2019

Posters

Hofmann, M. M., and Fleischmann, A. München sucht nummerierte Wildbienen – Wildbienenmarkierung im Botanischen Garten zur Erforschung von Flugdistanzen und Lebensdauer der Bienen. 17. Münchner Wissenschaftstage, Munich, Germany, 25-28 Nov. 2017.

Hofmann, M. M., Fleischman, A., and Renner, S. S. Tracking of 2600 individuals in an urban garden shows that small European solitary bees have mean foraging distances below 185 m. 20th annual meeting of the Society for Systematic Biology (GfBS), Munich, Germany, 24-27 Feb. 2019.

Contents

Summary

Numerous studies are documenting a global decrease in insect diversity and abundance, and the public is becoming more and more aware of the need to better protect biodiversity. Especially bees are now at the center of attention, as they have been promoted as a key taxon in conservation campaigns, citizen petitions, and efforts to modify nature protection laws. Reasons for the biodiversity loss are manifold, with habitat destruction and fragmentation as well as agricultural intensification being major factors. However, causation and interaction among factors are hard to disentangle, and effect sizes depend on the system one observes. This dissertation, which comprises ten chapters, deals with changes in Munich´s wild bee populations as a study system in which to address insect diversity changes in an urban context. Specifically, I investigated the factors influencing wild bees (not the domesticated honey bee) in different city biotopes. For comparison, I also studied German-wide correlations between bee extinction risks, their habitats, and various intrinsic and extrinsic traits. By comparing present (2017-2019) Munich species spectra with spectra from twenty years ago as well as by using Red List Data back to 40 years ago, I investigated how bee faunas have changed over time and which factors best explain the changes.

In 2017 and 2018, I monitored bees at three protected sites of 150 and 20 ha and on nine 1000 m^2-large flower strips within the city perimeter, compiled live-history parameters and habitat niche preferences of all species recorded in Munich since 1795, and analyzed correlations among these parameters and the persistence of species at the three sites for which data from 20 years ago were available. I also used Red List Data for all of Germany's bees to assess German-wide correlations of five life-history and three habitat niche parameters with bee persistence. To assess the included factors´ predictive power, I used known extinctions of the past 40 years. The results show that late-season emergence and restricted habitat use strongly increase extinction risk, using Hierarchical Bayesian models that allowed me to analyze all factors simultaneously while including a phylogeny for most of Germany's bees (chapter 2).

I then tested these German-wide 'extinction predictors' in the city of Munich by comparing species spectra from the 1990ies with my own from the Munich Botanical Garden (20 ha, chapter 3 and 4), the Allacher Lohe (150 ha, chapter 4) and the Virginia Depot (20 ha, chapter 4). I found an increase not only in species numbers at two of these sites but also of warm-loving species, most likely linked to shorter winters and warmer springs and summers compared to 20 years ago. The climate change benefits thermophilic species, which have been spreading in southern Germany since the 2000s. Moreover, opposed to the German-wide trend, late-flying bees persist well in urban protected habitats probably due to the more constant availability of flowers in cities compared to agricultural landscapes.

As bees need suitably-spaced foraging resources and nesting sites, effective conservation requires data on how far these resources can be apart while still supporting healthy bee populations. Of 436 Central European species, 92% are only 4.5 to 13.5 mm long, yet few data are available for flight distances in small bees. Using apiarist's tags and color codes, and a citizen science approach, I individually marked 2689 males and females of four oligolectic and two polylectic species of Osmiini with body lengths of 6 to 15 mm and long-term stable populations at my botanical garden study site and then monitored their foraging

distances. Based on 1045 re-sightings, mean female flight distances ranged from 73 to 121 m and male distances from 59 to 100 m, with maximal distances being up to seven times larger. Based on these results, 150 m would appear to be a good rule-of-thumb for planning the locations of conservation measures, such as flower strips (chapter 5). Prior to my work, flower strips had been mainly studied in an agricultural context, and I therefore decided to study their effectiveness in Munich, using eight 1000 m^2-large flower strips established in 2017 and one from 2015. I found out that these small and young strips already support 21% of the 324 species recorded for Munich since 1795 and 29% of the 232 species recorded between 1997 and 2017, attesting to bees' ability to detect and use new resources quickly (chapter 6).

Another way of urban biodiversity enrichment is the creation of green roofs. Although this habitat has low plant diversity, my survey of the literature (35 studies that have appeared between 1992 and 2017) showed that 236 species of wild bees have been recorded on green roofs worldwide, with high numbers of thermophilic and cavity-nesting species (chapter 7). Ground-nesting species are underrepresented in this habitat, because the substrate thickness is insufficient for them. This was in stark contrast to a gravel pit (circa 18 ha) that I studied in the East of Munich and found 48 species of bees, of which 54% were ground-nesting (chapter 8). For comparison, in Germany, Austria and Switzerland, 50% of the 745 bees known from this region are nesting in self-burrowed tunnels in the ground.

During the many hours of monitoring Munich´s bees, I was able to observe and photographically document the copulation of *Nomada flavoguttata*, which to my knowledge is a first, although M. Schindler had studied mating in *Nomada fucata* and *N. lathburiana* in the lab. The bee male wrapped its antenna around the antenna of the female, possibly to transfer male antennal secretions to the female (chapter 9).

Taken together, the results of my work show that cities can sustain a high bee diversity, especially if sites are protected from human interference, albeit not from climate warming, the urban heat effect, nitrogen input, light pollution, and other factors. As long as sites provide both foraging and nesting resources, bees quickly colonize and appear able to form stable populations. Likely, urban bee conservation will become increasingly important in times of biodiversity loss, as cities could provide safe havens from the negative effects of agricultural intensification.

Chapter 1

General Introduction

THE EFFECTS OF URBANIZATION ON BIODIVERSITY

According to United Nations (UN) data on ‘The World´s Cities in 2018,’ more than 50% of the world´s 7.7 billion people live in urban settlements (https://www.un.org/en/events/citiesday/assets/pdf/the_worlds_cities_in_2018_data_booklet.pdf, last accessed 08 Dec. 2019). These estimates clearly depend on the definition of what constitutes a city. According to the UN’s definition (United Nations 2018), ‘city proper’ refers to a city´s administrative boundary, ‘urban agglomeration’ to the extent of the contiguous urban area, and ‘metropolitan area’ to the interlinked commerce and commuting patterns of nearby areas. Another way to define a city is by a high population density and strong constructional development (Pickett et al. 2001). If the current rate of urbanization stays unchanged, models predict an increase in urban land cover by 1.7 million km² by 2050, which would be approximately 1.4 times the area of 2012 (Zhou et al. 2019). As foraging and nesting resources of wildlife are eliminated due to surface sealing, and animals and plants become exposed to pollutants as well as light pollution, traffic, and other anthropogenic stressors, urbanization reduces both species richness and evenness for most biotic communities (Grimm et al. 2008, Hernandez et al. 2009). However, the degree of urbanization within cities varies (as is evident from the above definitions of what constitutes a city), and with this also the influence of cities on biodiversity.

Generally, the core area is densely built up and highly developed, while the suburban areas surrounding the city center are increasingly natural (Magura et al. 2013). In cities with the strongest urbanization, the species richness of most plants, vertebrates, and a few groups of invertebrates is reduced, compared to the species richness of surrounding suburban areas, which presumably provide a baseline of what might be the natural diversity in the respective region (McKinney 2008, Shochat et al. 2010). Bird species richness generally is negatively affected by urbanization, while bird abundance marginally increases at urban sites, and highest abundance occurs in suburban areas (Batáry et al. 2018, meta-analysis of 37 studies of bird species richness and 20 studies of abundance). A study of arthropods in the city of Debrecen (Hungary) showed that different trophic levels react differently to urbanization: while predatory spiders did not differ in their taxonomic or functional diversity along an urbanization gradient because of their higher recolonization capability compared to lower trophic levels, rove beetles and woodlice were taxonomically more diverse in rural, less urbanized sites (Nagy et al. 2018).

The first studies on urban ecology were conducted in Europe and Australia in the 1970´s (Davis 1978, Sukopp et al. 1979), but cities only became a main focus in biodiversity research in the 21th century, even leading to the establishment of the ‘Journal of Urban Ecology’ (Grimm et al. 2008). An important aspect in urban biodiversity research is biotic homogenization, which is considered to be higher in cities than rural areas (McKinney 2005). Biotic homogenization is defined as “the replacement of local biotas with non-indigenous species,” which “often replaces unique endemic species with already widespread species” (McKinney and Lockwood 1999: p. 450). This process happens because habitat modification through construction and the accompanying alteration of the environment cause strong disturbances, excluding native species, while sometimes helping the introduction of exotic species (Hassal 2014). Species that are well-adapted to urban environments can spread worldwide, while many local species disappear since they are not adapted to the narrow physical environment that cities provide (McKinney 2005). Through these processes, the local biodiversity of a city can both increase or decrease, while the global biodiversity decreases.

Another reason for urban diversity increase is that cities show high small-scale heterogeneity (Baldock et al. 2019). Therefore, cities constitute a complex mosaic of different habitats suitable especially for smaller taxa with small habitat ranges, like many arthropods. For species with small home ranges, cities offer a variety of habitat niches with varying nesting opportunities, places to hide, and foraging sites.

WORLDWIDE BIODIVERSITY DECLINE

In the last decades, arthropod abundance and species diversity are declining worldwide, both in tropical and temperate habitats (Sánchez-Bayo and Wyckhuys 2019). For instance, dry weight biomass of arthropods in Puerto Rico´s Luquillo rainforest captured in sweep samples between 1976 and 2012 has declined four- to eightfold, and for sticky traps 30 to 60 times, with severe consequences for insectivorous species of higher trophic levels, which show parallel declines (Lister and Garcia 2018). Similarly, flying insect biomass in 63 German nature protection areas on average has declined by 76%, with mid-summer declines of 82%, between 1989 and 2016 (Hallmann et al. 2017), and arthropod biomass, abundance, and species numbers in forests and grassland have decreased by 67%, 78%, and 34% respectively between 2008 and 2017 (Seibold et al. 2019). Reasons for the decline are manifold, ranging from high nitrogen levels and reduced food and nesting resources to habitat loss, exposure to agrochemicals, pathogens and parasites, and for some groups also climate change (Potts et al. 2010, Goulson et al. 2015, Sánchez-Bayo and Wyckhuys 2019, Seibold et al. 2019).

Amongst the best studied arthropod groups are pollinators, particularly bees. There are almost 18.000 bee species known worldwide, which belong to nearly 500 genera (Michener 2007). All bees form a monophyletic group within the order of Hymenoptera. The foraging preferences of wild bees vary from being specialized on the pollen of one or a few plant species, which is called oligolecty, to being a generalist that can use many different plants as a pollen source to supply the brood cells, which is called polylecty (Cane and Sipes 2006). Not only do bees differ in their foraging specialization, but also in their nesting biology. Some species are cavity nesters, using already existing hollows to build their nest in. This can be big cavities like the nests of mice and birds, where bumblebees or honeybees can establish a new colony, or beetle grooves in dead wood or other hollow spaces like snail shells or hollow plant stems for solitary species. Cavity nesters are often found in artificial nesting aids as well (Michener 2007). Other species bite their nest tunnels into dead wood or the marrow of plant stems, and again others dig underground tunnels where they build their brood cells (Amiet and Krebs 2014). About a quarter of the wild bee species have stopped building their own brood cells, but have instead developed a parasitic lifestyle, laying their eggs in the nests of other bee species, where their offspring grows on the food that the host species has collected for its own offspring, which is killed in the stage of an egg or early larva either by the cuckoo bee adult or its offspring (Wiesbauer 2017). In Germany, Liechtenstein, Austria, and Switzerland, for instance, 184 of 745 bee species have such a parasitic lifestyle (Zurbuchen and Müller 2012). The vast majority of wild bees in Central Europe are solitary, while relatively few species in the genera *Bombus*, *Halictus*, and *Lasioglossum* are semisocial or eusocial, where work is divided among one or a few queens and many female workers (Michener 2007).

In the last years, public awareness of wild bees has increased, and numerous activities and information brochures have been produced by nature conservation organizations to improve the conditions for this group of insects. In Bavaria, this reached a political level in 2019, when almost 1.8 million voting-age Bavarian citizens signed a referendum for anchoring the protection of nature and especially bees in the law (https://volksbegehren-artenvielfalt.de, last accessed 12 Jul. 2019). Bees have been seen as providing especially important ecosystem services. Ecosystem services are benefits that humans gain from the environment, including provisioning services, which involve the production of renewable resources, and regulating services, like pest or disease control (Ehrlich and Ehrlich 1981). Biodiverse communities are considered to be more productive and stable (resilient against disturbance) and thus more reliably providing such services (Cardinale et al. 2012). Where pollinators disappear, such ecosystem services are not ensured any longer, which leads to decreased fruit-set in crops and wild plants (Steffan-Dewenter et al. 2005). This is indeed an alarming perspective, as we are already facing severe losses in species abundances. Currently, about half of the bees in Germany are threatened according to the German Red List (Westrich et al. 2011) or the Red Lists of the federal states (see Table 1).

Table 1: Proportion of threatened species in the Red Lists of Germany and its federal states

Country/Region	Species assessed	Red List species	Reference
Germany	557	47.9 %	Westrich et al. 2011
Baden-Wuerttemberg	460	45.2 %	Westrich et al. 2000
Bavaria	506	54 %	Mandery et al. 2003a
Berlin	298	39.9 %	Saure et al. 2005
Brandenburg	383	38.4 %	Dathe and Saure 2000
Hesse	424	43 %	Tischendorf et al. 2009
Lower Saxony and Bremen	341	62.2 %	Theunert 2002
Northrhine-Westphalia	364	51.9 %	Esser et al. 2010
Saxony	407	70.5 %	Burger 2005
Saxony-Anhalt	405	64.9 %	Burger et al. 2004
Schleswig-Holstein	296	58 %	Smissen 2001
Thuringia	422	57.6 %	Burger 2010

A major factor driving bee decline is the altered land-use (Potts et al. 2010, Sánchez-Bayo and Wyckhuys 2019). The effect of agriculture on arthropod decline in Germany is particularly pronounced at the landscape level (Seibold et al. 2019). Intensive agriculture constitutes a problem due to the uniformity of landscapes because of monocultures, leading to restricted flower availability, and due to agrochemicals, especially neonicotinoids (Goulson 2013, Goulson et al. 2015). The reproductive success of *Bombus terrestris* and *Osmia bicornis* is negatively correlated with neonicotinoid residues (Woodcock et al. 2017), the neonicotinoid clothianidin affects the visual guidance and navigational memory in *Osmia cornuta* (Jin et al. 2015), and traces of neonicotinoids are found in 75% of 198 honey samples collected throughout the world, indicating that both the honey bee and wild bees are exposed to this agrochemical worldwide (Mitchell et al. 2017). The issue of neonicotinoids not only affects arthropods but also has far-reaching consequences for higher trophic levels (Hallmann et al. 2014). For instance, higher-level consumers in a Japanese lake are affected by the zooplankton biomass decrease that correlates with neonicotinoid applications to watersheds since 1993, leading to a smelt harvest collapse from 240 to 22 tons (Yamamuro et al. 2019). With agriculture being such a strong driver in bee decline, the question arises whether urban spaces, which lack agrochemicals, crop-related mowing regimes, and show a higher heterogeneity compared to large crop monocultures could become an important wild bee habitat.

BEE DIVERSITY IN CITIES

In body size, bees range from 3 mm (Exely 1974: *Euryglossella* and *Quashihesma,*) to 63 mm (Messer 1984: *Megachile (Chalicodoma) pluto*) worldwide and from 4.5 mm to 24 mm in Germany (Hofmann et al. 2019), and their habitat ranges vary correspondingly. Compared to larger-bodied vertebrates and many other insects, however, the bee species occurring in Germany all have small home ranges because they are central-place foragers and because most species are solitary and smaller than 15 mm. A heterogeneous urban landscape might therefore support bee populations, at least for the small-bodied species, and should therefore be targeted by urban conservation efforts (Hall et al. 2017). Diverse bee communities can be found in cities, especially cavity nesters and pollen generalists (see Hall et al. 2017 for references). For community gardens in the heavily developed neighborhoods of the Bronx and East Harlem in New York, for instance, 54 species of wild bees have been reported (Matteson et al. 2008). Westchester County, a New York suburb, even hosts 110 species of wild bees in its residential gardens (Fetridge et al. 2008). A five-year study in Berlin found 262 species of bees using the net-sampling method (Saure 1996). In Lyon, 291 species were found between 2011 and 2012 using both pan traps and insect nets along an urbanization gradient (Fortel et al. 2014). In this study, bee abundance was negatively correlated with the amount of sealed surface, but at intermediate levels of sealed surface, the diversity of parasitic species and cavity-nesting species was highest (Fortel et al. 2014). Similarly, diversity and abundance of bees and hoverflies in the UK were negatively correlated with higher levels of urbanization and presumably surface sealing, and sites with high flowering plant diversity had the most diverse pollinator assemblages (Bates et al. 2011).

Likewise, Banaszak-Cibicka and Zmihorski (2012) found 104 species in Poznan, Poland, with some species being more abundant in the city center, whilst others preferred the suburban region, indicating that urbanization can influence wild bee species composition. Urban greenspace with suitable foraging resources for flies, bees, and butterflies, the main pollinators in the temperate zone, can be manifold, ranging from allotments, gardens and balconies to parks, cemeteries and churchyards. Especially residential gardens and allotments (i.e. community gardens) have a high pollinator biodiversity (Baldock et al. 2019). Another greenspace of increasing size and importance are green roofs, which are now mandatory on flat-topped buildings in Switzerland and a few other European countries and supported by incentives in the USA (Brenneisen 2006, Stutz 2010). They can increase habitat connectivity especially in highly urbanized areas (Braaker et al. 2014), and provide additional habitat space, where a lot of surface is sealed with buildings, streets and pavements.

RESEARCH QUESTIONS AND STUDY APPROACHES

The focus of this dissertation is on changes in the species diversity of wild bees in the city of Munich over the past 20 years. My goal was to identify factors that influence species diversity (chapter 2) and changes in community composition (chapter 3 and chapter 4). I made use of data on the population development and degree of threat of the German wild bee fauna as stated in successive editions of relevant Red Lists for Germany and correlated these data with information of live history parameters of the species, such as the extent of pollen specialization, sociality, flight times, and a fine-grained data collection on their habitat niches, using Hierarchical Bayesian Models (chapter 2). In Hierarchical Bayesian Models the prior distribution of some model parameters depends on other parameters, which are inferred using Bayesian methods (Kruschke 2010). These are based on Bayes´ theorem, which describes the probability of a parameter based on prior knowledge of factors potentially being related to the event as opposed to the frequentist approach, which is purely based on the inference of probabilities from long-term frequencies. Hierarchical Bayesian Models allowed me to include the phylogenetic relationship of bees as one of the explanatory factors that might influence the Red List status of wild bees. For most of the German wild bees barcodes of multiple specimens per species are available (Schmidt et al. 2015). Barcodes are sequences of the cytochrome oxidase subunit I, which were used to calculate a maximum-likelihood phylogeny, which was then included in the applied model. With this bee phylogeny in the background, I was able to examine the predictive power of different life-history parameters as well as habitats and their elevation of wild bees for their Red List Status and therefore the role of inherited and external factors as contributors to extinction. I could also test my models against known bee extinction rates based on data of the last 50 to 150 years (Westrich et al. 2011).

In Germany, the first wild bee Red List was published over forty years ago by Rühl (1977), followed by the Red Lists of Warncke and Westrich (1984), Westrich et al. (1998), Westrich et al. (2008), and finally Westrich et al. (2011). The Red List status of the wild bees published in the latest publication (Westrich et al. 2011) was determined based on the data of seven bee specialists, each with a different regional focus: P. Westrich for Baden-Wuerttemberg, U. Frommer for Hesse, K. Mandery for Northern Bavaria, H. Riemann for Bremen and Lower Saxony, H. Ruhnke for Saxony-Anhalt, C. Saure for Berlin and Brandenburg, and J. Voith for Southern Bavaria and the German Alps. Assessing the Red List Status of wild bees raises several difficulties: For some species, species boundaries have changed due to new findings in the field of phylogenetics based on the analysis of DNA in addition to the classical morphological features. For instance, cryptic species have been detected within one former species, while on the other hand, names can also become synonymized when it turns out that they refer to the same species. One example is the case of *Andrena flavilabris* and *A. decipiens* described by Schenk in 1874 and 1861 respectively. Until about 2008, *A. flavilabris* was considered the spring-time generation of *A. decipiens*, but genetic research has shown that Schenk was correct in treating them as two species (Mandery et al. 2008). In other cases, it is still not clear whether two species names are synonymous or not. *Andrena alutacea*, for example, is considered a synonym of *A. proxima* by Dubitzky and Schönitzer (2001) and Gusenleitner and Schwarz (2002), but is ranked as a species by Schmid-Egger (2005). For such taxonomically difficult species it is problematic to use historic data to evaluate the development of populations, because the determination of the specimen in the past might have followed another classification than the one used for the Red List. Moreover, monitoring and mapping intensities differ strongly between areas, so that species-rich areas are simply the best-assessed areas. Although the interest in bees is increasing, there are still areas with deficits in the faunal assessment of wild bees because small bees are often difficult to determine in the field. Another problem is the low degree of digitally available records. Approaches such as the ‘Wildbienen-Kataster’ (http://www.wildbienen-kataster.de/, last accessed 03 Jun. 2019), a digital data base for Baden-Wuerttemberg created by the Stuttgart State Museum of Natural History, or the ‘Arbeitsatlas der Bienen und Wespen Bayerns’ (http://www.buw-bayern.de/, last accessed 03 Jun. 2019) for Bavaria, initiated by Mandery and colleagues, are rare attempts to make voucher information available online and thus easy to access for abundance analyses. Nevertheless, the authors of the fifth Red List of wild bees in Germany (Westrich et al. 2011) managed to assess the threat status of 557 species: 39 species are currently considered extinct, 26 almost extinct, 31 highly threatened, 78 strongly threatened, 85 threatened, 42 near-threatened, 34 threatened to an unknown extent, 207 not threatened, and for 15 species, data are deficient.

To test possible predictors of population vulnerability with field data, I carried out bee occurrence mapping in the city of Munich. I was able to re-monitor two well-studied biotopes within the city perimeter of Munich (chapter 4), the Allacher Lohe nature reserve and the Virginia Depot, where data for the last 20 or more years are available via a species and biotope monitoring program (ABSP München Stadt) funded by the Bavarian Environmental Protection Agency (Bayerisches Landesamt für Umwelt). As the species spectrum of wild bees is shifting over the year, I visited all studied sites in regular intervals (every two to three weeks). Monitoring walks were conducted between 10 am and 4 pm on sunny, warm days with little or no wind. The mapping did not follow a strict route, but instead, I searched for bees on flowers and likely nesting sites. If possible, species were identified directly in the field and documented via macro-photography in a standardized setup: for detailed pictures, the bees were caught with an insect net and cooled down for 10 minutes in an Eppendorf cupped plastic vial stored on ice in a cooled box. When the bees became cold anesthetized, they were transferred onto scale paper (using a small box lined with millimeter paper on its bottom) and photographed from all sides. Within one to two minutes, they warmed up again and were released at the location they were caught. After determining the photos to species level, they were uploaded to the virtual research environment 'Diversity Workbench,' a platform operated by the IT group of the Bavarian Natural History Collections, which is located in the Botanical Institute and headed by a curator of the Munich herbarium. The platform allows researchers associated with the herbarium to store bio-and geodiversity data and will make the bee photographs generated as part of this dissertation available for other researchers.

For species that are taxonomically difficult to distinguish by morphology alone, like most members of the genera *Sphecodes*, *Lasioglossum* or *Halictus*, I collected voucher specimens, preferably males (for morphological re-identification by genitalia preparations), and identified them morphologically and via DNA barcoding. For DNA extraction, the QIAGEN DNeasy®-Blood and Tissue Kit (Qiagen GmbH, Hilden, Germany) was used. DNA was extracted from one leg per bee**.** The mitochondrial gene fragment of the cytochrome c oxidase (COI) with a 658 bp target region near the 5´terminus of COI was amplified**.** Polymerase chain reactions (PCR) were performed using standard conditions. Amplified products were sequenced on an ABI 3100 Avant capillary sequencer (Applied Biosystems), and forward and reverse sequences were manually edited and assembled, using Sequencher 5.1 (Gene Codes Corporation, Ann Arbor, Michigan, USA) and BLAST-search in GenBank. DNA barcodes were uploaded to NCBI. The voucher specimens have been deposited in the Zoologische Staatssammlung Munich (ZSM).

Besides the Allacher Lohe and the Virginia Depot, I used the Munich Botanical Garden as my main study site. It has monitoring data for bees extending back over twenty years starting with data from 1990, with highest data availability for the years 1996-1998. This allowed me to assess changes in the species composition of a basically unchanged, ideal habitat, as the garden layout and species-rich outdoor plantings of the Munich Botanical Garden have not changed over the past 20 years (chapter 3). Additionally, this site enabled me to conduct experiments on the flight distances of cavity-nesting wild bees (chapter 5). Habitats suitable for bees need both sufficient nesting and foraging resources (Westrich 1996), and these need to be within the flight range of single females (Gathmann and Tscharntke 2002, Greenleaf et al. 2007). Foraging ranges of most wild bees, however, are unknown, although such information is crucial for planning conservation measures. Therefore, I examined the flight distances of numerous males and females of six solitary bee species in the Botanical Garden, by marking them with colored number tags or colored dots using a mark-observe approach (chapter 5).

In spring 2017 and summer 2018, I also scientifically accompanied the establishment of inner-city flower strips by the Landesbund für Vogelschutz (LBV), a nature conservation organization, assessed the wild bee assemblage on the flower strips and on nearby control areas and monitored the development of these strips over the two years to understand which plants are most useful for bees and also can establish successfully in an urban context (chapter

6). Data on such habitat-enhancement measures in cities are much scarcer than in the agricultural context, where numerous studies are available (for references see Dicks et al. 2012).

The selection of the three sites described above allowed me to investigate and disentangle the effects of change in floral availability, nesting resources, and temperature changes (from anthropogenic climate warming), which are all factors influencing wild bees niche (Table 2 and first parts of the Introduction to this thesis). The sites Allacher Lohe, Virginia Depot, and the Munich Botanical Garden have changed differently in these aspects over the last 20 years. While the Allacher Lohe has seen a decrease in foraging and nesting resources due to heavy construction work at the site, the Virginia Depot´s flower and nesting resources have increased over time because of the efforts of nature conservation organisations, and the Munich Botanical Garden has stayed basically constant as regards these two factors. All three sites have experienced an increase in temperature in spring and summer and a shorter winter period within the last twenty years (Zohner and Renner 2014). The investigation of the newly established flower strips, on the other hand, allowed me to analyse the effect of an increase in floral and nesting resources without the factor temperature, as the long-term trend of increasing temperatures should not apply within a two-year investigation period (Table 2). Thus, my expectation was that if an increase in temperature benefits wild bees, as these are generally most species rich in Mediterranean type habitats (Michener 2007), this effect would become clear at the Munich Botanical Garden site, as all other factors were constant there, while it would be masked at the other sites because of the changes there in floral and nesting site availability. On the other hand, the 20-year-long data from the Allach and Virginia Depot sites, as well as the two-year data from the flower strips, would allow me to detect any effects of changing floral resources and changing nesting resources on wild bee diversity, with the expectation that an increase in floral and nesting resources would also lead to an increase in bee species numbers.

Table 2. Development of floral and nesting resources as well as spring and summer temperatures at the studied sites Allacher Lohe, Virginia Depot, the Botanical Garden and the flowers strips. ↗ indicates increases in the respective parameter, ↘ decreases, and = indicates no change in the parameter.

	Allacher Lohe	**Virginia Depot**	**Munich Botanical Garden**	**Flower strips**
Floral resources	↘	↗	=	↗
Nesting resources	↘	↗	=	↗
Temperature	↗	↗	↗	=

Another issue in bee conservation is the question of replacement habitats. As mentioned above, the proportion of green roofs in cities is increasing, as does the number of studies about this topic. In Munich, building owners can apply for a grant when they want to convert their roof into a green roof with a soil layer of at least 8 cm ("Sonderprogramm zur Förderung der Begrünung der Landeshauptstadt München", available at https://lhm-author.muenchen.swm.de/rathaus/home/Stadtverwaltung/baureferat/foerderprogramm-priv-gruen_alt/dachgruen.html, last accessed 04 Dec. 2019). To investigate the impact of green roofs on wild bees, I compiled studies of bees on green roofs worldwide and created a species list of all wild bees reported in these studies to be found on green roofs. The studies showed that green roofs can be used by some, but not all wild bee species to a varying extent and that intensive green roofs are more species-rich than extensive roofs (chapter 7), therefore it is worth to consider this newly created habitat for conservation purpose. The second replacement habitat I investigated was a partly renatured gravel pit. Due to the gravel excavation, such pits simulate dynamic river landscapes, which have become increasingly scarce. I made a species list of the Obermayr gravel pit in Riem, Munich, and compared it with the results from other studies in Central European gravel pits (chapter 8). Thanks to the open soil spots in the gravel pits, these are an especially valuable habitat for ground-nesting species.

During my field work, I observed many species of wild bees in their natural environment. By chance, I noticed the copulation of nomad bees in Allach, where I saw the remarkable behaviour of antennal grabbing. Little has been published to this topic so far, although I found an unpublished doctoral thesis by M. Schindler (2005) in which the behavior was described for other species of *Nomada*. In collaboration with Dr. Schindler, I found gland structures on the antennae of *Nomada flavoguttata*, using SEM studies, similar to those he had found in *N. fucata* and *N. lathburiana* before (chapter 9).

Chapter 2

Narrow habitat breadth and late-summer emergence increase extinction vulnerability in Central European bees

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Narrow habitat breadth and late-summer emergence increases extinction vulnerability in Central European bees

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Evaluating intrinsic and extrinsic traits that predispose species to local extinction is important for targeting conservation efforts. Among the species of special concern in Europe are bees, which, along with butterflies, are the best monitored insects. Bees are most species-rich in Mediterranean-type climates with short winters, warm springs, and dry summers. In Central Europe, climate warming *per se* is, therefore, expected to benefit most bee species, while pesticides and the loss of habitats and plant diversity should constitute threats. Here, we use the bee fauna of Germany, which has been monitored for Red Lists for over 40 years, to analyse the effects of habitat breadth, pollen specialization, body size, nesting sites, sociality, duration of flight activity, and time of emergence during the season. We tested each factor's predictive power against changes in commonness and Red List status, using phylogenetically informed hierarchical Bayesian (HB) models. Extinction vulnerability is strongly increased in bees flying in late summer, with a statistical model that included flight time, habitat preference, and duration of activity correctly predicting the vulnerability status of 85% of the species. Conversely, spring emergence and occurrence in urban areas each reduce vulnerability, pointing to intensive land use especially harming summer-active bees, with the combination of these factors currently shifting Germany's bee diversity towards warm-adapted, spring-flying, city-dwelling species.

1. Introduction

Bee diversity in the USA and Europe appears to be declining due to intensive agriculture, habitat loss, and the increased use of herbicides and insecticides, all of which negatively affect food sources and nesting opportunities [1–4]. Climate warming *per se* should benefit, not harm, bee diversity because most bees do well in Mediterranean-type climates [5], with the exception of a few cool-adapted groups, such as bumblebees [6]. A recent study of bee diversity in a protected urban garden in Germany indeed supported an increase in warm-adapted species with climate warming, based on inventories taken 20 years apart [7]. In non-protected areas, however, reduced floral and nesting resources due to human land use negatively impact bee diversity and abundance [1,3,8,9], potentially masking the expected positive effect of shorter winters and warmer springs and summers.

The effect of reduced and temporally shifted floral resources (because of earlier flowering under climate change) on the decline of wild bees in Europe is evident from a study of population trends in 57 species (from 10 genera) in the Netherlands, which found that late-flowering pollen and nectar sources have declined more strongly than early-flowering ones, leading to stronger declines in late-flying bees [10]. Earlier studies on bumblebee decline also implicate changes in agricultural practices. Thus, in Ireland, late-nesting bumblebee species associated with grassy habitats are declining, probably due to the agricultural trend of replacing hay with silage, leading to earlier mowing [11]. Similarly, bumblebee species in Britain, Canada, and China with late-active queens are especially susceptible to decline [12]. All this differentially affects the relative extinction risks of early- and late-flying bees. In addition, climate warming is uneven among seasons [13,14]. For instance, climate warming from 1960 to 2016 across 53 German weather stations shows strong March–May and July–August warming, while June, September, and October have hardly changed over those 56 years (inset figure 2*a*). If spring-warming and the early mass-flowering of herbaceous crops [10] benefit spring-flying bees, while agricultural activities during summer and autumn are detrimental to late-flying bees, this might lead to a shift in the relative vulnerability of spring- versus summer-active species.

Here, we use the German bee fauna as a system in which to study extinction risk predictors. Germany harbours 561 bee species in 35 genera [15], most of which have been barcoded with multiple specimens per species [16]. In terms of both taxonomy and ecology, Germany's bees are comparatively well known, with red-listing having been carried out for at least 40 years [15,17]. We, therefore, decided to rely on Red List status and whether status assessments have changed since 1977 as a proxy for species' extinction risks. Of the 445 bees included in this study, about 23% are pollen specialists (oligolectic), 227 (51%) build their nests in the ground and flight times fall between late February (first species of *Andrena* and *Osmia*, early-emerging overwintering queens of *Bombus*) and mid-October (e.g. species of *Colletes* and freshly emerged sexuals of *Lasioglossum* and *Halictus*).

Specifically, we set out to investigate whether early-season and late-season species differ in their Red List status and how their abundances and long-term population trends have changed over the past 40 years. Our expectation was that bees active in the fast-warming spring might do better than those later in the year. In addition, we were interested in how bees of different habitats may have fared over the past half-century. About 51.6% of Germany's land surface consists of arable land [18], 14% of urban areas [18], and 32% of forests, percentages that have changed little over the past 20 years, except for a slight increase in the percentage of urban area [19] (see electronic supplementary material, figure S1: land use 2000–2017). If urbanization and climate warming are less of a threat to bees than is intensive agriculture, this might lead to bees in urban or forest habitats doing better than those in open, non-urban habitats. We used hierarchical Bayesian (HB) models, which allowed us to control for phylogenetic structure in the data, to analyse the simultaneous effects of the biotic and abiotic traits relevant to our questions, namely habitat breadth (using a fine-grained categorization that included all types of vegetation mentioned in the autecological literature on the bees in question, namely meadows, forests, hedgerows, urban areas, raw-soil sites, and wasteland as well as altitudinal distribution), pollen specialization, body size, nesting preference, mean flight time, and duration of flight activity.

2. Material and methods

(a) Phylogeny

Cytochrome oxidase subunit I sequences of most bees that occur in Germany are available from the barcoding study of Schmidt *et al.* [16]. Where necessary, we downloaded additional sequences from GenBank in April 2018 (electronic supplementary material, table S3), resulting in a matrix of 553 species (TreeBase accession 23291). Maximum-likelihood tree inference relied on RAxML v. 8.0 [20]. Phylogenetic signal in species-level extinction risk and habitat breadth was measured with Pagel's λ [21], using the 'phylosig' function in the R package 'phytools' v. 0.2-1 [22] (figure 1).

(b) Trait scoring

We obtained information on life-history traits and extinction vulnerability status for 445 out of 561 German bee species, thus covering 79% of the German bee fauna [15] (electronic supplementary material, table S1). For each species, we scored its current Red List status either as an ordinal vector (1, not threatened; 2, near-threatened; 3, threatened; 4, highly threatened; 5, almost extinct; 6, extinct; figure 2*a*) or as a binary character (0, not threatened; 1, threatened; electronic supplementary material, figure S2) as well as abundance and long-term population trends from Westrich *et al.* [15]. The Red List status was determined based on the data of seven bee specialists, each with a different regional focus: P. Westrich for Baden-Wuerttemberg, U. Frommer for Hesse, K. Mandery for Northern Bavaria, H. Riemann for Bremen and Lower Saxony, H. Ruhnke for Saxonx-Anhalt, C. Saure for Berlin and Brandenburg, and J. Voith for Southern Bavaria and the German Alps. In terms of Red List status, 16 species are considered extinct, 26 almost extinct, 61 highly threatened, 100 threatened, 38 near-threatened, and 187 not threatened. For 17 species, the data were insufficient to assess their Red List status, leaving 428 red-listed species in our statistical models. Information on current commonness status from the Red Lists was available for all 445 species, long-term population trends, based on data of the past 50–150 years, were known for 404 species (table 1).

We scored species' pollen preferences (pollen specialization) (polylectic, oligolectic, or cuckoo) based on Westrich [23] and Scheuchl & Willner [24]. In a few cases, data were complemented with information from the International Union for the Conservation of Nature (IUCN) Red List [25]. Mesolectic species, which use pollen from a few genera of plants, were included in the category polylectic; kleptoparasitic and social parasitic species were placed in the category cuckoo. In total, 218 species were assigned the category 'polylectic', 102 'oligolectic', and 125 'cuckoo'. Species' nest location (above or below ground) was scored based on the literature [23,24], with 213 species nesting solely below ground and 232 above or below ground or in host nests. Sociality was coded as a binary trait, and all species not explicitly stated to be social in Westrich [23] or Scheuchl & Willner [24] were considered solitary, regardless of whether they are parasitic, form nest aggregations, or nest alone (268 species were social, 178 solitary).

The mean body length of females (as a proxy for body size) was recorded in millimetres based on Amiet *et al.* [26–30], von Hagen & Aichhorn [31], Schmid-Egger & Scheuchl [32], Dathe & Scheuchl [33], and Scheuchl [34,35]. For bumblebees, the size of female workers, not queens, was used for the analysis.

The average duration of flight activity per year (duration of flight activity; see electronic supplementary material, table S2) and the average month of flight activity (mean flight month) were scored based on Westrich [23] and Scheuchl & Willner [24] who have for many years monitored relative bee abundances and flight times in southwestern Germany. To calculate the duration of activity for bivoltine species, we used the cumulative span of occurrence, summing the duration of activity of the first and the second generation. To obtain the mean flight month, we calculated the mean of the first and last month of activity.

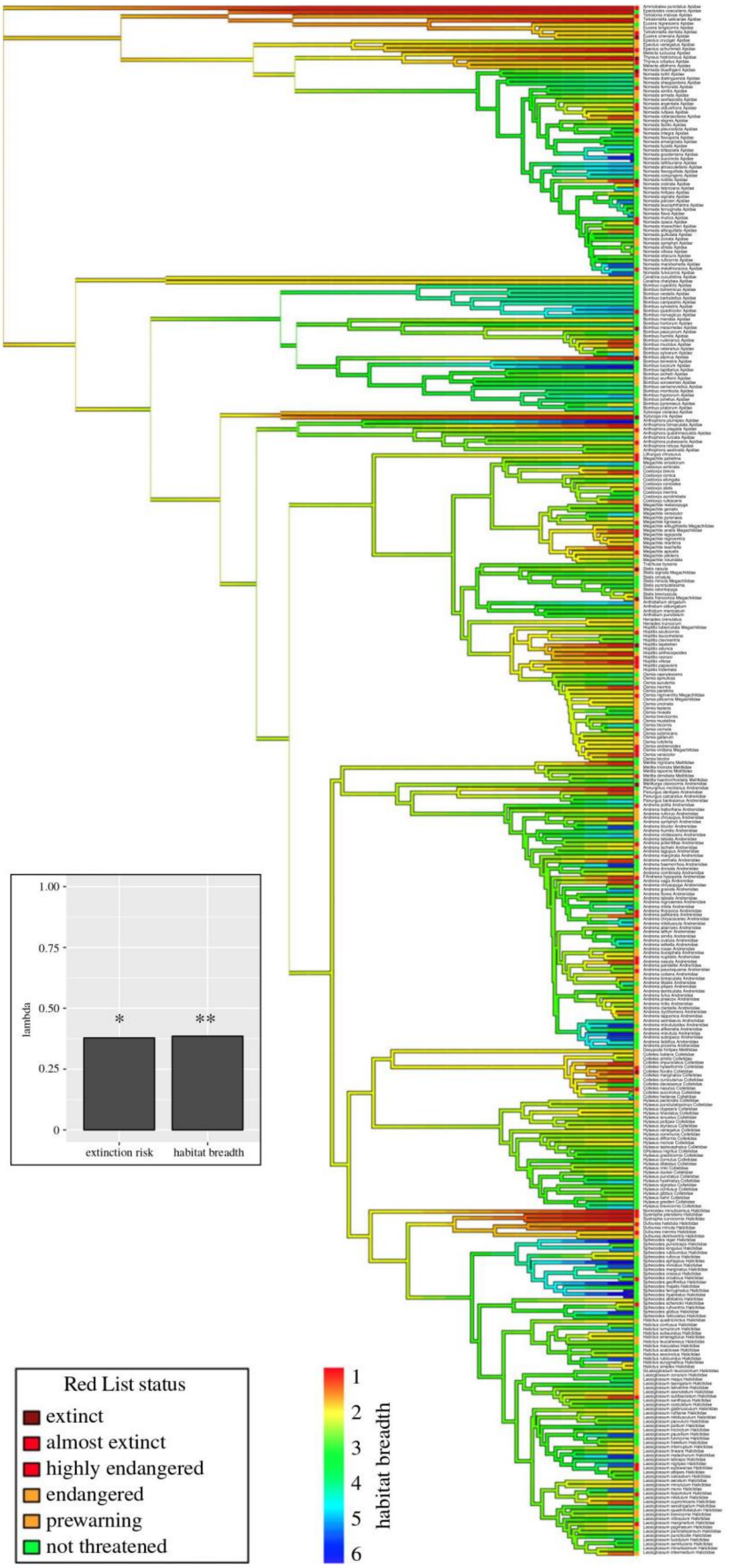

Figure 1. Phylogeny of 367 bee species occurring in Germany. Habitat breadth of species is indicated by colours of branches and Red List status by coloured squares next to tip labels. The inset shows the lambda estimates for Red List status and habitat breadth (*$p < 0.05$, **$p < 0.01$).

Habitat preferences were taken from Westrich [23] and Scheuchl & Willner [24] with six categories: forests and heaths, including alluvial forests (forests); raw-soil sites with little vegetation, such as sand dunes, heathland, steppes, and sand or gravel pits; urban areas, including gardens and parks; meadows (mown at least once a year); hedgerows; wasteland and

Table 1. Accuracy of predictions of species-level Red List status, abundance status, and long-term population trends. Overall classification rates from multivariate generalized linear models including 14 predictor variables (see figure 2) and pairwise interaction terms among them or without interaction terms (in parentheses). Type 1 error: species erroneously predicted endangered by the model. Type 2 error: species erroneously predicted to be not endangered. *N*, number of bee species included in the models.

	classification rate	type 1 error	type 2 error	*N*
Red List status	85% (77%)	9% (15%)	6% (8%)	428
abundance	84% (78%)	10% (13%)	6% (9%)	445
long-term trend	81% (75%)	11% (16%)	7% (9%)	404

nutrient-poor sites. Species occurring everywhere or with no specific habitat preferences were scored as ubiquists. In a second step, we scored habitat breadth as the number of habitats a species is found in (thus ranging from 1 to 6). Ubiquists were assigned a habitat breadth value of 6. Species' altitudinal distribution (altitude) was scored as lowlands from 0 to 300 m, colline from 300 to 800 m, montane from 800 to 1600 m, subalpine from 1600 to 2100 m, and alpine from 2100 to 3000 m [23,24].

(c) Hierarchical Bayesian modelling

We applied an HB approach (following [36]) for testing effects of species-level traits on extinction risk. This allowed us to control for phylogenetic structure in the data and to simultaneously fit slope parameters of biotic and abiotic traits relevant to our questions without concerns of *p*-value correction or multiple testing. To test for multicollinearity of our 14 predictor variables, we used a variance inflation factor (VIF) analysis, implemented in the R function 'vif', from the package 'HH' [37]. This analysis showed high variance inflation (greater than 10) for habitat breadth, because the six habitat types (*urban areas*, *hedgerows*, *forests*, *raw-soil sites*, *meadows*, and *wasteland*) together explain a significant proportion of habitat breadth. Thus, we decided to analyse specific habitat preferences in a separate analysis. After having separated habitat breadth and habitat preferences, all VIF were smaller than 2, indicating sufficient independence among predictor variables. We also calculated a correlation dendrogram, showing that Pearson's correlation coefficients among predictor variables are less than 0.5 (electronic supplementary material, figure S3).

We applied both binary and ordinal models, treating Red List status as a binary character (see above; figure 2*a*). To account for phylogenetic structure in the data, genus- and family-level random effects were incorporated in the models (note that the phylogeny could not be incorporated as a distance matrix in the analysis because this is only possible for continuous, not binary or ordinal, dependent variables). Six continuous and eight binary variables were used as predictor variables (see *Trait scoring*); continuous variables: *body size*, *mean flight month*, *duration of activity*, *altitude*, *habitat breadth*; binary variables: *pollen specialization* (oligolecty versus polylecty/cuckoo), *sociality* (social versus solitary), nest location (belowground versus aboveground ± belowground), *urban areas* (yes/no), *hedgerows* (yes/no), *forests* (yes/no), *raw-soil sites* (yes/no), *meadows* (yes/no), and *wasteland* (yes/no).

Regression components of the ordinal models are of the form:

Life-history traits and habitat breadth model:

$$\begin{aligned}&\text{ordered logit (redlist ordinal}_i) \\ &\quad = \beta_1\ x \text{ duration of activity}_i + \beta_2\ x \text{ mean flight month} \\ &\quad + \beta_3\ x \text{ body size}_i + \beta_4\ x \text{ pollen specialization}_i \\ &\quad + \beta_5\ x \text{ sociality}_i + \beta_6\ x \text{ nest location}_i \\ &\quad + \beta_7\ x \text{ habitat breadth}_i + \text{genus}_i + \text{family}_i.\end{aligned}$$

Habitat preference model:

$$\begin{aligned}&\text{ordered logit(redlist ordinal}_i) \\ &\quad = \beta_1\ x \text{ urban areas}_i + \beta_2\ x \text{ hedgerows}_i + \beta_3\ x \text{ wasteland}_i \\ &\quad + \beta_4\ x \text{ meadows}_i + \beta_5\ x \text{ raw-soil}_i + \beta_6\ x \text{ forest}_i \\ &\quad + \beta_7\ x \text{ altitude}_i + \text{genus}_i + \text{family}_i.\end{aligned}$$

The duration of activity, mean flight month, body size, pollen specialization, sociality, nest location, habitat breadth, urban areas, hedgerows, altitude, wasteland, meadows, raw-soil, and forest refer to species values (*i*) in electronic supplementary material, table S1, β refers to the estimated slopes of the respective variable (figure 2) and genus and family refer to the genus- and family-level random intercept effects inserted in the model.

Regression components of the binary models are of the form:

Life-history trait and habitat breadth model:

$$\begin{aligned}&\text{redlist binary}_i \sim \text{Bernoulli}(p_i) \\ &\text{logit}(p_i) = \alpha + \beta_1\ x \text{ duration of activity}_i + \beta_2\ x \text{ mean flight month} \\ &\qquad + \beta_3\ x \text{ body size}_i + \beta_4\ x \text{ pollen specialization}_i \\ &\qquad + \beta_5\ x \text{ sociality}_i + \beta_6\ x \text{ nest location}_i \\ &\qquad + \beta_7\ x \text{ habitat breadth}_i + \text{genus}_i + \text{family}_i.\end{aligned}$$

Habitat preference model:

$$\begin{aligned}&\text{redlist binary}_i \sim \text{Bernoulli}(p_i) \\ &\text{logit}(p_i) = \alpha + \beta_1\ x \text{ urban areas}_i \\ &\qquad + \beta_2\ x \text{ hedgerows}_i + \beta_3\ x \text{ wasteland}_i \\ &\qquad + \beta_4\ x \text{ meadows}_\text{i} + \beta_5\ x \text{ raw} - \text{soil}_i \\ &\qquad + \beta_6\ x \text{ forest}_i + \beta_7\ x \text{ altitude}_i + \text{genus}_i + \text{family}_i\end{aligned}$$

The term α refers to the intercept and β to the estimated slopes of the respective variable.

We additionally applied the same models, using current abundance status or long-term population trends instead of Red List status as response variables (electronic supplementary material, figures S1 and S2). Again, we applied both binary and ordinal models, treating abundance and population trend either as ordinal vectors or binary characters (abundance ordinal vector: 1, abundant; 2, common; 3, frequent; 4, occasional; 5, rare; 6, extremely rare; 7, extinct; abundance binary: 0, abundant to frequent; 1, rare to extinct; population trend ordinal vector: 1, increase; 2, no change; 3, small decline; 4, decline; 5, large decline; 6, extinct; population trend binary: 0, no decline; 1, decline).

To examine relative effect sizes of predictor variables, we standardized all variables by subtracting their mean and dividing by 2 s.d. before analysis [38]. The resulting posterior distributions are a direct statement of the relative effect of each tested trait on species-level extinction vulnerability. The effective posterior means for the respective relationships are shown in figure 1*a*; electronic supplementary material figures S2 and S3. To parametrize our models, we used the JAGS implementation [39] of Markov chain Monte Carlo (MCMC) methods in the R package R2JAGS [40]. The R code for our HB models is provided in the electronic supporting material as Note S1. We ran three parallel MCMC chains for 20 000 iterations with a 5000-iteration burn-in and evaluated model convergence with the Gelman and Rubin [41] statistic. Non-informative priors were specified for all parameter distributions, including normal priors for α and β coefficients (fixed effects; mean = 0; variance = 1000), and uniform priors between 0 and 100 for the variance of the genus random intercept effect, based on De Villemereuil *et al.* [42].

In table 1, we summarize the statistical results.

(d) Classification rates and recursive partitioning analysis

Multivariate generalized linear models were applied to test how well the combination of scored traits explains species-level extinction risk, i.e. testing for type 1 and type 2 errors (species erroneously considered as not endangered by the model or species erroneously considered endangered by the model). The models included all 14 predictor variables and an interaction for each pair of them to account for possible interactions among traits and Red List status, abundance, and population trend as binary dependent variables (table 1). Overall, Red List status was predicted with an accuracy of 85%; false positives (type 1 error) occurred for 9% of species and false negatives (type 2 error) for 6%. For recursive partitioning analyses (figure 3) of the four best predictor variables (habitat breadth, urban areas, duration of activity, and mean flight month), we used the 'rpart' option in the R library [43], setting the minimum node size to 15 (minimum number of species contained in each terminal node).

All statistical analyses were conducted in R 3.2.2 [44].

3. Results

Early-emerging bees had the lowest extinction probabilities, late-emerging bees the highest (figures 2 and 3), and extinction risk was also significantly increased in species with narrow habitat breadths (figures 1 and 2) or short flight periods, irrespective of whether extinction risk was coded as an ordinal (figure 2) or a binary character (electronic supplementary material, figure S2). Large-bodied species were slightly more vulnerable to extinction (figure 2*a*). Pollen preference, sociality, and nest location had no statistical effect on vulnerability. When we ran the analysis again, replacing the response variable 'extinction risk' with either 'bee abundance' or 'long-term population trends', the logistic regression (table 1) and HB models (compare figure 2*a* with electronic supplementary material, figure S4*a*,*b*) showed similar results, with similar effect sizes of predictor variables.

The fine-grained habitat scoring possible because of the relatively well-known autecology of Germany's bees revealed that occurrence in urban habitats, for example gardens and parks, as well as hedge habitats, strongly lowers a species' extinction risk compared with occurrence in any of the other five habitat types (figure 2*a*). High-altitude bees (coded as a continuous trait; Material and methods) also have a reduced extinction risk (figure 2*a*). Occurrence in forests and nutrient-poor sites, such as raw-soils, meadows, and wastelands had no statistical effect on vulnerability.

A logistic regression model, using the predictor variables (figure 2*a*) and pairwise interaction terms among them, correctly predicted the extinction risk of 85% of the 428 species for which we had information on Red List status (table 1). Nine per cent (38 species) were erroneously predicted as endangered (type 1 error) and 6% (26 species) were erroneously predicted as not endangered (type 2 error). Whether a species was misclassified or not did not show a phylogenetic signal (electronic supplementary material, figure S5).

4. Discussion

The three strongest extinction-predicting factors for the bees with data on both life-history traits and Red List status over the past 40 years (445 species or 79% of the German bee fauna) were narrow habitat preferences, a short flight time, and late-summer emergence (figures 1*b* and 3). By contrast, spring emergence reduced extinction risk. Shorter winters, earlier springs, and increased average monthly temperatures in Central Europe should benefit many species of bees because the superfamily Apoidea worldwide is most species-rich in Mediterranean-type climates [5]. For Germany, March–May and July–August have warmed more strongly than other months (inset figure 2*a*), a pattern that *per se* cannot explain why spring-active species should have a lower extinction risk than species active later in the year. The phenological mismatch between pollinators and flowers is also an unlikely explanation because current data indicate strongly buffered synchronization mechanisms between bees' flight times and the flowering time of their pollen and nectar sources, probably because mutualistic interactions depend on such buffering for their persistence [45,46]. This leaves lack of pollen and nectar sources as the most probable explanation for why late-flying bees are declining more strongly than bees that reproduce early in the year when mass-flowering crops (e.g. *Brassica napus*), flowering trees and shrubs (e.g. *Salix* spp., *Prunus* spp.), and flowering herbs in improved grasslands and field margins (e.g. *Taraxacum* spp., *Cardamine pratensis*, and *Ranunculus* spp.) still provide early-season floral resources [10]. Intensive land use (with monocultures, fertilizers, insecticides, and herbicides) and habitat fragmentation, rather than changes in the relative area of arable or built-up land and forest, thus emerge as the most probable factors driving the decline of wild bee species in Germany.

A caveat applying to this study is that local extinction may be common in rare species, including species for which the area under study (Germany) represents the edge of their distribution ranges. Rare species might be less reliably monitored than more abundant species, so that their changing Red List status over the past 40 years may be less well understood than that of common species. However, models that included abundance and population trends as separate parameters yielded the same results (see electronic supplementary material, figure S4). Occurrence in urban areas lowered a species' extinction risk, under both the ordinal and the binary model (figure 2; electronic supplementary material, S2). Between 2000 and 2017, Germany's urban areas have been increasing in surface (electronic supplementary material, figure S1), and they support numerous bees that find nest sites, pollen, and nectar in city gardens, probably benefitting from lower pesticide use there compared to arable land [47,48]. However, the monitoring of changes in land use in Germany is at a coarse-scale, and it is therefore problematic to link them to bee decline.

That high-altitude bees have low extinction risks may be due to Germany's montane and alpine regions being less impacted by modern human land use than are its lowlands.

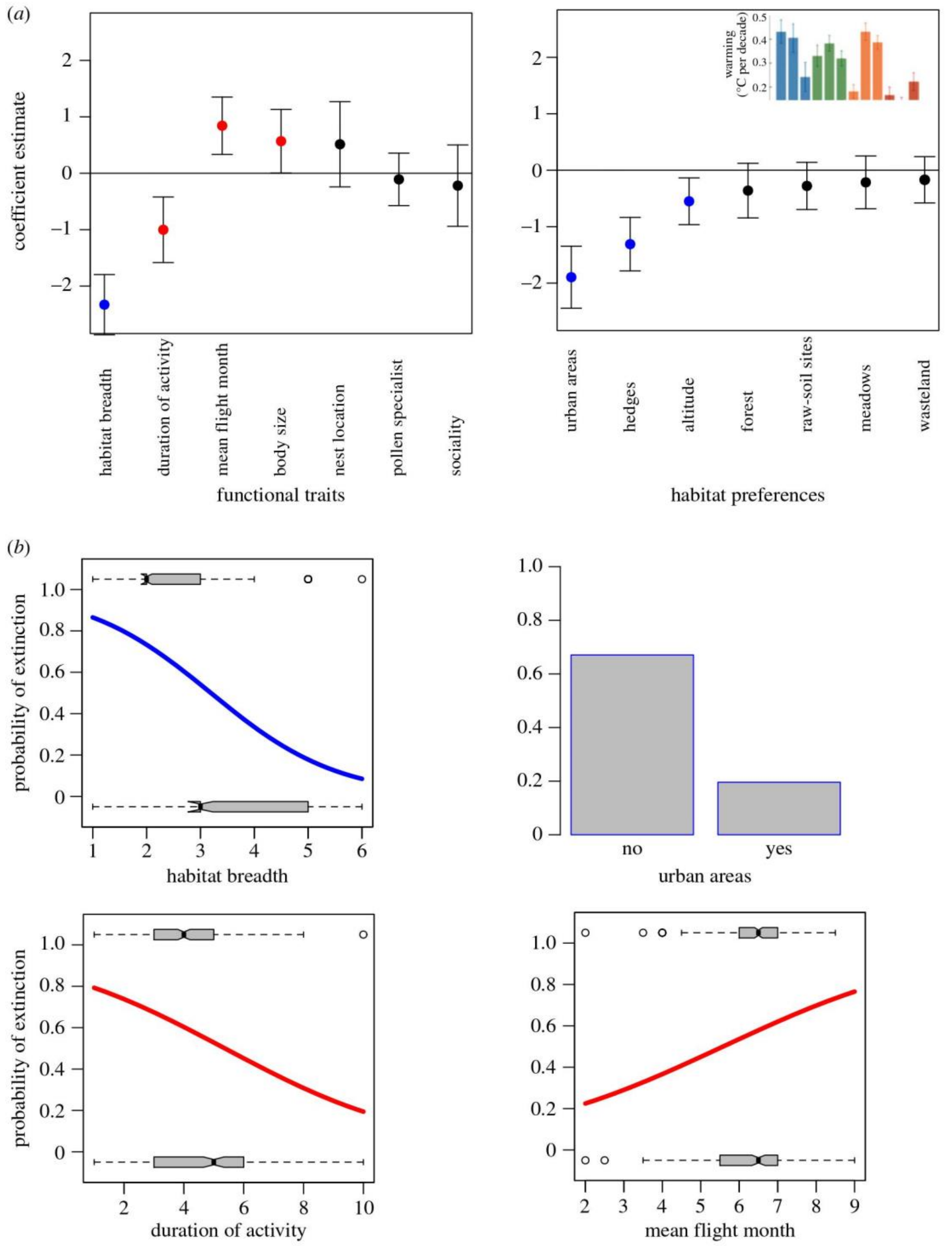

Figure 2. Extinction risk of 428 bee species occurring in Germany is linked to their habitat breadth, occurrence in urban habitats, and flight time. (*a*) Coefficient estimates (effective posterior means ± 95% credible intervals) for the effects of species-specific functional traits (duration of flight activity, mean flight month, body size, pollen specialization, sociality, nest location) and habitat breadth on species' Red List status (coded as ordinal variable). Positive estimates correspond to increasing extinction risk status. The right panel shows the effects of species-specific habitat preferences (urban areas, hedgerows, altitude, forest, raw-soil sites, meadows, and wasteland) on species' Red List status. HB linear models were applied, including genus and family random effects to account for phylogenetic signal in the data. All variables were standardized to allow for direct effect size comparisons. Red dots indicate significant functional traits and blue dots indicate significant habitat traits. Inset shows the seasonal differences in climate warming from 1960 to 2016 across 53 German weather stations (°C increase in air temperature per decade; adapted from [14]). (*b*) The univariate probability of species-specific extinction risk (not threatened, 0; threatened, 1) in relation to the four best explanatory traits, habitat breadth, occurrence in urban areas, duration of activity, and mean flight month ($p < 0.05$ in univariate generalized linear models).

The higher extinction risk of large-bodied species (figure 2*a*) agrees with the studies of Bartomeus *et al*. [46] and Scheper *et al*. [10] who both found that body size has a negative effect on wild bee population persistence, regardless of whether bumblebees were included or excluded in the analyses. A plausible explanation is that the larger pollen requirements of larger species [49] result in stronger food limitations compared to smaller bees. Larger bees also have larger foraging ranges [50–52], which may increase their exposure to pesticides.

An earlier study of traits affecting bees' extinction vulnerability that also incorporated phylogenetic relationships did

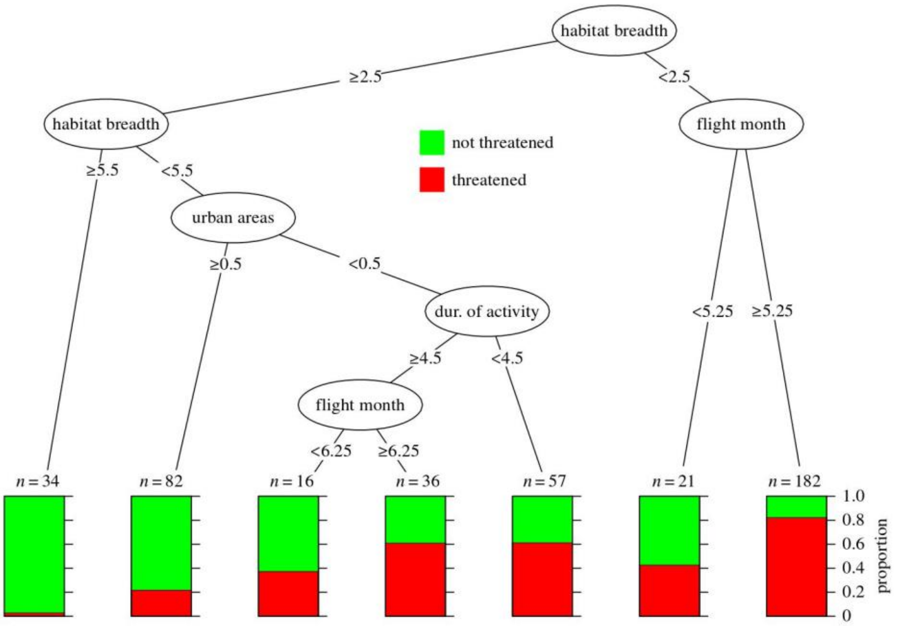

Figure 3. Recursive partitioning tree for the effect of habitat requirements and flight time on Red List status in 428 German bee species. Habitat breadth, occurrence in urban areas, duration of activity, and mean flight month were evaluated as potential split points. The number of species (*n*) contained in each terminal node shown within graphs.

not rely on Red Lists, but instead used relative abundances inferred from museum specimens (of 438 species in 47 genera) collected over 140 years in the northeastern USA [10]. The results revealed greatest declines (of collected specimens) in species with a narrow dietary breadth (pollen specialization), a short flight time (days of adult activity per year), and a large body size (intertegular distance in millimetres). Flight times were not included as a risk factor, so results cannot be compared with the present study. Meta-analyses of datasets collected either throughout the world ([8]: 19 studies) or throughout Europe ([3]: 30 studies) also did not include time of flight activity. The one study that did address a possible effect of time of flight activity on population trends—in 57 species from 10 genera in the Netherlands—found stronger declines in late-flying bees than early-flying ones [10] in agreement with our findings.

Overall, these results from a large sample of species from Central Europe that have been monitored for a comparatively long time highlight that intensive agriculture, with its negative repercussions for summer-active bees, is currently shifting faunistic diversity (at least for bees) towards warm-adapted, early-flying, city-dwelling species.

Data accessibility. All DNA sequences have been submitted to NCBI (https://www.ncbi.nlm.nih.gov) under the accession numbers listed in electronic supplementary material, table S3. All trait scoring is shown in electronic supplementary material, tables S1 and S2.

Authors' contributions. M.M.H. gathered data and observations; C.M.Z. conducted statistical analyses; S.S.R. and M.M.H. designed the study and wrote the first draft; all authors worked on the final manuscript.

Competing interests. The authors declare no competing financial interests.

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References

1. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010 Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* **25**, 345–353. (doi:10.1016/j.tree.2010.01.007)
2. Goulson D, Nicholls E, Botías C, Rotheray EL. 2015 Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* **347**, 1255957. (doi:10.1126/science.1255957)
3. De Palma A, Kuhlmann M, Roberts SP, Potts SG, Börger L, Hudson LN, Lysenko I, Newbold T, Purvis A. 2015 Ecological traits affect the sensitivity of bees to land use pressures in European agricultural landscapes. *J. Appl. Ecol.* **52**, 1567–1577. (doi:10.1111/1365-2664.12524)
4. Hass AL *et al.* 2018 Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proc. R. Soc. B* **285**, 20172242. (doi:10.1098/rspb.2017.2242)
5. Michener CD. 2007 *The bees of the world*, 2nd edn. Baltimore, MD: Johns Hopkins.
6. Kerr JT *et al.* 2015 Climate change impacts on bumblebees converge across continents. *Science* **349**, 177–180. (doi:10.1126/science.aaa7031)
7. Hofmann MM, Fleischmann A, Renner S. 2018 Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. *Oecologia* **187**, 701–706. (doi:10.1007/s00442-018-4110-x)
8. Williams NM, Crone EE, T'ai HR, Minckley RL, Packer L, Potts SG. 2010 Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.* **143**, 2280–2291. (doi:10.1016/j.biocon.2010.03.024)
9. Forrest JRK, Thorp RW, Kremen C, Williams NM. 2015 Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. *J. Appl. Ecol.* **52**, 706–715. (doi:10.1111/1365-2664.12433)
10. Scheper J, Reemer M, van Kats R, Ozinga WA, van der Linden GTJ, Schamin'ee JHJ, Siepel H, Kleijn D.

2014 Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proc. Natl Acad. Sci. USA* **111**, 17 552 – 17 557. (doi:10.1073/pnas.1412973111)

11. Fitzpatrick Ú, Murray TE, Paxton RJ, Breen J, Cotton D, Santorum V, Brown MJ. 2007 Rarity and decline in bumblebees—a test of causes and correlates in the Irish fauna. *Biol. Conserv.* **136**, 185 – 194. (doi:10.1016/j.biocon.2006.11.012)
12. Williams P, Colla S, Xie Z. 2009 Bumblebee vulnerability: common correlates of winners and losers across three continents. *Conserv. Biol.* **23**, 931 – 940. (doi:10.1111/j.1523-1739.2009.01176.x)
13. Thackeray SJ *et al.* 2016 Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241 – 245. (doi:10.1038/nature18608)
14. Renner SS, Zohner CM. 2018 Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* **49**, 165 – 182. (doi:10.1146/annurev-ecolsys-110617-062535)
15. Westrich P, Frommer U, Mandery K, Riemann H, Ruhnke H, Saure C, Voith J. 2011 Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. In *Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 3: Wirbellose Tiere* (*Teil 1*), vol. 70 (eds M Binot-Hafke *et al.* (Red.)), pp. 373–416. Landwirtschaftsverlag, Münster, Germany: Naturschutz und Biologische Vielfalt.
16. Schmidt S, Schmid-Egger C, Morinière J, Haszprunar G, Hebert PDN. 2015 DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea *partim*. *Mol. Ecol. Res.* **15**, 985 – 1000. (doi:10.1111/1755-0998.12363)
17. Rühl D. 1977 Rote Liste ausgewählter Gruppen der Hautflügler (Hymenoptera). Blatt-, Halm- und Holzwespen (Symphyta), Stechimmen und Goldwespen (Aculeata). 1. Fassung, Stand 15.3.1977. In *Rote Liste der gefährdeten Tiere und Pflanzen in der Bundesrepublik Deutschland*, vol. 1 (eds J Blab, E Nowak, W Trautmann, H Sukopp (Hrsg.)), pp. 22 – 30. Greven, Germany: Kilda Verlag, Naturschutz aktuell.
18. Statistisches Bundesamt, FS3 Land- und Forstwirtschaft, Fischerei R, 5.1. 2016 Bodenfläche nach Art der tatsächlichen Nutzung 2015. Wiesbaden.
19. Bundesministerium für Ernährung und Landwirtschaft (Hrsg.) 2016 Ergebnisse der Bundeswaldinventur 2012. Berlin.
20. Stamatakis A. 2014 RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**, 1312 – 1313. (doi:10.1093/bioinformatics/btu033)
21. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877 – 884. (doi:10.1038/44766)
22. Revell LJ. 2012 Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217 – 223. http://cran.r-project.org/web/packages/phytools (accessed: 15 May 2018). (doi:10.1111/j.2041-210X.2011.00169.x)
23. Westrich P. 1990 Die Wildbienen Baden-Württembergs. 2., verbesserte Aufl., Ulmer, Stuttgart.
24. Scheuchl E, Willner W. 2016 Taschenlexikon der Wildbienen Mitteleuropas: alle Arten im Porträt. Wiebelsheim, Germany: Quelle et Meyer Verlag.
25. IUCN. 2017 The IUCN Red List of Threatened Species. Version 2018-1. http://www.iucnredlist.org
26. Amiet F, Müller A, Neumeyer R. 1999 *Fauna Helvetica 9. Apidae 2: Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha*. Neuchatel, Switzerland: Centre Suisse de Cartographie de la Faune.
27. Amiet F, Herrmann M, Müller A, Neumeyer R. 2001 *Fauna Helvetica 9. Apidae 3: Lasioglossum, Halictus*. Neuchatel, Switzerland: Centre Suisse de Cartographie de la Faune.
28. Amiet F, Herrmann M, Müller A, Neumeyer R. 2004 *Fauna Helvetica 9. Apidae 4: Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis*. Neuchatel, Switzerland: Centre Suisse de Cartographie de la Faune.
29. Amiet F, Herrmann M, Müller A, Neumeyer R. 2007 *Fauna Helvetica 9. Apidae 5: Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa*. Neuchatel, Switzerland: Centre Suisse de Cartographie de la Faune.
30. Amiet F, Herrmann M, Müller A, Neumeyer R. 2010 *Apidae 6: Andrena, Melitturga, Panurginus, Panurgus*, vol. 26. Neuchatel, Switzerland: Centre Suisse de Cartographie de la Faune.
31. von Hagen E, Aichhorn A. 2003 *Hummeln: bestimmen, ansiedeln, vermehren, schützen*. Nottuln, Germany: Fauna Verlag.
32. Schmid-Egger C, Scheuchl E. 1997 *Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Bd. III: Andrenidae*. Velden, The Netherlands: Eigenverlag.
33. Dathe HH, Scheuchl E, Ockermüller E. 2016 Illustrierte Bestimmungstabelle für die Arten der Gattung *Hylaeus* F.(Maskenbienen) in Deutschland, Österreich und der Schweiz. Entomologica Austriaca. Suppl. 1.
34. Scheuchl E. 1996 *Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs (Band 2)*. Velden, The Netherlands: Eigenverlag.
35. Scheuchl E. 2008 Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Bd. 1: Anthophoridae. 2. erweiterte Auflage. Velden, The Netherlands.
36. Zohner CM, Benito BM, Svenning J-C, Renner SS. 2016 Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nat. Clim. Change* **6**, 1120 – 1123. (doi:10.1038/nclimate3138)
37. Heiberger RM. 2016 HH: statistical analysis and data display: Heiberger and Holland. R package version 3.1 – 25. See http:// CRAN.R-project.org/package = HH (accessed: 6 June 2016).
38. Gelman A, Hill J. 2007 *Data analyses using regression and multilevel/hierarchical models*. Cambridge, UK: Cambridge University Press.
39. Plummer M. 2003 JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In *Proc. 3rd Int. Workshop on distributed statistical computing* (eds K Hornik, F Leisch, A Zeileis). Vienna, Austria: Technische Universität Wien.
40. Su Y-S, Yajima M. 2014 R2jags v 0.04-03. http://CRAN.R-project.org/
41. Gelman A, Rubin DB. 1992 Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457 – 472. (doi:10.1214/ss/1177011136)
42. De Villemereuil P, Wells JA, Edwards RD, Blomberg SP. 2012 Bayesian models for comparative analysis integrating phylogenetic uncertainty. *BMC Evol. Biol.* **12**, 102. (doi:10.1186/1471-2148-12-102)
43. Thernau T, Atkinson B, Ripley B. 2015 rpart: recursive partitioning and regression trees. R package version 4.1-10. See http://CRAN.R-project.org/package=rpart (accessed 20 July 2016).
44. R Core Team. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org (accessed: 1 July 2018).
45. Bartomeus I, Ascher JS, Wagner D, Danforth BN, Colla S, Kornbluth S, Winfree R. 2011 Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl Acad. Sci. USA* **108**, 20 645 – 20 649. (doi:10.1073/pnas.1115559108)
46. Bartomeus I, Ascher JS, Gibbs J, Danforth BN, Wagner DL, Hedtke SM, Winfree R. 2013 Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proc. Natl Acad. Sci. USA* **110**, 4656 – 4660. (doi:10.1073/pnas.1218503110)
47. Baldock K *et al.* 2015 Where is the UK's pollinator biodiversity? Comparing flower-visitor communities between cities, farmland and nature reserves using visitation networks. *Proc. R. Soc. B* **282**, 20142849. (doi:10.1098/rspb.2014.2849)
48. Samuelson AE, Gill RJ, Brown MJ, Leadbeater E. 2018 Lower bumblebee colony reproductive success in agricultural compared with urban environments. *Proc. R. Soc. B* **285**, 20180807. (doi:10.1098/rspb.2018.0807)
49. Müller A, Diener S, Schnyder S, Stutz K, Sedivy C, Dorn S. 2006 Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee – flower relationships. *Biol. Conserv.* **130**, 604 – 615. (doi:10.1016/j.biocon.2006.01.023)
50. Gathmann A, Tscharntke T. 2002 Foraging ranges of solitary bees. *J. Anim. Ecol.* **71**, 757 – 764. (doi:10.1046/j.1365-2656.2002.00641.x)
51. Greenleaf SS, Williams NM, Winfree R, Kremen C. 2007 Bee foraging ranges and their relationship to body size. *Oecologia* **153**, 589 – 596. (doi:10.1007/s00442-007-0752-9)
52. Hofmann MM, Fleischmann A, Renner SS. Tracking of 2600 individuals shows that small European solitary bees have median foraging distances below 185 m. Submitted for publication.

Supplementary material from

Narrow habitat breadth and late-summer emergence increase extinction vulnerability in Central European bees

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Supplementary figures S1-S5

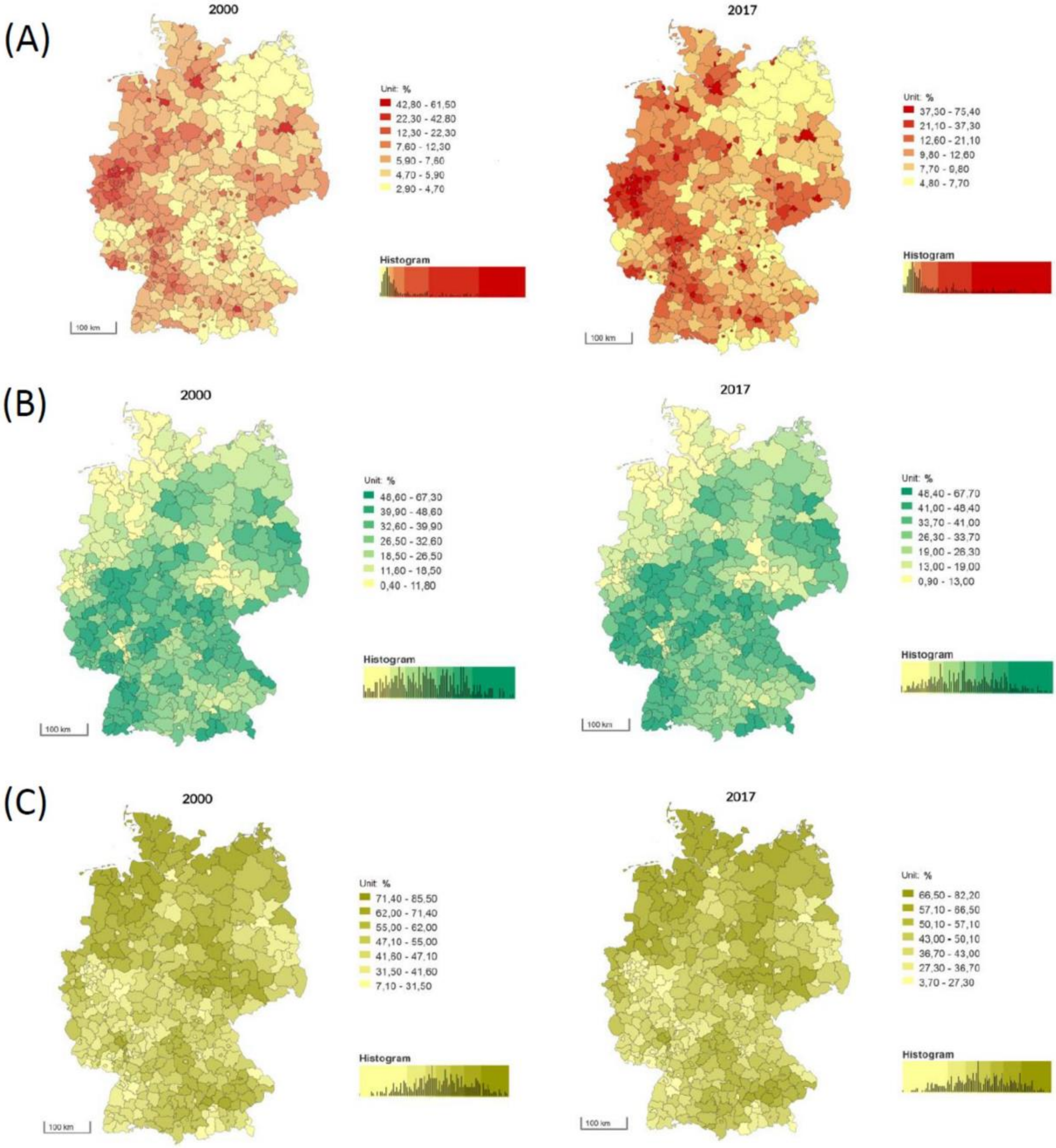


Figure S1 | Percentages of (A) human settlements and the transport infrastructure, (B) woodland, and (C) arable land in 2000 and 2017.

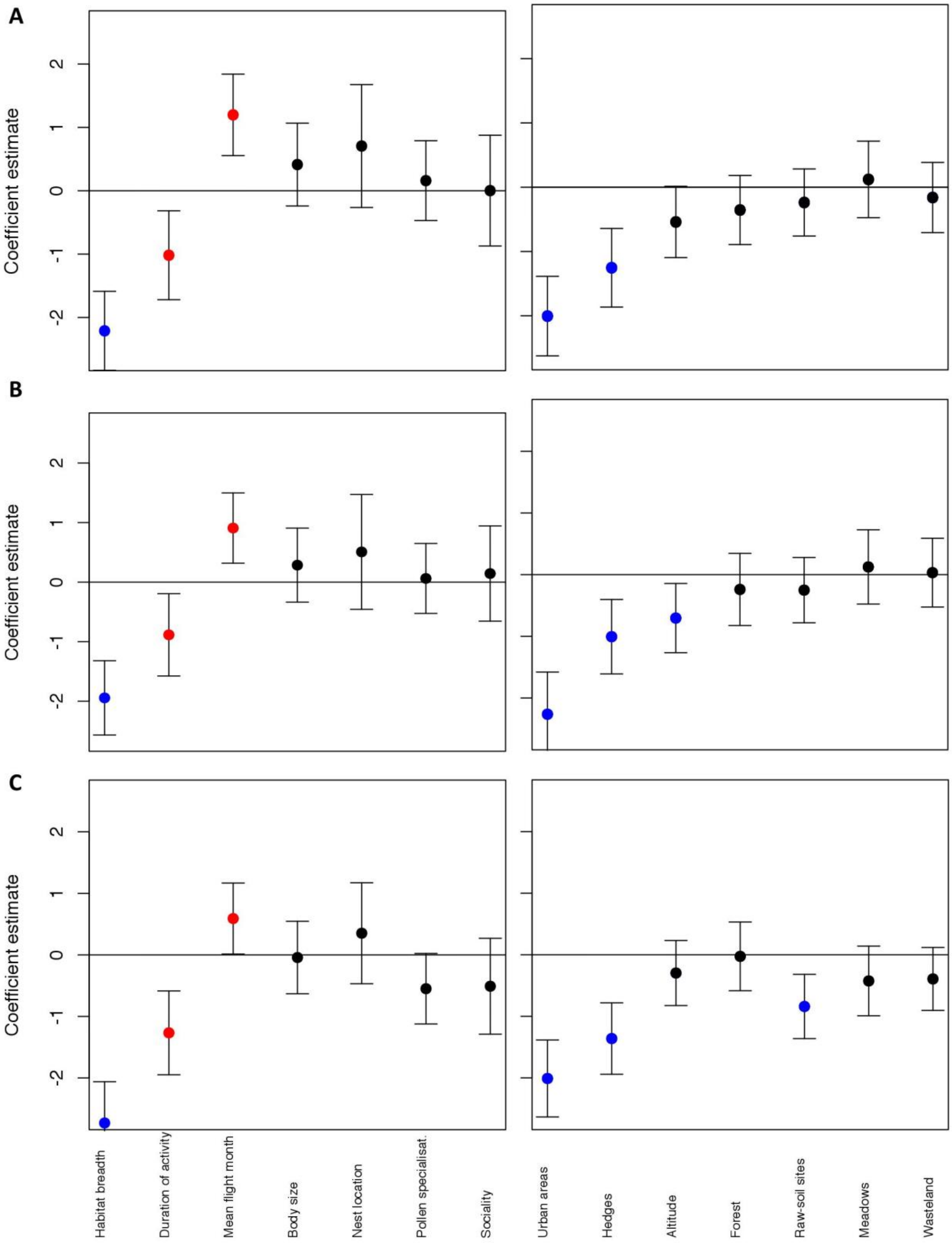


Figure S2 | Extinction risk (A), population trends (B) and abundance (C) of bee species occurring in Germany modeled as binary characters. a, Coefficient estimates (effective posterior means ± 95% credible intervals) for the effects of species-specific functional traits (duration of activity, mean flight month, body size, pollen specialization, sociality, nest location) and habitat requirements (habitat breadth, urban areas, hedgerows, altitude, wasteland, meadows, raw-soil sites, forest) on Red List status (A), population trends (B), and abundance (C) (coded as binary variables). Hierarchical Bayesian linear models were applied, including genus and family random effects to account for phylogenetic signal in the data. All variables were standardized to allow for direct effect size comparisons. $N = 428$ (A), 404 (B), and 445 (C) species.

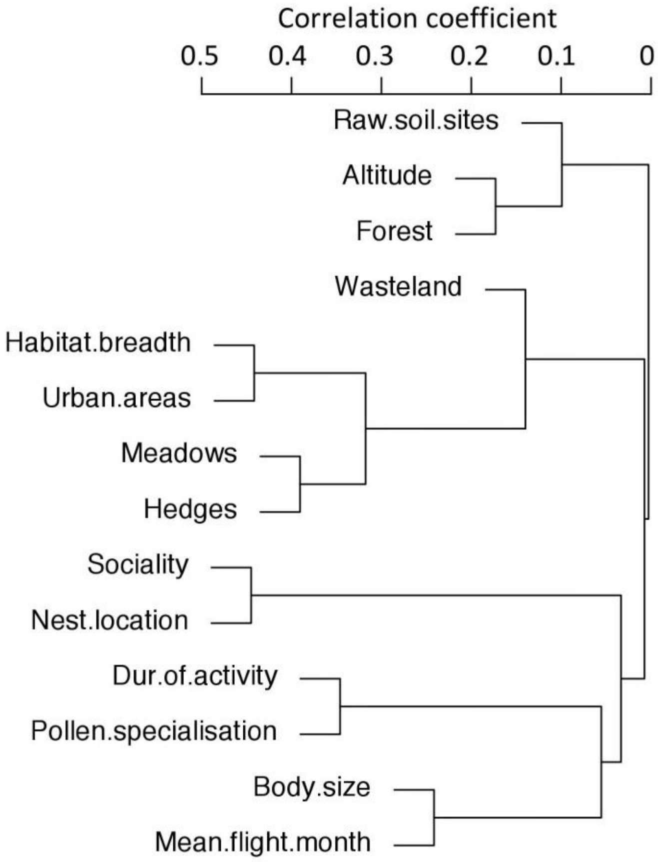


Figure S3 | Correlation dendrogram for the 14 variables used to predict extinction risk. Pearson's correlation coefficients were calculated. All correlation coefficients are < 0.5, indicating sufficient independence among predictor variables.

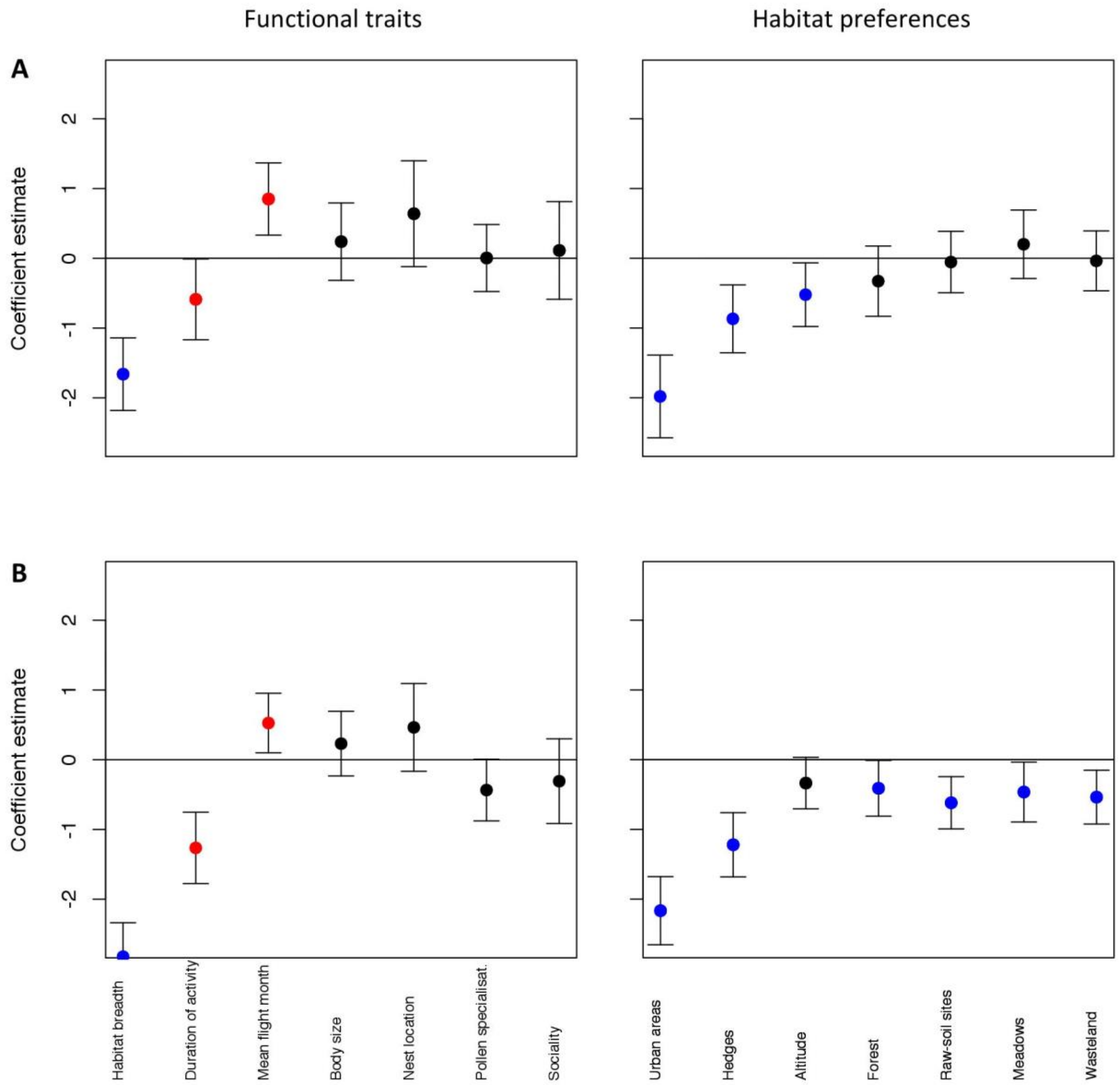


Figure S4 | Population trends (A) and abundance (B) of Germany's bee species are linked to habitat breadth, occurrence in urban areas, and flight time (duration and month of year). a, Coefficient estimates (effective posterior means ± 95% credible intervals) for the effects of species-specific functional traits (duration of activity, mean flight month, body size, pollen specialization, sociality, nest location) and habitat requirements (habitat breadth, urban areas, hedgerows, altitude, wasteland, meadows, raw-soil sites, forest) on population trends (A) and abundance (B) (coded as ordinal variables). Hierarchical Bayesian linear models were applied, including genus and family random effects to account for phylogenetic signal in the data. All variables were standardized to allow for direct effect size comparisons. $N = 404$ (A) and 445 (B) species.

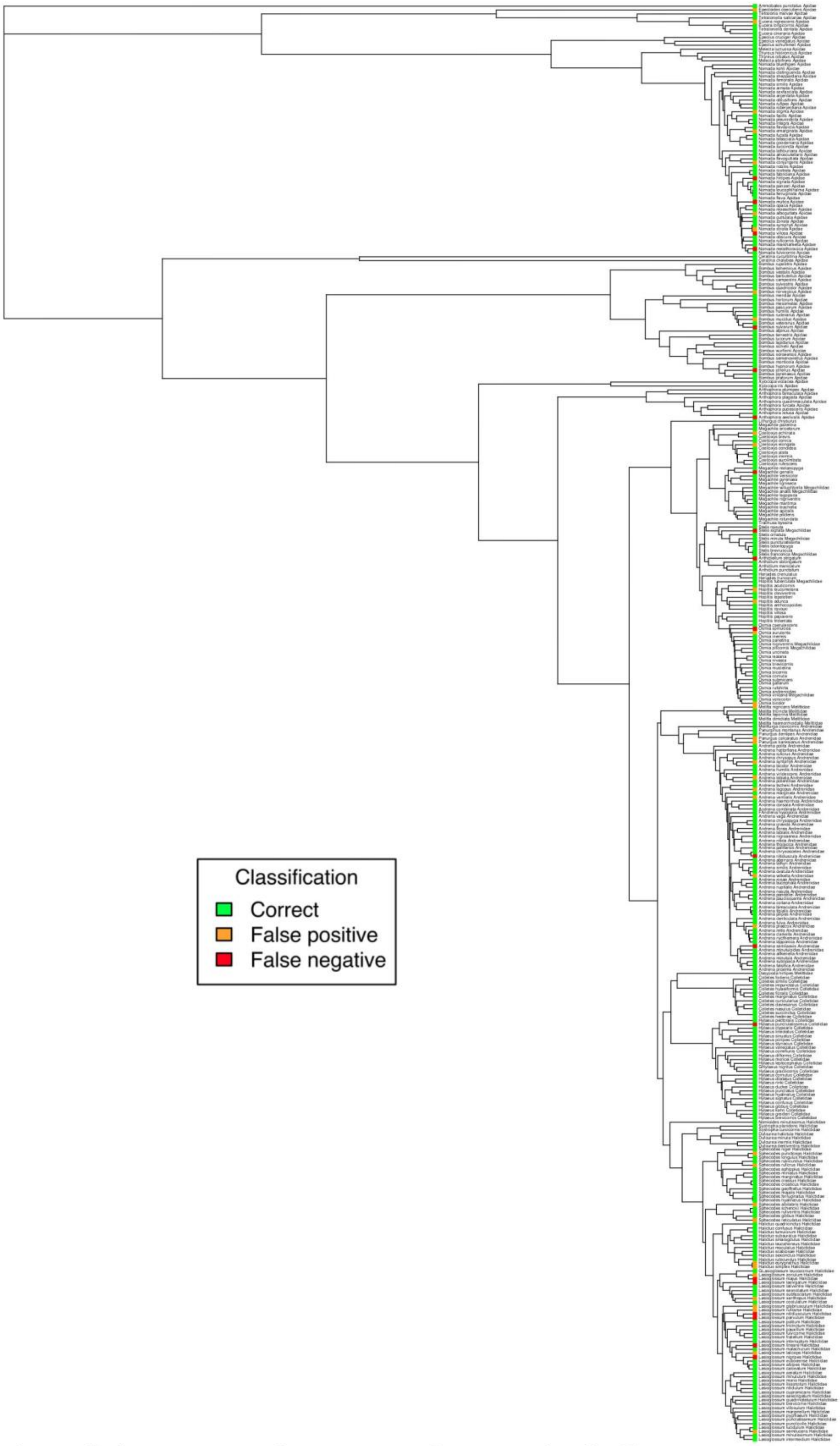


Figure S5 | Phylogeny of 367 bee species occurring in Germany showing for which species, Red List status was misclassified by the generalized linear model. False positives (Type 1 error): species erroneously predicted endangered (see Table 1). False negatives (Type 2 error): species erroneously predicted to be not endangered. For both false positives and false negatives Lambda <0.01.

Table S1: The 17 traits and their states for all species coded

Species	Red.list	Abundance	Population.trend	Pollen.specialisation	Nest.location	Sociality	Mean.flight.month	Duration.of.activity	Size.mean	Altitude.mean	Forest	Raw.soil	Urban.areas	Meadows	Hedgerows	Wasteland	Habitat.breadth
Dufourea halictula (NYLANDER, 1852)	4	4	4	oligolectic	ground	solitary	7,5	2	4,5	400	0	1	0	0	0	1	2
Hylaeus clypearis (SCHENCK, 1853)	1	3	2	polylectic	above	solitary	7,5	4	4,5	800	0	0	0	0	1	1	2
Hylaeus pictipes NYLANDER, 1852	1	3	2	polylectic	above	solitary	7	3	4,5	800	0	1	0	0	1	1	3
Hylaeus styriacus FÖRSTER, 1871	1	3	2	polylectic	above	solitary	7	3	4,5	800	1	0	0	0	1	1	3
Lasioglossum glabriusculum (MORAWITZ, 1872)	1	3	2	polylectic	ground	social	7	7	4,5	800	0	1	0	0	0	1	2
Lasioglossum lucidulum (SCHENCK, 1861)	1	2	2	polylectic	ground	solitary	7	7	4,5	400	0	1	0	1	1	1	4
Lasioglossum minutissimum (KIRBY, 1802)	1	4	2	polylectic	ground	solitary	6,5	6	4,5	800	0	1	0	1	0	1	3
Lasioglossum politum (SCHENCK, 1853)	1	3	2	polylectic	ground	social	6,5	8	4,5	400	0	1	1	1	0	1	4
Nomada bluethgeni STÖCKHERT, 1943	6	7	6	cuckoo	host nest	cuckoo	6	5	4,5	400	0	1	0	1	0	0	2
Nomioides minutissimus (ROSSI, 1790)	4	6	4	polylectic	ground	solitary	7	3	4,5	400	0	1	0	0	0	0	1
Stelis minima SCHENCK, 1861	1	4	2	cuckoo	host nest	cuckoo	7	3	4,5	800	0	0	1	1	1	1	4
Hylaeus brevicornis NYLANDER, 1852	1	2	2	polylectic	above	solitary	7,5	4	5	800	0	0	1	1	1	1	4
Hylaeus gracilicornis (MORAWITZ, 1867)	1	4	insufficient data	polylectic	above	solitary	7	3	5	400	1	1	0	0	1	0	3
Hylaeus moricei (FRIESE, 1898)	3	4	3	polylectic	above	solitary	7	3	5	400	1	0	0	0	1	1	3
Lasioglossum aeratum (KIRBY, 1802)	3	4	3	polylectic	ground	social	6,5	6	5	1050	0	1	0	0	0	1	2
Lasioglossum marginellum (SCHENCK, 1853)	4	5	3	polylectic	ground	solitary	6,5	4	5	400	0	1	0	0	0	0	1
Sphecodes longulus VON HAGENS, 1882	1	3	2	cuckoo	host nest	cuckoo	6	7	5,25	800	1	1	1	1	1	1	6
Halictus smaragdulus VACHAL, 1895	3	4	3	polylectic	ground	social	6	5	5,5	800	0	1	0	0	0	1	2
Hylaeus gredleri FÖRSTER, 1871	1	2	2	polylectic	above	solitary	7	3	5,5	800	1	0	1	0	1	1	4
Hylaeus kahri FÖRSTER, 1871	1	4	insufficient data	polylectic	above	solitary	7,5	4	5,5	800	0	0	0	0	0	1	1
Hylaeus leptocephalus (MORAWITZ, 1870)	1	3	2	polylectic	above	solitary	7	5	5,5	800	0	0	1	0	1	1	3
Hylaeus lineolatus (SCHENCK, 1861)	3	4	3	polylectic	above	solitary	7,5	4	5,5	400	0	1	0	0	1	0	2
Hylaeus punctatus (BRULLÉ, 1832)	1	3	2	polylectic	above	solitary	6,5	4	5,5	400	0	0	1	0	1	1	3
Hylaeus sinuatus (SCHENCK, 1853)	1	3	2	polylectic	above	solitary	7	3	5,5	800	1	0	0	0	1	1	3
Lasioglossum cupromicans (PÉREZ, 1903)	3	5	insufficient data	polylectic	ground	solitary	6,5	6	5,5	1900	0	1	0	0	0	0	1
Lasioglossum morio (FABRICIUS, 1793)	1	1	2	polylectic	ground	social	6,5	8	5,5	1050	1	1	1	1	1	1	6
Lasioglossum pauxillum (SCHENCK, 1853)	1	1	2	polylectic	ground	social	6,5	8	5,5	800	1	1	1	1	1	1	6
Lasioglossum semilucens (ALFKEN, 1914)	1	3	2	polylectic	ground	solitary	5	6	5,5	400	0	1	0	0	1	1	3
Lasioglossum tarsatum (SCHENCK, 1868)	4	4	4	polylectic	ground	solitary	6	5	5,5	400	0	1	0	0	0	0	1
Nomada distinguenda MORAWITZ, 1874	3	4	insufficient data	cuckoo	host nest	cuckoo	7	7	5,5	800	1	1	1	1	1	1	6
Nomada kohli SCHMIEDEKNECHT, 1882	4	4	4	cuckoo	host nest	cuckoo	6,5	4	5,5	400	0	1	0	1	1	1	4
Sphecodes geoffrellus (KIRBY, 1802)	1	2	2	cuckoo	host nest	cuckoo	7	7	5,5	1500	1	1	1	1	1	1	6
Sphecodes hyalinatus VON HAGENS, 1882	1	1	2	cuckoo	host nest	cuckoo	7	7	5,5	1050	1	1	1	1	1	1	6
Sphecodes marginatus VON HAGENS, 1882	1	3	insufficient data	cuckoo	host nest	cuckoo	6,5	4	5,5	800	0	1	0	0	0	0	1
Sphecodes miniatus VON HAGENS, 1882	1	3	insufficient data	cuckoo	host nest	cuckoo	6,5	6	5,5	1500	1	1	1	1	1	1	6
Sphecodes niger VON HAGENS, 1874	1	3	2	cuckoo	host nest	cuckoo	7	7	5,5	1050	1	1	1	1	1	1	6
Stelis breviuscula (NYLANDER, 1848)	1	2	2	cuckoo	host nest	cuckoo	7	5	5,5	800	0	0	0	1	1	0	2
Stelis minuta LEPELETIER & SERVILLE, 1825	1	4	insufficient data	cuckoo	host nest	cuckoo	7,5	4	5,5	800	0	1	0	0	1	1	3
Andrena minutula (KIRBY, 1802)	1	1	2	polylectic	ground	solitary	5,5	6	6	1050	1	1	1	1	1	1	6
Dufourea alpina MORAWITZ, 1865	unknown	6	2	polylectic	ground	solitary	7	3	6	1900	0	1	0	0	0	0	1
Dufourea minuta LEPELETIER, 1841	3	4	3	oligolectic	ground	solitary	7,5	4	6	1450	1	0	0	0	0	0	1
Lasioglossum intermedium (SCHENCK, 1868)	3	4	3	polylectic	ground	solitary	6	5	6	1800	0	1	0	0	0	0	1
Lasioglossum lissonotum (NOSKIEWICZ, 1926)	4	5	3	polylectic	ground	social	6	5	6	800	0	1	0	0	0	1	2
Lasioglossum nitidiusculum (KIRBY, 1802)	2	3	3	polylectic	ground	solitary	6,5	6	6	400	0	1	0	0	1	1	3
Lasioglossum nitidulum (FABRICIUS, 1804)	1	2	2	polylectic	ground	social	6,5	8	6	800	0	1	1	0	0	0	2
Lasioglossum parvulum (SCHENCK, 1853)	2	4	3	polylectic	ground	solitary	7	7	6	800	1	1	1	1	1	1	6
Lasioglossum pygmaeum (SCHENCK, 1853)	3	4	insufficient data	polylectic	ground	solitary	6,5	6	6	400	0	1	0	0	0	1	2
Nomada atroscutellaris STRAND, 1921	2	3	3	cuckoo	host nest	cuckoo	5	3	6	800	0	1	1	1	1	1	5
Nomada discedens PÉREZ, 1884	5	6	insufficient data	cuckoo	host nest	cuckoo	6	1	6	400	0	1	0	0	0	0	1
Nomada flavoguttata (KIRBY, 1802)	1	1	2	cuckoo	host nest	cuckoo	5,5	6	6	1050	1	1	1	1	1	1	6
Nomada fuscicornis NYLANDER, 1848	1	3	2	cuckoo	host nest	cuckoo	7,5	4	6	800	0	1	0	0	1	1	3
Nomada obtusifrons NYLANDER, 1848	4	4	4	cuckoo	host nest	cuckoo	7,5	2	6	1050	1	1	0	0	1	0	3
Nomada sheppardana (KIRBY, 1802)	1	1	2	cuckoo	host nest	cuckoo	5,5	6	6	800	1	1	0	0	1	1	4
Sphecodes puncticeps THOMSON, 1870	1	3	2	cuckoo	host nest	cuckoo	6,5	6	6	800	0	1	0	0	0	1	2
Andrena alfkenella PERKINS, 1914	2	4	3	polylectic	ground	solitary	6,5	4	6,5	800	0	0	0	1	1	1	3
Andrena falsifica PERKINS, 1915	1	3	2	polylectic	ground	solitary	4	3	6,5	800	1	0	0	1	1	1	4
Andrena minutuloides PERKINS, 1914	1	1	2	polylectic	ground	solitary	6,5	6	6,5	800	1	1	1	1	1	1	6
Andrena potentillae PANZER, 1809	4	5	3	oligolectic	ground	solitary	4	3	6,5	400	0	1	0	0	0	1	2
Andrena semilaevis PÉREZ, 1903	3	4	3	polylectic	ground	solitary	6	3	6,5	1050	0	1	0	1	1	1	4
Anthidium strigatum (PANZER, 1805)	2	3	4	polylectic	above	solitary	7	3	6,5	800	0	1	1	0	1	1	4
Camptopoeum frontale (FABRICIUS, 1804)	4	6	3	oligolectic	ground	solitary	7,5	2	6,5	400	0	1	0	0	0	0	1
Ceratina cyanea (KIRBY, 1802)	1	2	2	polylectic	above	solitary	7	7	6,5	800	0	0	1	1	1	1	4
Epeolus alpinus FRIESE, 1893	unknown	6	2	cuckoo	host nest	cuckoo	6,5	2	6,5	1500	0	1	0	0	0	0	1
Hylaeus cardioscapus COCKERELL, 1924	unknown	6	insufficient data	polylectic	above	solitary	7	3	6,5	400	0	0	0	0	1	0	1
Hylaeus communis NYLANDER, 1852	1	1	2	polylectic	above	solitary	7,5	6	6,5	1050	0	1	1	0	1	0	3
Hylaeus dilatatus (KIRBY, 1802)	1	3	2	polylectic	above	solitary	7,5	4	6,5	800	0	1	0	0	1	1	3
Hylaeus hyalinatus SMITH, 1842	1	1	2	polylectic	above	solitary	7	5	6,5	800	0	1	1	1	1	1	5
Hylaeus rinki (GORSKI, 1852)	1	4	2	polylectic	above	solitary	7	3	6,5	800	1	0	0	0	1	0	2
Lasioglossum brevicorne (SCHENCK, 1868)	3	4	3	oligolectic	ground	social	7	7	6,5	800	0	1	0	0	1	0	2
Lasioglossum convexiusculum (SCHENCK, 1853)	4	5	3	polylectic	ground	solitary	6,5	4	6,5	800	0	0	0	0	0	1	1
Lasioglossum fulvicorne (KIRBY, 1802)	1	1	2	polylectic	ground	solitary	6,5	8	6,5	1050	1	1	1	1	1	1	6
Lasioglossum interruptum (PANZER, 1798)	3	3	4	polylectic	ground	social	7	7	6,5	800	0	0	0	1	0	1	2
Lasioglossum laticeps (SCHENCK, 1868)	1	2	2	polylectic	ground	social	6,5	8	6,5	800	0	1	0	1	1	1	4
Lasioglossum minutulum (SCHENCK, 1853)	3	4	3	polylectic	ground	solitary	6,5	6	6,5	800	0	0	0	1	0	1	2
Lasioglossum punctatissimum (SCHENCK, 1853)	1	3	2	polylectic	ground	solitary	7	7	6,5	400	0	1	0	0	1	1	3
Lasioglossum puncticolle (MORAWITZ, 1872)	3	4	3	polylectic	ground	social	7	7	6,5	400	0	1	0	1	1	1	4
Lasioglossum quadrisignatum (SCHENCK, 1853)	4	5	3	polylectic	ground	solitary	6,5	6	6,5	800	0	0	0	0	1	1	2
Lasioglossum rufitarse (ZETTERSTEDT, 1838)	1	3	2	polylectic	ground	solitary	7	7	6,5	1050	1	1	0	0	1	0	3
Lasioglossum sexstrigatum (SCHENCK, 1868)	1	3	2	polylectic	ground	solitary	7	7	6,5	400	1	1	1	0	0	1	4
Lasioglossum tricinctum (SCHENCK, 1874)	3	4	3	polylectic	ground	social	6,5	6	6,5	400	0	1	0	0	0	1	2
Lasioglossum villosulum (KIRBY, 1802)	1	2	2	polylectic	ground	solitary	6,5	8	6,5	800	1	1	1	1	1	1	6
Nomada errans LEPELETIER, 1841	4	5	3	cuckoo	host nest	cuckoo	7	3	6,5	400	0	1	1	1	1	1	5
Nomada posthuma BLÜTHGEN, 1949	unknown	5	insufficient data	cuckoo	host nest	cuckoo	6	3	6,5	400	1	0	0	0	0	0	1
Osmia andrenoides SPINOLA, 1808	4	4	4	oligolectic	above	solitary	6,5	4	6,5	800	0	1	0	0	0	1	2
Osmia crenulata (NYLANDER, 1856)	1	3	2	oligolectic	above	solitary	7,5	4	6,5	800	0	0	0	1	1	0	2
Osmia truncorum (LINNAEUS, 1758)	1	2	2	oligolectic	above	solitary	7,5	4	6,5	800	0	0	0	1	1	0	2
Osmia versicolor LATREILLE, 1811	5	6	4	polylectic	above	solitary	5,5	4	6,5	800	0	1	0	0	0	1	2
Osmia viridana MORAWITZ, 1874	4	6	3	polylectic	above	solitary	5,5	4	6,5	800	0	1	0	0	0	1	2
Panurginus herzi MORAWITZ, 1892	unknown	6	2	polylectic	ground	solitary	7	3	6,5	1450	0	0	0	1	0	0	1
Panurginus montanus GIRAUD, 1861	1	4	2	oligolectic	ground	solitary	7	3	6,5	1900	0	0	0	1	0	0	1
Sphecodes crassus THOMSON, 1870	1	1	2	cuckoo	host nest	cuckoo	7	7	6,5	1050	1	1	1	1	1	1	6
Sphecodes croaticus MEYER, 1922	4	4	insufficient data	cuckoo	host nest	cuckoo	7,5	6	6,5	800	0	1	0	0	0	1	2
Stelis odontopyga NOSKIEWICZ, 1926	3	4	3	cuckoo	host nest	cuckoo	7	3	6,5	1050	0	1	0	1	1	0	3
Stelis ornatula (KLUG, 1807)	1	3	2	cuckoo	host nest	cuckoo	6	5	6,5	1050	0	1	0	0	1	1	3
Stelis signata (LATREILLE, 1809)	3	4	3	cuckoo	host nest	cuckoo	6,5	4	6,5	800	0	1	1	0	1	1	4
Andrena subopaca NYLANDER, 1848	1	2	2	polylectic	ground	solitary	5,5	6	7	1050	1	1	1	1	1	1	6
Andrena viridescens VIERECK, 1916	2	3	3	oligolectic	ground	solitary	5	3	7	800	0	1	1	1	1	1	5
Anthidium nanum MOCSÁRY, 1879	3	4	3	oligolectic	above	solitary	7,5	4	7	800	0	0	0	0	1	1	2
Ceratina cucurbitina (ROSSI, 1792)	1	3	2	polylectic	above	solitary	7	5	7	800	0	1	1	0	1	1	4
Coelioxys echinata FÖRSTER, 1853	1	4	1	cuckoo	host nest	cuckoo	7,5	2	7	800	0	1	0	0	1	1	3
Epeolus cruciger (PANZER, 1799)	3	3	4	cuckoo	host nest	cuckoo	7,5	2	7	400	0	1	0	0	1	1	3
Halictus confusus SMITH, 1853	1	3	2	polylectic	ground	solitary	5,5	7	7	1050	0	1	0	0	0	1	2
Halictus tumulorum (LINNAEUS, 1758)	1	1	2	polylectic	ground	social	6,5	6	7	1050	1	1	1	1	1	1	6
Hylaeus annulatus (LINNAEUS, 1758)	unknown	6	2	polylectic	above	solitary	7,5	4	7	1050	1	0	1	1	1	1	5
Hylaeus confusus NYLANDER, 1852	1	2	2	polylectic	above	solitary	6,5	6	7	1050	1	1	1	0	1	0	4
Hylaeus cornutus CURTIS, 1831	1	3	insufficient data	polylectic	above	solitary	7	3	7	800	0	1	0	1	1	1	4
Hylaeus duckei (ALFKEN, 1904)	3	4	3	polylectic	above	solitary	6,5	4	7	800	0	1	0	0	0	1	2
Hylaeus gibbus SAUNDERS, 1850	1	2	2	polylectic	above	solitary	7	5	7	1050	0	1	0	0	1	1	3
Hylaeus pectoralis FÖRSTER, 1871	3	3	4	polylectic	above	solitary	7	5	7	400	1	0	0	1	1	0	2
Hylaeus variegatus (FABRICIUS, 1798)	2	3	3	polylectic	ground	solitary	7,5	4	7	800	0	1	0	0	0	1	2
Lasioglossum fratellum (PÉREZ, 1903)	1	3	2	polylectic	ground	solitary	7	7	7	1500	1	1	0	0	1	0	3
Lasioglossum lativentre (SCHENCK, 1853)	2	3	3	polylectic	ground	solitary	7	7	7	800	0	0	0	1	1	1	3
Lasioglossum lineare (SCHENCK, 1868)	3	3	4	polylectic	ground	social	6	7	7	800	0	1	0	0	0	1	2
Lasioglossum quadrinotatum (KIRBY, 1802)	3	4	3	polylectic	ground	solitary	7	7	7	400	0	0	0	1	0	1	2
Nomada facilis SCHWARZ, 1967	3	5	insufficient data	cuckoo	host nest	cuckoo	6,5	4	7	800	0	1	0	1	1	0	3
Nomada integra BRULLÉ, 1832	3	4	insufficient data	cuckoo	host nest	cuckoo	6	5	7	800	0	1	0	1	1	0	3
Ammobates punctatus (FABRICIUS, 1804)	4	5	3	cuckoo	host nest	cuckoo	7	3	7,5	800	0	1	0	0	0	0	1
Andrena nanaeformis NOSKIEWICZ, 1925	6	7	6	polylectic	ground	solitary	5,5	4	7,5	400	0	1	0	0	0	0	1
Biastes brevicornis (PANZER, 1798)	5	6	3	cuckoo	host nest	cuckoo	7	3	7,5	400	0	0	0	0	0	1	1
Dufourea dentiventris (NYLANDER, 1848)	3	3	4	oligolectic	ground	solitary	7,5	2	7,5	1050	0	0	0	0	1	1	2
Dufourea inermis (NYLANDER, 1848)	4	4	4	oligolectic	ground	solitary	7,5	2	7,5	1500	0	0	0	0	1	1	2
Epeolus variegatus (LINNAEUS, 1758)	2	3	3	cuckoo	host nest	cuckoo	7	3	7,5	800	0	1	0	0	0	1	2
Halictus leucaheneus EBMER, 1972	3	3	4	polylectic	ground	social	6,5	6	7,5	800	1	1	0	0	0	1	3
Halictus subauratus (ROSSI, 1792)	1	3	2	polylectic	ground	social	5,5	6	7,5	800	0	1	0	0	0	1	2
Hylaeus difformis (EVERSMANN, 1852)	1	4	2	polylectic	above	solitary	7	3	7,5	800	1	0	0	1	1	0	3
Hylaeus punctulatissimus SMITH, 1842	3	3	insufficient data	oligolectic	above	solitary	6,5	4	7,5	800	0	1	1	0	0	1	3
Lasioglossum quadrinotatulum (SCHENCK, 1861)	3	4	3	polylectic	ground	solitary	7	7	7,5	400	0	1	0	1	0	1	3
Nomada baccata SMITH, 1844	4	4	4	cuckoo	host nest	cuckoo	8	3	7,5	400	0	1	0	0	0	0	1
Nomada guttulata SCHENCK, 1861	1	4	2	cuckoo	host nest	cuckoo	5,5	4	7,5	800	0	0	1	1	1	1	4
Osmia gallarum SPINOLA, 1808	2	4	3	oligolectic	above	solitary	6	5	7,5	800	0	0	0	0	1	1	2
Osmia spinulosa (KIRBY, 1802)	3	3	4	oligolectic	above	solitary	7	5	7,5	1050	0	1	0	1	1	0	3
Osmia submicans MORAWITZ, 1870	4	5	3	polylectic	above	solitary	5,5	2	7,5	800	0	1	0	0	1	1	3
Rhophitoides canus (EVERSMANN, 1852)	2	4	3	oligolectic	ground	solitary	7	3	7,5	400	0	0	0	0	0	1	1
Sphecodes ephippius (LINNAEUS, 1767)	1	1	2	cuckoo	host nest	cuckoo	6,5	8	7,5	1050	1	1	1	1	1	1	6
Sphecodes ferruginatus VON HAGENS, 1882	1	3	2	cuckoo	host nest	cuckoo	7	7	7,5	1500	1	1	1	1	1	1	6
Sphecodes rufiventris (PANZER, 1798)	1	3	2	cuckoo	host nest	cuckoo	6,5	6	7,5	800	0	1	0	0	1	1	3
Andrena labiata FABRICIUS, 1781	1	2	2	polylectic	ground	solitary	5,5	4	8	1050	0	0	1	1	1	1	4
Andrena nitidiuscula SCHENCK, 1853	3	3	4	oligolectic	ground	solitary	7	3	8	800	0	1	1	1	1	1	5
Coelioxys afra LEPELETIER, 1841	3	4	3	cuckoo	host nest	cuckoo	7	3	8	800	0	1	0	0	0	1	2

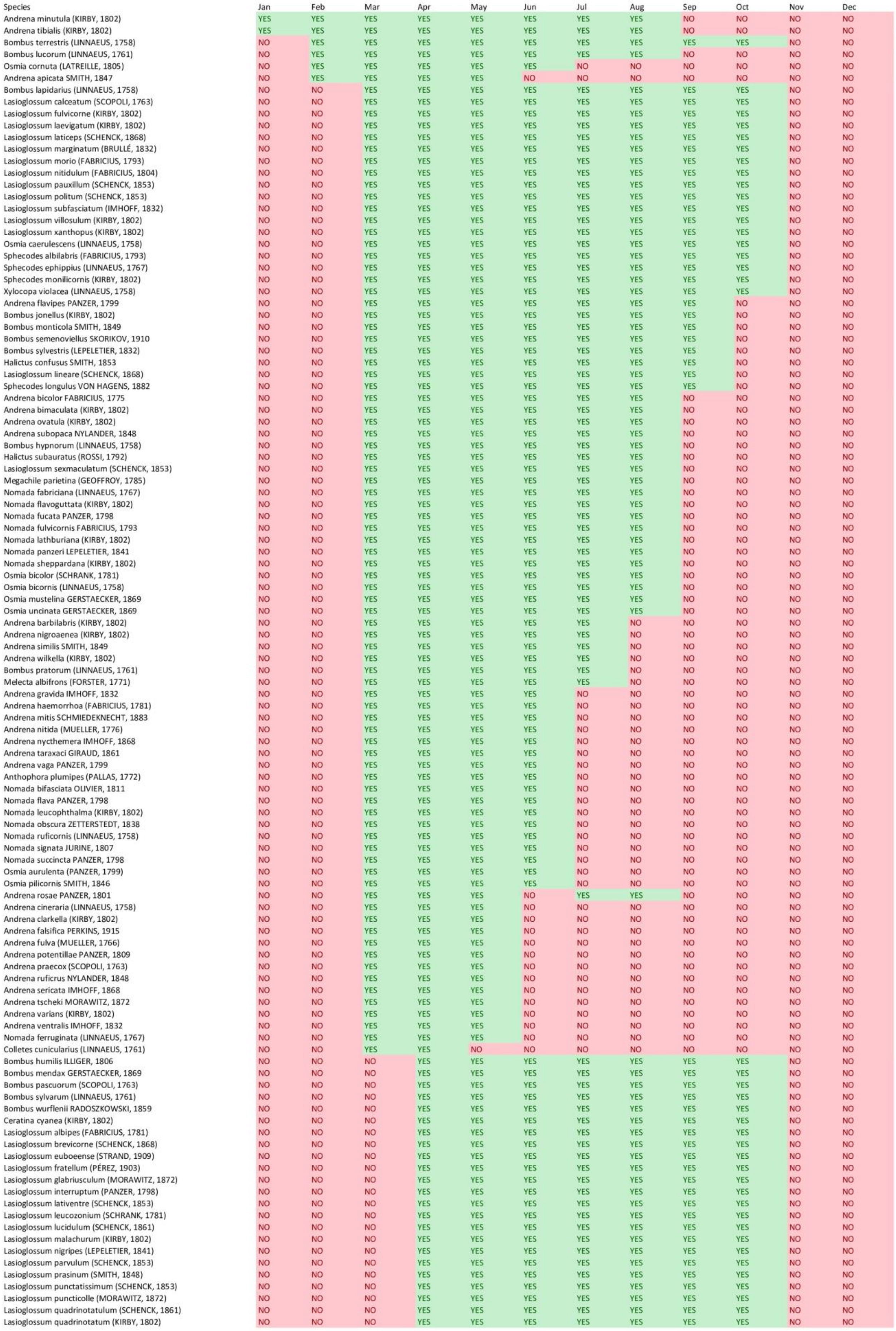
Coelioxys brevis EVERSMANN, 1852	4	5	3	cuckoo	host nest	cuckoo	7	3	8	400	0	1	0	0	0	0	1
Colletes mlokossewiczi RADOSZKOWSKI, 1891	unknown	6	insufficient data	oligolectic	ground	solitary	7	3	8	400	0	1	0	0	0	1	2
Hylaeus nigritus (FABRICIUS, 1798)	1	1	2	oligolectic	above	solitary	7	5	8	1050	0	1	1	1	0	1	4
Hylaeus signatus (PANZER, 1798)	1	1	2	oligolectic	above	solitary	6,5	6	8	800	0	1	1	0	1	1	4
Lasioglossum albipes (FABRICIUS, 1781)	1	1	2	polylectic	ground	social	7	7	8	1500	1	0	1	0	1	1	4
Lasioglossum laeve (KIRBY, 1802)	5	6	4	polylectic	ground	solitary	6,5	6	8	800	0	0	0	0	1	1	2
Lasioglossum marginatum (BRULLÉ, 1832)	unknown	6	2	polylectic	ground	social	6,5	8	8	800	0	0	0	1	0	1	2
Lasioglossum prasinum (SMITH, 1848)	4	4	4	polylectic	ground	solitary	7	7	8	400	0	1	0	0	0	0	1
Nomada alboguttata HERRICH-SCHÄFFER, 1839	1	3	2	cuckoo	host nest	cuckoo	4,5	2	8	400	0	1	0	0	0	0	1
Nomada argentata HERRICH-SCHÄFFER, 1839	4	4	4	cuckoo	host nest	cuckoo	8	3	8	800	0	1	0	0	0	1	2
Nomada obscura ZETTERSTEDT, 1838	1	4	2	cuckoo	host nest	cuckoo	4,5	4	8	1050	1	1	0	0	1	0	3
Nomada opaca ALFKEN, 1913	4	5	3	cuckoo	host nest	cuckoo	5,5	2	8	400	1	0	0	0	1	0	2
Nomada piccioliana MAGRETTI, 1883	3	4	3	cuckoo	host nest	cuckoo	6	3	8	800	0	0	0	1	0	1	2
Nomada rhenana MORAWITZ, 1872	3	4	insufficient data	cuckoo	host nest	cuckoo	6	5	8	400	0	1	1	1	1	1	5
Nomada roberjeotiana PANZER, 1799	3	4	insufficient data	cuckoo	host nest	cuckoo	8	3	8	800	0	1	0	0	0	0	1
Nomada rufipes FABRICIUS, 1793	2	3	3	cuckoo	host nest	cuckoo	8	3	8	1050	0	1	0	0	1	0	2
Nomada zonata PANZER, 1798	2	4	2	cuckoo	host nest	cuckoo	6	5	8	400	0	1	0	0	1	1	3
Osmia leucomelana (KIRBY, 1802)	1	2	2	polylectic	above	solitary	7	3	8	1050	0	1	0	0	1	1	3
Panurgus calcaratus (SCOPOLI, 1763)	1	3	2	oligolectic	ground	solitary	7,5	4	8	1050	0	1	0	0	1	1	3
Panurgus dentipes LATREILLE, 1811	3	4	3	oligolectic	ground	solitary	7,5	4	8	800	0	0	0	0	0	1	1
Sphecodes cristatus VON HAGENS, 1882	3	4	insufficient data	cuckoo	host nest	cuckoo	6,5	2	8	800	0	1	0	0	0	1	2
Stelis phaeoptera (KIRBY, 1802)	3	4	3	cuckoo	host nest	cuckoo	6,5	6	8	1050	0	0	0	1	1	1	3
Andrena coitana (KIRBY, 1802)	3	4	3	polylectic	ground	solitary	7,5	4	8,5	1050	1	0	0	0	1	0	2
Andrena pallitarsis PÉREZ, 1903	5	6	4	oligolectic	ground	solitary	7,5	2	8,5	400	0	0	0	0	0	1	1
Andrena ventralis IMHOFF, 1832	1	3	2	oligolectic	ground	solitary	4	3	8,5	800	0	1	0	0	0	0	1
Anthidium punctatum LATREILLE, 1809	2	3	3	polylectic	above	solitary	7	5	8,5	1050	0	0	1	0	1	1	3
Anthophora bimaculata (PANZER, 1798)	3	4	3	polylectic	ground	solitary	7	5	8,5	800	0	1	0	0	0	0	1
Anthophora pubescens (FABRICIUS, 1781)	5	6	4	polylectic	ground	solitary	7	3	8,5	800	0	0	1	1	0	0	2
Eucera alticincta (LEPELETIER, 1841)	6	7	6	oligolectic	ground	solitary	8	3	8,5	400	0	1	0	0	1	0	2
Lasioglossum calceatum (SCOPOLI, 1763)	1	1	2	polylectic	ground	social	6,5	8	8,5	1050	1	1	1	1	1	1	6
Lasioglossum laevigatum (KIRBY, 1802)	3	3	4	polylectic	ground	solitary	6,5	8	8,5	1050	0	1	0	1	1	1	4
Lasioglossum malachurum (KIRBY, 1802)	1	2	2	polylectic	ground	social	7	7	8,5	800	1	1	1	1	1	1	6
Megachile apicalis SPINOLA, 1808	4	5	3	polylectic	ground and above	solitary	7	3	8,5	800	0	0	0	1	1	0	2
Megachile rotundata (FABRICIUS, 1787)	1	3	2	polylectic	ground and above	solitary	7,5	4	8,5	800	0	1	0	0	1	1	3
Nomada conjungens HERRICH-SCHÄFFER, 1839	1	3	2	cuckoo	host nest	cuckoo	5,5	4	8,5	800	0	0	1	1	1	1	4
Nomada similis MORAWITZ, 1872	3	4	insufficient data	cuckoo	host nest	cuckoo	7,5	4	8,5	1050	1	1	0	0	1	1	4
Osmia parietina CURTIS, 1828	3	4	3	polylectic	above	solitary	6	5	8,5	1050	1	0	0	0	1	0	2
Osmia rufohirta LATREILLE, 1811	3	3	4	polylectic	above	solitary	6	5	8,5	800	0	1	0	0	0	1	2
Pseudapis femoralis (PALLAS, 1773)	6	7	6	polylectic	ground	solitary	6,5	2	8,5	400	0	1	0	0	0	1	2
Sphecodes majalis PÉREZ, 1903	1	5	2	cuckoo	host nest	cuckoo	4,5	2	8,5	400	0	0	0	1	1	1	3
Sphecodes monilicornis (KIRBY, 1802)	1	1	2	cuckoo	host nest	cuckoo	6,5	8	8,5	800	1	1	1	1	1	1	6
Sphecodes reticulatus THOMSON, 1870	1	3	2	cuckoo	host nest	cuckoo	7	7	8,5	800	0	1	0	0	1	1	3
Stelis nasuta (LATREILLE, 1809)	6	7	6	cuckoo	host nest	cuckoo	6,5	4	8,5	800	0	1	0	0	0	1	2
Systropha curvicornis (SCOPOLI, 1770)	3	4	3	oligolectic	ground	solitary	7	3	8,5	400	0	0	0	0	0	1	1
Andrena argentata SMITH, 1844	3	3	4	polylectic	ground	solitary	6,5	5	9	400	0	1	0	0	0	0	1
Andrena paucisquama NOSKIEWICZ, 1924	5	6	insufficient data	oligolectic	ground	solitary	5,5	2	9	400	0	0	0	1	1	1	3
Anthidium oblongatum (ILLIGER, 1806)	2	3	3	polylectic	above	solitary	7	3	9	800	0	0	1	0	1	1	3
Ceratina chalybea CHEVRIER, 1872	3	4	3	polylectic	above	solitary	6,5	6	9	400	0	0	0	0	0	1	1
Osmia rapunculi (LEPELETIER, 1841)	1	2	2	oligolectic	above	solitary	6,5	4	9	1050	0	0	1	1	1	1	4
Colletes daviesanus SMITH, 1846	1	2	2	oligolectic	ground	solitary	7,5	4	9	1050	0	1	1	0	0	1	3
Colletes marginatus SMITH, 1846	3	4	3	polylectic	ground	solitary	8	3	9	800	0	1	0	0	0	1	2
Epeoloides coecutiens (FABRICIUS, 1775)	1	4	2	cuckoo	host nest	cuckoo	7,5	2	9	800	1	0	0	0	1	0	2
Eucera salicariae (LEPELETIER, 1841)	3	4	3	polylectic	ground	solitary	7	3	9	400	0	1	0	0	1	0	2
Halictus maculatus SMITH, 1848	1	2	2	polylectic	ground	social	6,5	6	9	800	0	1	0	0	1	1	3
Lasioglossum leucozonium (SCHRANK, 1781)	1	1	2	polylectic	ground	solitary	7	7	9	1050	1	1	1	1	1	1	6
Lasioglossum sexmaculatum (SCHENCK, 1853)	3	5	insufficient data	polylectic	ground	solitary	5,5	6	9	400	0	1	0	0	0	0	1
Nomada fabriciana (LINNAEUS, 1767)	1	1	2	cuckoo	host nest	cuckoo	5,5	6	9	1050	1	1	1	1	1	1	6
Nomada femoralis MORAWITZ, 1869	4	5	3	cuckoo	host nest	cuckoo	5,5	4	9	800	0	1	0	1	1	1	4
Nomada ferruginata (LINNAEUS, 1767)	1	3	2	cuckoo	host nest	cuckoo	4	3	9	800	0	1	0	0	1	0	2
Nomada fucata PANZER, 1798	1	2	2	cuckoo	host nest	cuckoo	5,5	6	9	800	1	1	1	1	1	1	6
Osmia caerulescens (LINNAEUS, 1758)	1	2	2	polylectic	above	solitary	6,5	8	9	800	0	1	1	0	1	1	4
Osmia claviventris THOMSON, 1872	1	2	2	polylectic	above	solitary	7	3	9	1050	0	1	0	0	1	1	3
Osmia ravouxi PÉREZ, 1902	4	4	4	polylectic	above	solitary	6	5	9	800	0	1	0	0	0	1	2
Sphecodes pellucidus SMITH, 1845	2	3	3	cuckoo	host nest	cuckoo	6,5	6	9	1050	0	1	0	0	1	1	3
Sphecodes scabricollis WESMAEL, 1835	3	4	insufficient data	cuckoo	host nest	cuckoo	7	5	9	800	1	1	1	1	1	1	6
Thyreus orbatus (LEPELETIER, 1841)	4	5	3	cuckoo	host nest	cuckoo	7	5	9	1050	0	1	0	1	0	0	2
Andrena bicolor FABRICIUS, 1775	1	1	2	polylectic	ground	solitary	5,5	6	9,5	1050	1	1	1	1	1	1	6
Andrena chrysopus PÉREZ, 1903	2	4	2	oligolectic	ground	solitary	5,5	2	9,5	400	0	1	0	0	0	0	1
Andrena chrysosceles (KIRBY, 1802)	1	2	2	polylectic	ground	solitary	5	3	9,5	400	0	0	1	1	1	1	4
Andrena dorsata (KIRBY, 1802)	1	2	2	polylectic	ground	solitary	6	5	9,5	800	0	1	0	0	1	1	3
Andrena marginata FABRICIUS, 1776	4	4	4	oligolectic	ground	solitary	8	3	9,5	800	0	1	0	0	0	1	2
Andrena ovatula (KIRBY, 1802)	1	2	2	polylectic	ground	solitary	5,5	6	9,5	1050	0	1	1	1	1	1	5
Andrena ruficrus NYLANDER, 1848	3	4	insufficient data	oligolectic	ground	solitary	4	3	9,5	1050	1	1	0	0	1	0	3
Andrena symphyti SCHMIEDEKNECHT, 1883	1	5	insufficient data	oligolectic	ground	solitary	5	3	9,5	400	0	1	0	0	1	0	2
Anthidium byssinum (PANZER, 1798)	3	3	4	oligolectic	ground	solitary	7	3	9,5	1050	0	1	0	1	1	0	3
Coelioxys inermis (KIRBY, 1802)	1	3	2	cuckoo	host nest	cuckoo	7,5	6	9,5	800	0	0	1	1	1	1	4
Colletes impunctatus NYLANDER, 1852	3	5	3	polylectic	ground	solitary	7	3	9,5	1050	0	1	0	0	0	0	1
Epeolus schummeli SCHILLING, 1849	5	6	3	cuckoo	host nest	cuckoo	7	3	9,5	400	0	1	0	0	0	0	1
Halictus eurygnathus BLÜTHGEN, 1931	1	3	2	polylectic	ground	solitary	6,5	6	9,5	800	0	1	0	0	0	1	2
Halictus simplex BLÜTHGEN, 1923	1	2	2	polylectic	ground	solitary	6	5	9,5	1050	0	1	0	0	0	1	2
Lasioglossum euboeense (STRAND, 1909)	4	5	3	polylectic	ground	social	7	7	9,5	800	0	1	0	0	0	1	2
Lasioglossum nigripes (LEPELETIER, 1841)	4	4	4	polylectic	ground	social	7	7	9,5	1050	1	1	1	1	1	1	6
Lasioglossum subfasciatum (IMHOFF, 1832)	5	5	4	polylectic	ground	solitary	6,5	8	9,5	800	0	0	0	0	0	1	1
Lasioglossum zonulum (SMITH, 1848)	1	2	2	polylectic	ground	solitary	7	7	9,5	800	1	1	1	1	1	1	6
Megachile leachella CURTIS, 1828	3	4	3	polylectic	ground and above	solitary	7	5	9,5	800	0	1	0	0	0	0	1
Megachile pilidens ALFKEN, 1924	3	4	4	polylectic	ground and above	solitary	7	5	9,5	800	0	1	0	0	0	1	2
Nomada flavopicta (KIRBY, 1802)	1	3	2	cuckoo	host nest	cuckoo	7,5	6	9,5	400	1	1	1	1	1	1	6
Nomada hirtipes PÉREZ, 1884	3	4	3	cuckoo	host nest	cuckoo	5	3	9,5	800	0	0	0	1	1	0	2
Nomada moeschleri ALFKEN, 1913	1	5	2	cuckoo	host nest	cuckoo	6	3	9,5	800	0	0	1	1	1	0	3
Osmia acuticornis DUFOUR & PERRIS, 1840	4	5	3	polylectic	above	solitary	7	3	9,5	800	0	1	0	0	0	1	2
Osmia anthocopoides SCHENCK, 1853	3	3	4	oligolectic	above	solitary	6,5	4	9,5	1050	0	1	0	0	0	0	1
Osmia inermis (ZETTERSTEDT, 1838)	4	5	4	polylectic	above	solitary	6,5	4	9,5	1900	0	1	0	0	0	0	1
Osmia leaiana (KIRBY, 1802)	3	4	3	oligolectic	above	solitary	6	5	9,5	1050	0	0	0	1	1	1	3
Osmia niveata (FABRICIUS, 1804)	3	3	4	oligolectic	above	solitary	5,5	4	9,5	800	0	0	1	1	1	1	4
Osmia uncinata GERSTÄCKER, 1869	3	4	3	polylectic	above	solitary	5,5	6	9,5	1050	1	0	0	0	1	0	2
Rophites algirus PÉREZ, 1895	3	4	3	oligolectic	ground	solitary	6,5	2	9,5	800	0	1	0	0	0	1	2
Rophites quinquespinosus SPINOLA, 1808	4	5	3	oligolectic	ground	solitary	7	3	9,5	400	0	1	0	0	1	1	3
Sphecodes rubicundus VON HAGENS, 1875	3	4	3	cuckoo	host nest	cuckoo	6	3	9,5	400	0	0	0	1	1	0	2
Sphecodes ruficrus (ERICHSON, 1835)	1	5	2	cuckoo	host nest	cuckoo	5	3	9,5	400	0	1	0	0	0	1	2
Stelis punctulatissima (KIRBY, 1802)	1	2	2	cuckoo	host nest	cuckoo	7	5	9,5	800	0	1	1	0	1	1	4
Andrena angustior (KIRBY, 1802)	1	3	2	polylectic	ground	solitary	8	3	10	400	0	1	0	1	1	0	3
Andrena proxima (KIRBY, 1802)	1	3	2	oligolectic	ground	solitary	5	3	10	1050	0	0	1	1	1	1	4
Colletes fodiens (GEOFFROY, 1785)	3	4	3	oligolectic	ground	solitary	7,5	2	10	800	0	1	0	0	0	1	2
Colletes similis SCHENCK, 1853	2	3	3	oligolectic	ground	solitary	7,5	4	10	800	0	1	0	1	0	1	3
Dufourea paradoxa (MORAWITZ, 1867)	unknown	6	2	polylectic	ground	solitary	7,5	4	10	1900	0	1	0	0	0	0	1
Eucera cineraria EVERSMANN, 1852	6	7	6	oligolectic	ground	solitary	6	3	10	400	0	1	0	0	0	1	2
Lasioglossum costulatum (KRIECHBAUMER, 1873)	3	3	4	oligolectic	ground	solitary	6,5	6	10	1050	0	1	0	1	1	1	4
Nomada braunsiana SCHMIEDEKNECHT, 1882	5	6	insufficient data	cuckoo	host nest	cuckoo	6,5	4	10	1050	0	0	0	1	1	1	3
Nomada leucophthalma (KIRBY, 1802)	1	2	2	cuckoo	host nest	cuckoo	4,5	4	10	1050	1	1	0	0	1	0	3
Nomada mutabilis MORAWITZ, 1870	5	6	4	cuckoo	host nest	cuckoo	6	3	10	800	0	1	0	1	0	0	2
Nomada pleurosticta HERRICH-SCHÄFFER, 1839	4	5	3	cuckoo	host nest	cuckoo	7	3	10	400	0	1	0	1	1	1	4
Nomada ruficornis (LINNAEUS, 1758)	1	2	2	cuckoo	host nest	cuckoo	4,5	4	10	800	0	0	1	1	1	0	3
Nomada striata FABRICIUS, 1793	1	2	2	cuckoo	host nest	cuckoo	6	5	10	1050	0	1	0	1	1	0	3
Nomada symphyti STÖCKHERT, 1930	3	5	3	cuckoo	host nest	cuckoo	5,5	2	10	400	1	1	0	0	1	0	3
Osmia bicornis (LINNAEUS, 1758)	1	1	2	polylectic	above	solitary	5	5	10	800	1	1	1	1	1	1	6
Osmia loti MORAWITZ, 1867	unknown	6	2	polylectic	above	solitary	7,5	4	10	1500	0	1	0	0	0	0	1
Osmia pilicornis SMITH, 1846	3	5	insufficient data	polylectic	above	solitary	4,5	4	10	800	1	0	0	0	1	0	2
Sphecodes gibbus (LINNAEUS, 1758)	1	1	2	cuckoo	host nest	cuckoo	7	7	10	1500	1	1	1	1	1	1	6
Sphecodes schenckii VON HAGENS, 1882	5	6	insufficient data	cuckoo	host nest	cuckoo	6,5	6	10	400	0	1	0	0	0	1	2
Stelis franconica BLÜTHGEN, 1930	6	7	6	cuckoo	host nest	cuckoo	6	3	10	1200	0	1	0	0	0	1	2
Andrena combinata (CHRIST, 1791)	3	4	3	polylectic	ground	solitary	5,5	2	10,5	800	0	0	0	1	0	1	2
Andrena hypopolia SCHMIEDEKNECHT, 1883	4	6	4	polylectic	ground	solitary	6,5	4	10,5	400	0	1	0	0	0	0	1
Andrena lagopus (LATREILLE, 1809)	1	3	2	oligolectic	ground	solitary	5	3	10,5	800	0	1	0	1	1	1	4
Andrena praecox (SCOPOLI, 1763)	1	3	2	oligolectic	ground	solitary	4	3	10,5	800	0	1	0	0	1	0	2
Andrena simillima SMITH, 1851	5	6	3	polylectic	ground	solitary	8	3	10,5	1500	0	1	0	0	0	0	1
Bombus pyrenaeus PÉREZ, 1879	1	4	2	polylectic	ground and above	social	7	5	10,5	2300	1	0	0	0	1	0	2
Coelioxys lanceolata NYLANDER, 1852	4	6	3	cuckoo	host nest	cuckoo	6,5	2	10,5	950	1	0	0	0	1	0	2
Coelioxys mandibularis NYLANDER, 1848	1	3	2	cuckoo	host nest	cuckoo	7	3	10,5	1050	0	1	1	1	1	1	5
Colletes hylaeiformis EVERSMANN, 1852	5	6	insufficient data	oligolectic	ground	solitary	8	3	10,5	400	0	1	0	0	0	1	2
Halictus rubicundus (CHRIST, 1791)	1	3	2	polylectic	ground	social	6,5	6	10,5	1050	1	1	1	1	1	1	6
Lasioglossum sexnotatum (KIRBY, 1802)	3	4	4	polylectic	ground	solitary	7	7	10,5	400	0	1	0	0	0	1	2
Nomada emarginata MORAWITZ, 1877	1	4	2	cuckoo	host nest	cuckoo	7	5	10,5	800	0	0	0	1	1	1	3
Nomada panzeri LEPELETIER, 1841	1	2	2	cuckoo	host nest	cuckoo	5,5	6	10,5	1050	1	1	1	1	1	1	6
Osmia aurulenta (PANZER, 1799)	1	3	2	polylectic	above	solitary	5	5	10,5	800	0	1	0	1	1	1	4
Osmia bicolor (SCHRANK, 1781)	1	3	2	polylectic	above	solitary	5	5	10,5	800	1	1	0	0	1	1	4
Osmia papaveris (LATREILLE, 1799)	5	5	4	polylectic	ground	solitary	6	3	10,5	800	0	0	0	0	1	1	2
Sphecodes spinulosus VON HAGENS, 1875	3	4	insufficient data	cuckoo	host nest	cuckoo	6	3	10,5	800	0	0	0	1	1	1	3
Systropha planidens GIRAUD, 1861	4	4	4	oligolectic	ground	solitary	7	3	10,5	400	0	0	0	0	0	1	1
Thyreus histrionicus (ILLIGER, 1806)	6	7	6	cuckoo	host nest	cuckoo	7,5	2	10,5	800	0	1	0	0	0	0	1
Andrena denticulata (KIRBY, 1802)	2	3	3	oligolectic	ground	solitary	7,5	2	11	800	1	1	0	0	1	1	4
Andrena haemorrhoa (FABRICIUS, 1781)	1	1	2	polylectic	ground	solitary	4,5	4	11	800	1	1	1	1	1	1	6
Andrena humilis IMHOFF, 1832	2	3	3	oligolectic	ground	solitary	6	3	11	1050	1	1	0	1	1	1	5
Andrena pandellei PÉREZ, 1895	3	3	4	oligolectic	ground	solitary	5,5	2	11	800	0	0	0	1	1	1	3
Andrena sericata IMHOFF, 1868	unknown	6	2	oligolectic	ground	solitary	4	3	11	800	0	0	0	0	1	0	1
Andrena similis SMITH, 1849	3	4	insufficient data	oligolectic	ground	solitary	5	5	11	400	0	1	0	1	1	0	3

Andrena synadelpha PERKINS, 1914	1	4	2	polylectic	ground	solitary	6	3	11	400	1	1	0	0	1	1	4
Andrena taraxaci GIRAUD, 1861	unknown	6	2	oligolectic	ground	solitary	4,5	4	11	800	0	1	0	1	1	1	4
Andrena varians (KIRBY, 1802)	1	3	2	polylectic	ground	solitary	4	3	11	800	1	0	1	1	1	1	5
Anthophora quadrimaculata (PANZER, 1798)	2	3	3	polylectic	ground	solitary	6,5	4	11	1050	0	1	1	1	0	0	3
Colletes floralis EVERSMANN, 1852	6	7	6	polylectic	ground	solitary	6,5	4	11	1050	0	1	0	0	0	0	1
Colletes halophilus VERHOEFF, 1944	unknown	6	2	oligolectic	ground	solitary	9	3	11	0	0	1	0	0	0	0	1
Colletes succinctus (LINNAEUS, 1758)	2	3	3	oligolectic	ground	solitary	8,5	2	11	400	0	1	0	0	1	0	2
Nomada armata HERRICH-SCHÄFFER, 1839	3	3	4	cuckoo	host nest	cuckoo	6,5	4	11	800	0	0	0	1	1	0	2
Nomada bifasciata OLIVIER, 1811	1	2	2	cuckoo	host nest	cuckoo	4,5	4	11	400	1	1	1	1	1	1	6
Nomada lathburiana (KIRBY, 1802)	1	2	2	cuckoo	host nest	cuckoo	5,5	6	11	1050	0	1	1	1	1	1	5
Nomada mutica MORAWITZ, 1872	4	5	3	cuckoo	host nest	cuckoo	5,5	4	11	800	1	1	0	0	1	1	4
Nomada stigma FABRICIUS, 1804	1	2	2	cuckoo	host nest	cuckoo	6	5	11	800	0	0	0	1	1	0	2
Nomada villosa THOMSON, 1870	3	4	insufficient data	cuckoo	host nest	cuckoo	5,5	4	11	800	0	0	1	1	1	0	3
Osmia brevicornis (FABRICIUS, 1798)	3	4	insufficient data	oligolectic	above	solitary	5,5	4	11	800	0	0	1	0	1	1	3
Osmia cerinthidis MORAWITZ, 1876	5	6	3	oligolectic	above	solitary	5,5	2	11	800	0	0	0	0	1	1	2
Osmia maritima FRIESE, 1885	unknown	6	2	polylectic	ground	solitary	6	3	11	0	0	1	0	0	0	0	1
Osmia tridentata DUFOUR & PERRIS, 1840	3	4	3	oligolectic	above	solitary	7	3	11	400	0	0	0	0	1	1	2
Osmia villosa (SCHENCK, 1853)	4	5	3	oligolectic	above	solitary	6	3	11	1500	0	1	0	0	0	0	1
Panurgus banksianus (KIRBY, 1802)	1	3	2	oligolectic	ground	solitary	7	3	11	1050	1	1	0	1	1	1	5
Ammobatoides abdominalis (EVERSMANN, 1852)	6	7	6	cuckoo	host nest	cuckoo	7	3	11,5	400	0	1	0	1	0	1	3
Andrena barbilabris (KIRBY, 1802)	2	3	3	polylectic	ground	solitary	5	5	11,5	400	0	1	0	0	1	1	3
Andrena florea FABRICIUS, 1793	1	3	2	oligolectic	ground	solitary	6,5	4	11,5	800	0	0	1	0	1	1	3
Andrena fucata SMITH, 1847	1	3	2	polylectic	ground	solitary	6	3	11,5	1050	1	0	0	0	0	0	1
Andrena mitis SCHMIEDEKNECHT, 1883	2	3	3	oligolectic	ground	solitary	4,5	4	11,5	400	1	1	0	1	0	0	3
Andrena nigriceps (KIRBY, 1802)	4	5	3	polylectic	ground	solitary	7	3	11,5	800	0	1	0	0	0	1	2
Andrena schencki MORAWITZ, 1866	4	6	4	polylectic	ground	solitary	6	3	11,5	400	0	0	0	1	0	1	2
Andrena wilkella (KIRBY, 1802)	1	3	2	oligolectic	ground	solitary	5	5	11,5	1050	0	1	0	1	1	1	4
Anthidium manicatum (LINNAEUS, 1758)	1	2	2	polylectic	above	solitary	7	3	11,5	800	0	1	1	0	1	0	3
Anthophora furcata (PANZER, 1798)	2	3	3	oligolectic	above	solitary	7	3	11,5	800	1	0	1	0	1	0	3
Bombus jonellus (KIRBY, 1802)	3	4	3	polylectic	ground and above	social	6	7	11,5	1050	1	1	0	0	1	1	4
Bombus pratorum (LINNAEUS, 1761)	1	1	2	polylectic	above	social	5	5	11,5	1500	1	0	1	1	1	1	5
Coelioxys aurolimbata FÖRSTER, 1853	2	3	3	cuckoo	host nest	cuckoo	7	3	11,5	400	0	1	0	1	1	1	4
Coelioxys conica (LINNAEUS, 1758)	2	3	3	cuckoo	host nest	cuckoo	6,5	4	11,5	1050	0	0	0	1	1	0	2
Coelioxys elongata LEPELETIER, 1841	1	4	insufficient data	cuckoo	host nest	cuckoo	7	5	11,5	800	0	1	0	1	1	1	4
Colletes hederae SCHMIDT & WESTRICH, 1993	1	3	insufficient data	oligolectic	ground	solitary	9	3	11,5	400	1	1	1	1	1	1	6
Eucera macroglossa ILLIGER, 1806	4	5	3	oligolectic	ground	solitary	7	3	11,5	800	0	1	0	0	0	1	2
Lasioglossum majus (NYLANDER, 1852)	3	4	4	polylectic	ground	solitary	6,5	6	11,5	800	1	0	0	1	1	1	4
Megachile analis NYLANDER, 1852	4	5	3	polylectic	ground	solitary	7	5	11,5	1500	0	1	0	0	0	0	1
Megachile melanopyga COSTA, 1863	5	6	4	polylectic	above	solitary	7,5	6	11,5	800	0	1	0	1	0	1	3
Megachile versicolor SMITH, 1844	1	2	2	polylectic	above	solitary	7	5	11,5	800	1	1	1	1	1	1	6
Melitta leporina (PANZER, 1799)	1	3	2	oligolectic	ground	solitary	7,5	4	11,5	400	0	0	1	1	0	1	3
Melitta nigricans ALFKEN, 1905	1	3	2	oligolectic	ground	solitary	7,5	2	11,5	400	0	0	0	0	1	0	1
Melitta tricincta KIRBY, 1802	2	3	2	oligolectic	ground	solitary	8,5	2	11,5	800	0	1	0	1	0	1	3
Nomada fulvicornis FABRICIUS, 1793	1	2	2	cuckoo	host nest	cuckoo	5,5	6	11,5	800	1	1	1	1	1	1	6
Nomada goodeniana (KIRBY, 1802)	1	1	2	cuckoo	host nest	cuckoo	5,5	3	11,5	800	1	1	1	1	1	1	6
Nomada marshamella (KIRBY, 1802)	1	1	2	cuckoo	host nest	cuckoo	5,5	4	11,5	800	1	1	1	1	1	1	6
Nomada signata JURINE, 1807	1	4	2	cuckoo	host nest	cuckoo	4,5	4	11,5	800	1	0	1	0	1	0	3
Nomada succincta PANZER, 1798	1	2	2	cuckoo	host nest	cuckoo	4,5	4	11,5	800	1	1	1	1	1	1	6
Osmia tuberculata NYLANDER, 1848	3	4	3	polylectic	above	solitary	6,5	2	11,5	1900	1	0	0	1	1	0	3
Andrena flavipes PANZER, 1799	1	2	2	polylectic	ground	solitary	6	7	12	800	1	1	1	1	1	1	6
Andrena tscheki MORAWITZ, 1872	3	4	3	oligolectic	ground	solitary	4	3	12	400	0	0	0	1	0	1	2
Bombus humilis ILLIGER, 1806	3	3	4	polylectic	above	social	7	7	12	1050	0	0	0	1	1	1	3
Bombus pascuorum (SCOPOLI, 1763)	1	1	2	polylectic	ground and above	social	7	7	12	1050	0	0	1	1	1	1	4
Bombus soroeensis (FABRICIUS, 1776)	2	3	3	polylectic	ground	social	6,5	6	12	1050	1	1	0	1	1	1	5
Coelioxys alata FÖRSTER, 1853	5	6	insufficient data	cuckoo	host nest	cuckoo	7	3	12	400	1	0	0	0	1	0	2
Coelioxys rufescens LEPELETIER & SERVILLE, 1825	2	4	3	cuckoo	host nest	cuckoo	7,5	4	12	1050	0	0	0	0	1	0	1
Lasioglossum xanthopus (KIRBY, 1802)	1	3	2	polylectic	ground	solitary	6,5	8	12	800	0	0	0	1	1	1	3
Megachile lapponica THOMSON, 1872	1	3	2	oligolectic	above	solitary	7	3	12	800	1	0	1	0	1	0	3
Megachile pyrenaea PÉREZ, 1890	3	5	3	polylectic	ground and above	solitary	8	3	12	800	0	1	0	0	0	1	2
Nomada flava PANZER, 1798	1	1	2	cuckoo	host nest	cuckoo	4,5	4	12	800	1	1	1	1	1	1	6
Nomada nobilis HERRICH-SCHÄFFER, 1839	6	7	6	cuckoo	host nest	cuckoo	5,5	2	12	800	0	0	0	0	0	1	1
Nomada sexfasciata PANZER, 1799	1	3	2	cuckoo	host nest	cuckoo	5	3	12	800	0	0	0	1	1	1	3
Osmia adunca (PANZER, 1798)	1	2	2	oligolectic	above	solitary	7,5	4	12	800	0	1	0	0	0	1	2
Osmia lepeletieri PÉREZ, 1879	6	7	6	oligolectic	above	solitary	7	3	12	1050	0	1	0	0	0	0	1
Andrena bucephala STEPHENS, 1846	3	4	3	polylectic	ground	solitary	4,5	2	12,5	800	0	0	0	1	1	0	2
Andrena clarkella (KIRBY, 1802)	1	3	2	oligolectic	ground	solitary	4	3	12,5	1050	1	0	0	0	1	0	2
Andrena ferox SMITH, 1847	4	5	3	polylectic	ground	solitary	5,5	2	12,5	800	1	0	0	0	1	0	2
Andrena lapponica ZETTERSTEDT, 1838	2	3	3	oligolectic	ground	solitary	5,5	4	12,5	1650	1	1	0	0	1	0	3
Andrena rosae PANZER, 1801	3	4	4	polylectic	ground	solitary	5,5	5	12,5	800	0	0	0	1	1	1	3
Bombus lucorum (LINNAEUS, 1761)	1	1	2	polylectic	ground	social	5,5	6	12,5	1050	1	1	1	1	1	1	6
Bombus monticola SMITH, 1849	1	4	2	polylectic	ground	social	6	7	12,5	1900	1	1	0	0	1	0	3
Bombus ruderarius (MÜLLER, 1776)	3	4	3	polylectic	above	social	6,5	6	12,5	1500	0	0	0	1	0	0	1
Bombus sylvarum (LINNAEUS, 1761)	2	3	3	polylectic	ground and above	social	7	7	12,5	1050	0	1	1	1	1	1	5
Colletes collaris DOURS, 1872	unknown	6	2	polylectic	ground	solitary	9	3	12,5	400	0	1	0	0	0	1	2
Megachile genalis MORAWITZ, 1880	4	5	3	oligolectic	above	solitary	7,5	4	12,5	800	0	1	0	0	1	1	3
Melitta haemorrhoidalis (FABRICIUS, 1775)	1	2	2	oligolectic	ground	solitary	7,5	4	12,5	1050	0	0	1	1	1	1	4
Nomada melathoracica IMHOFF, 1834	4	5	3	cuckoo	host nest	cuckoo	5,5	4	12,5	800	0	1	1	1	1	0	4
Nomada rostrata HERRICH-SCHÄFFER, 1839	5	6	3	cuckoo	host nest	cuckoo	5,5	2	12,5	400	0	1	0	0	0	0	1
Sphecodes albilabris (FABRICIUS, 1793)	1	3	2	cuckoo	host nest	cuckoo	6,5	8	12,5	800	0	1	0	0	0	1	2
Andrena chrysopyga SCHENCK, 1853	4	5	3	polylectic	ground	solitary	5	3	13	800	0	1	0	1	0	0	2
Andrena decipiens SCHENCK, 1861	4	5	4	polylectic	ground	solitary	7,5	4	13	400	0	1	0	0	0	0	1
Andrena fulva (MÜLLER, 1766)	1	2	2	polylectic	ground	solitary	4	3	13	800	1	0	1	0	1	0	3
Andrena gravida IMHOFF, 1832	1	1	2	polylectic	ground	solitary	4,5	4	13	800	1	1	1	1	1	1	6
Andrena nuptialis PÉREZ, 1902	5	6	3	polylectic	ground	solitary	6	4	13	900	0	0	0	0	1	1	2
Andrena nycthemera IMHOFF, 1868	3	4	3	oligolectic	ground	solitary	4,5	4	13	400	0	1	0	0	0	0	1
Andrena polita SMITH, 1847	4	4	4	oligolectic	ground	solitary	7	5	13	400	0	1	0	1	1	1	4
Andrena rogenhoferi MORAWITZ, 1872	unknown	6	2	polylectic	ground	solitary	6,5	4	13	1500	0	1	0	1	0	0	2
Andrena scotica PERKINS, 1916	1	3	2	polylectic	ground	solitary	5	3	13	800	0	1	1	1	1	0	4
Bombus hypnorum (LINNAEUS, 1758)	1	1	2	polylectic	above	social	5,5	6	13	1050	1	0	1	1	1	1	5
Bombus muscorum (LINNAEUS, 1758)	4	4	4	polylectic	above	social	7	5	13	800	0	1	0	1	1	0	3
Bombus pomorum (PANZER, 1805)	4	4	4	polylectic	ground	social	6	5	13	800	0	0	0	1	1	0	2
Bombus veteranus (FABRICIUS, 1793)	3	4	3	polylectic	above	social	6,5	6	13	800	0	0	0	1	1	0	2
Eucera dentata GERMAR, 1839	4	5	3	oligolectic	ground	solitary	7,5	4	13	800	0	1	0	0	0	1	2
Melecta albifrons (FORSTER, 1771)	1	1	2	cuckoo	host nest	cuckoo	5	5	13	1500	0	1	1	0	0	0	2
Melecta luctuosa (SCOPOLI, 1770)	3	4	3	cuckoo	host nest	cuckoo	5,5	4	13	800	0	1	0	0	1	0	2
Osmia nigriventris (ZETTERSTEDT, 1838)	5	6	4	polylectic	above	solitary	5,5	4	13	1650	1	0	0	0	1	0	2
Andrena apicata SMITH, 1847	3	3	insufficient data	oligolectic	ground	solitary	3,5	4	13,5	800	1	1	0	0	1	0	3
Andrena bimaculata (KIRBY, 1802)	2	3	3	polylectic	ground	solitary	5,5	6	13,5	400	0	1	0	0	0	0	1
Andrena curvungula THOMSON, 1870	3	3	4	oligolectic	ground	solitary	6	3	13,5	800	0	0	0	1	1	1	3
Andrena labialis (KIRBY, 1802)	2	3	3	oligolectic	ground	solitary	6	3	13,5	1050	0	0	0	1	1	0	2
Andrena lathyri ALFKEN, 1899	1	2	2	oligolectic	ground	solitary	5,5	4	13,5	800	0	0	1	1	1	0	3
Anthophora plagiata (ILLIGER, 1806)	4	6	4	polylectic	ground	solitary	5,5	4	13,5	1050	0	1	0	0	0	0	1
Bombus hortorum (LINNAEUS, 1761)	1	2	2	polylectic	ground and above	social	6	5	13,5	1050	0	0	1	1	1	1	4
Bombus semenoviellus SKORIKOV, 1910	1	5	insufficient data	polylectic	ground	social	6	7	13,5	400	1	1	0	1	0	1	4
Colletes cunicularius (LINNAEUS, 1761)	1	3	2	polylectic	ground	solitary	3,5	2	13,5	400	0	1	0	0	0	0	1
Colletes nasutus SMITH, 1853	4	5	3	oligolectic	ground	solitary	7	3	13,5	400	0	1	0	0	0	0	1
Halictus scabiosae (ROSSI, 1790)	1	3	2	polylectic	ground	social	6,5	6	13,5	800	0	1	0	0	1	1	3
Lithurgus chrysurus FONSCOLOMBE, 1834	5	6	insufficient data	oligolectic	above	solitary	7	3	13,5	400	1	1	0	0	0	0	2
Megachile willughbiella (KIRBY, 1802)	1	2	2	polylectic	ground and above	solitary	7	5	13,5	1050	0	0	1	1	1	0	3
Melitta dimidiata MORAWITZ, 1876	5	6	3	oligolectic	ground	solitary	5,5	4	13,5	800	0	0	0	1	0	1	2
Osmia cornuta (LATREILLE, 1805)	1	3	1	polylectic	above	solitary	4	5	13,5	800	0	1	1	0	1	0	3
Osmia mustelina GERSTÄCKER, 1869	4	5	3	polylectic	above	solitary	5,5	6	13,5	1050	0	1	0	0	0	1	2
Andrena agilissima (SCOPOLI, 1770)	3	4	3	oligolectic	ground	solitary	5,5	2	14	800	0	1	1	1	1	0	4
Andrena cineraria (LINNAEUS, 1758)	1	2	2	polylectic	ground	solitary	4	3	14	1050	0	1	1	1	1	1	5
Andrena nigroaenea (KIRBY, 1802)	1	3	2	polylectic	ground	solitary	5	5	14	1050	0	1	1	1	1	0	4
Andrena pilipes FABRICIUS, 1781	3	3	4	polylectic	ground	solitary	6,5	5	14	800	0	1	0	1	0	1	3
Andrena suerinensis FRIESE, 1884	4	5	3	oligolectic	ground	solitary	6	3	14	400	0	1	0	0	0	1	2
Andrena tibialis (KIRBY, 1802)	1	3	2	polylectic	ground	solitary	4,5	4	14	800	0	1	1	1	1	1	5
Andrena vaga PANZER, 1799	1	3	2	oligolectic	ground	solitary	4,5	4	14	800	0	1	0	0	0	0	1
Bombus lapidarius (LINNAEUS, 1758)	1	1	2	polylectic	above	social	6,5	8	14	1050	0	0	1	1	1	1	4
Bombus mesomelas GERSTÄCKER, 1869	6	7	6	polylectic	ground	social	7,5	6	14	1900	0	1	0	0	0	0	1
Bombus mucidus GERSTÄCKER, 1869	1	4	2	polylectic	ground	social	7,5	6	14	1900	0	0	0	0	1	0	1
Bombus terrestris (LINNAEUS, 1758)	1	1	2	polylectic	ground	social	5,5	8	14	800	0	0	1	1	1	1	4
Dasypoda hirtipes (FABRICIUS, 1793)	2	3	3	oligolectic	ground	solitary	7,5	4	14	800	0	1	0	0	1	1	3
Eucera longicornis (LINNAEUS, 1758)	2	3	3	oligolectic	ground	solitary	6	3	14	400	0	0	0	1	0	1	2
Eucera nigrescens PÉREZ, 1879	1	3	2	oligolectic	ground	solitary	5	3	14	400	0	0	0	1	1	0	2
Megachile ericetorum LEPELETIER, 1841	1	3	2	oligolectic	above	solitary	7	3	14	800	0	1	1	1	1	1	5
Megachile ligniseca (KIRBY, 1802)	4	5	3	polylectic	above	solitary	7,5	4	14	1050	1	0	0	0	1	0	2
Melitturga clavicornis (LATREILLE, 1806)	6	7	6	oligolectic	ground	solitary	7	3	14	800	0	1	0	1	1	1	4
Anthophora aestivalis (PANZER, 1801)	3	4	3	polylectic	ground	solitary	5,5	4	14,5	1050	0	1	0	0	1	1	3
Anthophora plumipes (PALLAS, 1772)	1	1	2	polylectic	ground	solitary	4,5	4	14,5	800	1	1	1	1	1	1	6
Anthophora retusa (LINNAEUS, 1758)	2	3	4	polylectic	ground	solitary	5,5	4	14,5	800	0	1	0	1	1	0	3
Bombus sichelii RADOSZKOWSKI, 1859	3	5	3	polylectic	ground	social	6,5	6	14,5	2300	1	0	0	0	1	0	2
Bombus wurflenii RADOSZKOWSKI, 1859	2	3	3	polylectic	ground	social	7	7	14,5	1500	1	1	0	1	1	0	4
Coelioxys conoidea (ILLIGER, 1806)	3	4	3	cuckoo	host nest	cuckoo	7	3	14,5	800	0	1	0	0	0	1	2
Halictus sexcinctus (FABRICIUS, 1775)	3	3	4	polylectic	ground	solitary	7	6	14,5	800	0	1	0	0	0	1	2
Megachile maritima (KIRBY, 1802)	3	3	4	polylectic	ground	solitary	7	3	14,5	800	0	1	0	0	0	1	2
Andrena hattorfiana (FABRICIUS, 1775)	3	3	4	oligolectic	ground	solitary	6,5	4	15	800	0	0	1	1	1	0	3
Andrena nitida (MÜLLER, 1776)	1	1	2	polylectic	ground	solitary	4,5	4	15	800	0	0	0	0	0	0	6
Andrena thoracica (FABRICIUS, 1775)	4	5	3	polylectic	ground	solitary	6,5	6	15	800	0	1	0	0	0	1	2
Bombus alpinus (LINNAEUS, 1758)	6	7	6	polylectic	ground	social	6,5	6	15	1900	0	0	0	0	0	1	1
Bombus sylvestris (LEPELETIER, 1832)	1	2	2	cuckoo	host nest	cuckoo	6	5	15	1050	1	0	1	1	1	1	5
Dasypoda argentata (PANZER, 1809)	5	6	4	oligolectic	ground	solitary	7,5	4	15	800	0	1	0	0	0	0	1
Megachile nigriventris SCHENCK, 1868	1	3	1	oligolectic	above	solitary	6,5	4	15	1050	1	0	0	0	1	0	2
Andrena aberrans EVERSMANN, 1852	5	6	3	oligolectic	ground	solitary	5	3	15,5	400	0	1	0	0	0	1	2

Bombus mendax GERSTÄCKER, 1869	1	4	2	polylectic	ground	social	7	7	15,5	2300	0	1	0	0	0	0	1
Halictus quadricinctus (FABRICIUS, 1776)	3	4	3	polylectic	ground	solitary	6,5	6	15,5	1050	0	1	0	0	0	1	2
Bombus gerstaeckeri MORAWITZ, 1882	unknown	6	2	oligolectic	ground	social	8	5	16	1900	0	0	0	0	1	1	2
Megachile lagopoda (LINNAEUS, 1761)	4	5	3	polylectic	ground and above	solitary	7	3	16	800	0	1	0	0	0	1	2
Bombus campestris (PANZER, 1801)	1	2	2	cuckoo	host nest	cuckoo	6,5	4	16,5	1050	0	0	1	1	1	1	4
Xylocopa iris (CHRIST, 1791)	6	7	6	polylectic	above	solitary	7	7	16,5	400	0	0	0	0	1	0	1
Andrena nasuta GIRAUD, 1863	4	4	4	oligolectic	ground	solitary	5,5	2	17	400	0	1	0	0	0	0	1
Bombus flavidus EVERSMANN, 1852	3	4	insufficient data	cuckoo	host nest	cuckoo	7,5	4	17	1900	1	0	0	0	1	0	2
Megachile parietina (GEOFFROY, 1785)	5	6	5	polylectic	above	solitary	5,5	6	17	800	0	1	0	0	0	1	2
Bombus barbutellus (KIRBY, 1802)	1	2	2	cuckoo	host nest	cuckoo	5,5	4	18	1050	0	0	1	1	1	1	4
Bombus norvegicus (SPARRE-SCHNEIDER, 1918)	1	3	2	cuckoo	host nest	cuckoo	6	5	20	1050	1	0	0	1	1	1	4
Bombus rupestris (FABRICIUS, 1793)	1	2	2	cuckoo	host nest	cuckoo	6	5	20	1050	0	0	1	1	1	1	4
Bombus vestalis (GEOFFROY, 1785)	1	3	2	cuckoo	host nest	cuckoo	6	5	21	800	0	0	1	1	1	1	4
Xylocopa violacea (LINNAEUS, 1758)	1	3	1	polylectic	above	solitary	6,5	8	22,5	800	0	0	1	1	0	0	2
Bombus bohemicus SEIDL, 1838	1	2	2	cuckoo	host nest	cuckoo	6	5	24	1050	0	0	1	1	1	1	4
Bombus quadricolor (LEPELETIER, 1832)	4	5	3	cuckoo	host nest	cuckoo	6,5	6	24	1050	1	1	0	1	1	1	5

Category	Variable name	Explanation
Response variables	**Redlist**	redlist status (extinction risk): 1=not threatened; 2=near-threatened; 3=threatened; 4=highly threatened; 5=almost extinct; 6=extinct
	Abundance	species abundance: 1=abundant; 2=common; 3=frequent; 4=occasional; 5=rare; 6=extremely rare; 7=extinct
	Population.trend	long-term population trend: 1=increase; 2=no change; 3=small decline; 4=decline; 5=large decline; 6=extinct
Functional traits	**Pollen.specialisation**	polylectic / oligolectic / cuckoo
	Nest.location	nesting: above ground / in ground and above ground / in ground / host nest
	Sociality	social / solitary / cuckoo
	Mean.flight.month	mean month of flight activity
	Duration.of.activity	duration of flight activity (in months)
	Size.mean	mean female body length
Habitat preferences	**Altitude.mean**	mean altitudinal occurrence (in meter above sea-level)
	Forest	occurrence in forests (1=yes; 0=no)
	Raw.soil	occurrence in raw-soil sites (1=yes; 0=no)
	Urban.areas	occurrence in urban areas (1=yes; 0=no)
	Meadows	occurrence in meadows (1=yes; 0=no)
	Hedgerows	occurrence in hedgerows (1=yes; 0=no)
	Wasteland	occurrence in wasteland (1=yes; 0=no)
	Habitat.breadth	number of habitats occupied by a species (1–6)

Table S2: Flight times for all bee species coded in this study



Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Andrena minutula (KIRBY, 1802)	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Andrena tibialis (KIRBY, 1802)	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Bombus terrestris (LINNAEUS, 1758)	NO	YES	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Bombus lucorum (LINNAEUS, 1761)	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia cornuta (LATREILLE, 1805)	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena apicata SMITH, 1847	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Bombus lapidarius (LINNAEUS, 1758)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum calceatum (SCOPOLI, 1763)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum fulvicorne (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum laevigatum (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum laticeps (SCHENCK, 1868)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum marginatum (BRULLÉ, 1832)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum morio (FABRICIUS, 1793)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum nitidulum (FABRICIUS, 1804)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum pauxillum (SCHENCK, 1853)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum politum (SCHENCK, 1853)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum subfasciatum (IMHOFF, 1832)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum villosulum (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum xanthopus (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Osmia caerulescens (LINNAEUS, 1758)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes albilabris (FABRICIUS, 1793)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes ephippius (LINNAEUS, 1767)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes monilicornis (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Xylocopa violacea (LINNAEUS, 1758)	NO	NO	YES	YES	YES	YES	YES	YES	YES	YES	NO	NO
Andrena flavipes PANZER, 1799	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus jonellus (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus monticola SMITH, 1849	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus semenoviellus SKORIKOV, 1910	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus sylvestris (LEPELETIER, 1832)	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO
Halictus confusus SMITH, 1853	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum lineare (SCHENCK, 1868)	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO
Sphecodes longulus VON HAGENS, 1882	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO	NO
Andrena bicolor FABRICIUS, 1775	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Andrena bimaculata (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Andrena ovatula (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Andrena subopaca NYLANDER, 1848	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Bombus hypnorum (LINNAEUS, 1758)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Halictus subauratus (ROSSI, 1792)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Lasioglossum sexmaculatum (SCHENCK, 1853)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Megachile parietina (GEOFFROY, 1785)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada fabriciana (LINNAEUS, 1767)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada flavoguttata (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada fucata PANZER, 1798	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada fulvicornis FABRICIUS, 1793	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada lathburiana (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada panzeri LEPELETIER, 1841	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada sheppardana (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia bicolor (SCHRANK, 1781)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia bicornis (LINNAEUS, 1758)	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia mustelina GERSTAECKER, 1869	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia uncinata GERSTAECKER, 1869	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO	NO
Andrena barbilabris (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO	NO
Andrena nigroaenea (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO	NO
Andrena similis SMITH, 1849	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO	NO
Andrena wilkella (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO	NO
Bombus pratorum (LINNAEUS, 1761)	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO	NO
Melecta albifrons (FORSTER, 1771)	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO	NO
Andrena gravida IMHOFF, 1832	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena haemorrhoa (FABRICIUS, 1781)	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena mitis SCHMIEDEKNECHT, 1883	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena nitida (MUELLER, 1776)	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena nycthemera IMHOFF, 1868	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena taraxaci GIRAUD, 1861	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena vaga PANZER, 1799	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Anthophora plumipes (PALLAS, 1772)	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada bifasciata OLIVIER, 1811	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada flava PANZER, 1798	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada leucophthalma (KIRBY, 1802)	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada obscura ZETTERSTEDT, 1838	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada ruficornis (LINNAEUS, 1758)	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada signata JURINE, 1807	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada succincta PANZER, 1798	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Osmia aurulenta (PANZER, 1799)	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Osmia pilicornis SMITH, 1846	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena rosae PANZER, 1801	NO	NO	YES	YES	YES	NO	YES	YES	NO	NO	NO	NO
Andrena cineraria (LINNAEUS, 1758)	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena clarkella (KIRBY, 1802)	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena falsifica PERKINS, 1915	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena fulva (MUELLER, 1766)	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena potentillae PANZER, 1809	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena praecox (SCOPOLI, 1763)	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena ruficrus NYLANDER, 1848	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena sericata IMHOFF, 1868	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena tscheki MORAWITZ, 1872	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena varians (KIRBY, 1802)	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Andrena ventralis IMHOFF, 1832	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Nomada ferruginata (LINNAEUS, 1767)	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO	NO
Colletes cunicularius (LINNAEUS, 1761)	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO	NO	NO
Bombus humilis ILLIGER, 1806	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Bombus mendax GERSTAECKER, 1869	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Bombus pascuorum (SCOPOLI, 1763)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Bombus sylvarum (LINNAEUS, 1761)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Bombus wurflenii RADOSZKOWSKI, 1859	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Ceratina cyanea (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum albipes (FABRICIUS, 1781)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum brevicorne (SCHENCK, 1868)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum euboeense (STRAND, 1909)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum fratellum (PÉREZ, 1903)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum glabriusculum (MORAWITZ, 1872)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum interruptum (PANZER, 1798)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum lativentre (SCHENCK, 1853)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum leucozonium (SCHRANK, 1781)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum lucidulum (SCHENCK, 1861)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum malachurum (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum nigripes (LEPELETIER, 1841)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum parvulum (SCHENCK, 1853)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum prasinum (SMITH, 1848)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum punctatissimum (SCHENCK, 1853)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum puncticolle (MORAWITZ, 1872)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum quadrinotatulum (SCHENCK, 1861)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum quadrinotatum (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO

Lasioglossum rufitarse (ZETTERSTEDT, 1838)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum sexnotatum (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum sexstrigatum (SCHENCK, 1868)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Lasioglossum zonulum (SMITH, 1848)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Nomada distinguenda MORAWITZ, 1874	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes crassus THOMSON, 1870	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes ferruginatus VON HAGENS, 1882	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes geoffrellus (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes gibbus (LINNAEUS, 1758)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes hyalinatus VON HAGENS, 1882	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes reticulatus THOMSON, 1870	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Xylocopa iris (CHRIST, 1791)	NO	NO	NO	YES	YES	YES	YES	YES	YES	YES	NO	NO
Andrena minutuloides PERKINS, 1914	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Andrena thoracica (FABRICIUS, 1775)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus alpinus (LINNAEUS, 1758)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus quadricolor (LEPELETIER, 1832)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus ruderarius (MUELLER, 1776)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus sichelii RADOSZKOWSKI, 1859	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus soroeensis (FABRICIUS, 1776)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Bombus veteranus (FABRICIUS, 1793)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Ceratina chalybea CHEVRIER, 1872	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Halictus eurygnathus BLÜTHGEN, 1931	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Halictus leucaheneus EBMER, 1972	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Halictus maculatus SMITH, 1848	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Halictus quadricinctus (FABRICIUS, 1776)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Halictus rubicundus (CHRIST, 1791)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Halictus scabiosae (ROSSI, 1790)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Halictus tumulorum (LINNAEUS, 1758)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Hylaeus confusus NYLANDER, 1852	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Hylaeus signatus (PANZER, 1798)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum aeratum (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum costulatum (KRIECHBAUMER, 1873)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum cupromicans (PÉREZ, 1903)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum laeve (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum majus (NYLANDER, 1852)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum minutissimum (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum minutulum (SCHENCK, 1853)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum nitidiusculum (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum pygmaeum (SCHENCK, 1853)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum quadrisignatum (SCHENCK, 1853)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Lasioglossum tricinctum (SCHENCK, 1874)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Osmia leaiana (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Sphecodes miniatus VON HAGENS, 1882	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Sphecodes niger VON HAGENS, 1874	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Sphecodes pellucidus SMITH, 1845	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Sphecodes puncticeps THOMSON, 1870	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Sphecodes rufiventris (PANZER, 1798)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Sphecodes schenckii VON HAGENS, 1882	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Stelis phaeoptera (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO	NO
Andrena dorsata (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Anthidium strigatum (PANZER, 1805)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Bombus bohemicus SEIDL, 1838	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Bombus hortorum (LINNAEUS, 1761)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Bombus norvegicus (SPARRE-SCHNEIDER, 1918)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Bombus pomorum (PANZER, 1805)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Bombus rupestris (FABRICIUS, 1793)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Bombus vestalis (GEOFFROY, 1785)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Halictus smaragdulus VACHAL, 1895	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Lasioglossum intermedium (SCHENCK, 1868)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Lasioglossum lissonotum (NOSKIEWICZ, 1926)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Lasioglossum semilucens (ALFKEN, 1914)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Lasioglossum tarsatum (SCHENCK, 1868)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Lithurgus chrysurus FONSCOLOMBE, 1834	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada bluethgeni STÖCKHERT, 1943	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada integra BRULLÉ, 1832	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada rhenana MORAWITZ, 1872	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada stigma FABRICIUS, 1804	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada striata FABRICIUS, 1793	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Nomada zonata PANZER, 1798	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia gallarum SPINOLA, 1808	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia parietina CURTIS, 1828	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia ravouxi PÉREZ, 1902	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Osmia rufohirta LATREILLE, 1811	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Stelis ornatula (KLUG, 1807)	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO	NO
Andrena labiata FABRICIUS, 1781	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Andrena lathyri ALFKEN, 1899	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Andrena nanaeformis NOSKIEWICZ, 1925	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Anthophora aestivalis (PANZER, 1801)	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Anthophora plagiata (ILLIGER, 1806)	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Anthophora retusa (LINNAEUS, 1758)	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Melecta luctuosa (SCOPOLI, 1770)	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Melitta dimidiata MORAWITZ, 1876	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Nomada femoralis MORAWITZ, 1869	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Nomada guttulata SCHENCK, 1861	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Nomada marshamella (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Nomada melathoracica IMHOFF, 1834	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Nomada mutica MORAWITZ, 1872	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Nomada villosa THOMSON, 1870	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Osmia nigriventris (ZETTERSTEDT, 1838)	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Osmia niveata (FABRICIUS, 1804)	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Osmia versicolor LATREILLE, 1811	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Osmia viridana MORAWITZ, 1874	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO	NO
Andrena aberrans EVERSMANN, 1852	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena chrysopyga SCHENCK, 1853	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena chrysosceles (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena lagopus (LATREILLE, 1809)	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena proxima (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena scotica PERKINS, 1916	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena symphyti SCHMIEDEKNECHT, 1883	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena viridescens VIERECK, 1916	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Eucera nigrescens PÉREZ, 1879	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada atroscutellaris STRAND, 1921	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada goodeniana (KIRBY, 1802)	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada hirtipes PÉREZ, 1884	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Nomada sexfasciata PANZER, 1799	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Sphecodes ruficrus (ERICHSON, 1835)	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO	NO
Andrena argentata SMITH, 1844	NO	NO	NO	YES	YES	NO	YES	YES	YES	NO	NO	NO
Andrena pilipes FABRICIUS, 1781	NO	NO	NO	YES	YES	NO	YES	YES	YES	NO	NO	NO
Andrena nuptialis PÉREZ, 1902	NO	NO	NO	YES	YES	NO	YES	YES	NO	NO	NO	NO
Andrena bucephala STEPHENS, 1846	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO	NO
Nomada alboguttata HERRICH-SCHÄFFER, 1839	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO	NO
Sphecodes majalis PÉREZ, 1903	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO	NO

Bombus mesomelas GERSTAECKER, 1869	NO	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO
Bombus mucidus GERSTAECKER, 1869	NO	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO
Coelioxys inermis (KIRBY, 1802)	NO	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO
Hylaeus communis NYLANDER, 1852	NO	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO
Megachile melanopyga COSTA, 1863	NO	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO
Nomada flavopicta (KIRBY, 1802)	NO	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO
Sphecodes croaticus MEYER, 1922	NO	NO	NO	NO	YES	YES	YES	YES	YES	YES	NO	NO
Andrena polita SMITH, 1847	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Anthidium punctatum LATREILLE, 1809	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Anthophora bimaculata (PANZER, 1798)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Bombus muscorum (LINNAEUS, 1758)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Bombus pyrenaeus PÉREZ, 1879	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Ceratina cucurbitina (ROSSI, 1792)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Coelioxys elongata LEPELETIER, 1841	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Halictus sexcinctus (FABRICIUS, 1775)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Hylaeus gibbus SAUNDERS, 1850	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Hylaeus hyalinatus SMITH, 1842	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Hylaeus leptocephalus (MORAWITZ, 1870)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Hylaeus nigritus (FABRICIUS, 1798)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Hylaeus pectoralis FÖRSTER, 1871	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Megachile analis NYLANDER, 1852	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Megachile leachella CURTIS, 1828	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Megachile pilidens ALFKEN, 1924	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Megachile versicolor SMITH, 1844	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Megachile willughbiella (KIRBY, 1802)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Nomada emarginata MORAWITZ, 1877	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Osmia spinulosa (KIRBY, 1802)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Sphecodes scabricollis WESMAEL, 1835	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Stelis breviuscula (NYLANDER, 1848)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Stelis punctulatissima (KIRBY, 1802)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Thyreus orbatus (LEPELETIER, 1841)	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO	NO
Andrena alfkenella PERKINS, 1914	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Andrena florea FABRICIUS, 1793	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Andrena hattorfiana (FABRICIUS, 1775)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Andrena hypopolia SCHMIEDEKNECHT, 1883	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Andrena rogenhoferi MORAWITZ, 1872	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Anthophora quadrimaculata (PANZER, 1798)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Osmia rapunculi (LEPELETIER, 1841)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Coelioxys conica (LINNAEUS, 1758)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Colletes floralis EVERSMANN, 1852	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Hylaeus duckei (ALFKEN, 1904)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Hylaeus punctatus (BRULLÉ, 1832)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Hylaeus punctulatissimus SMITH, 1842	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Lasioglossum convexiusculum (SCHENCK, 1853)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Lasioglossum marginellum (SCHENCK, 1853)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Megachile nigriventris SCHENCK, 1868	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Nomada armata HERRICH-SCHÄFFER, 1839	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Nomada braunsiana SCHMIEDEKNECHT, 1882	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Nomada facilis SCHWARZ, 1967	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Nomada kohli SCHMIEDEKNECHT, 1882	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Osmia andrenoides SPINOLA, 1808	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Osmia anthocopoides SCHENCK, 1853	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Osmia inermis (ZETTERSTEDT, 1838)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Osmia maritima FRIESE, 1885	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Sphecodes marginatus VON HAGENS, 1882	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Stelis nasuta (LATREILLE, 1809)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Stelis signata (LATREILLE, 1809)	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO	NO
Andrena curvungula THOMSON, 1870	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena fucata SMITH, 1847	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena humilis IMHOFF, 1832	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena labialis (KIRBY, 1802)	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena lapponica ZETTERSTEDT, 1838	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena schencki MORAWITZ, 1866	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena semilaevis PÉREZ, 1903	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena suerinensis FRIESE, 1884	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena synadelpha PERKINS, 1914	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Eucera cineraria EVERSMANN, 1852	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Eucera longicornis (LINNAEUS, 1758)	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Nomada moeschleri ALFKEN, 1913	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Nomada mutabilis MORAWITZ, 1870^	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Nomada piccioliana MAGRETTI, 1883	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Nomada posthuma BLÜTHGEN, 1949	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Osmia papaveris (LATREILLE, 1799)	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Osmia villosa (SCHENCK, 1853)	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Sphecodes rubicundus VON HAGENS, 1875	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Sphecodes spinulosus VON HAGENS, 1875	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Stelis franconica BLÜTHGEN, 1930	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO	NO
Andrena agilissima (SCOPOLI, 1770)	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Andrena chrysopus PÉREZ, 1903	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Andrena combinata (CHRIST, 1791)	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Andrena ferox SMITH, 1847	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Andrena nasuta GIRAUD, 1863	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Andrena pandellei PÉREZ, 1895	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Andrena paucisquama NOSKIEWICZ, 1924	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Nomada conjungens HERRICH-SCHÄFFER, 1839	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Nomada nobilis HERRICH-SCHÄFFER, 1839	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Nomada opaca ALFKEN, 1913	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Nomada rostrata HERRICH-SCHÄFFER, 1839	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Nomada symphyti STÖCKHERT, 1930	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Osmia cerinthidis MORAWITZ, 1876^	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Osmia submicans MORAWITZ, 1870	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO	NO
Bombus gerstaeckeri MORAWITZ, 1882	NO	NO	NO	NO	NO	YES	YES	YES	YES	YES	NO	NO
Andrena coitana (KIRBY, 1802)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Andrena decipiens SCHENCK, 1861	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Anthidium nanum MOCSÁRY, 1879	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Bombus flavidus EVERSMANN, 1852	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Coelioxys rufescens LEPELETIER & SERVILLE, 1825	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Colletes daviesanus SMITH, 1846	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Colletes similis SCHENCK, 1853	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Dasypoda argentata (PANZER, 1809)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Dasypoda hirtipes (FABRICIUS, 1793)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Dufourea minuta LEPELETIER, 1841	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Dufourea paradoxa (MORAWITZ, 1867)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Eucera dentata GERMAR, 1839	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Hylaeus annulatus (LINNAEUS, 1758)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Hylaeus brevicornis NYLANDER, 1852	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Hylaeus clypearis (SCHENCK, 1853)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Hylaeus dilatatus (KIRBY, 1802)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Hylaeus kahri FÖRSTER, 1871	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Hylaeus lineolatus (SCHENCK, 1861)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Hylaeus variegatus (FABRICIUS, 1798)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Megachile genalis MORAWITZ, 1880	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO

Megachile ligniseca (KIRBY, 1802)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Megachile rotundata (FABRICIUS, 1787)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Melitta haemorrhoidalis (FABRICIUS, 1775)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Melitta leporina (PANZER, 1799)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Nomada fuscicornis NYLANDER, 1848	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Nomada similis MORAWITZ, 1872	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Osmia adunca (PANZER, 1798)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Osmia crenulata (NYLANDER, 1856)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Osmia loti MORAWITZ, 1867	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Osmia truncorum (LINNAEUS, 1758)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Panurgus calcaratus (SCOPOLI, 1763)	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Panurgus dentipes LATREILLE, 1811	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Stelis minuta LEPELETIER & SERVILLE, 1825	NO	NO	NO	NO	NO	YES	YES	YES	YES	NO	NO	NO
Ammobates punctatus (FABRICIUS, 1804)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Ammobatoides abdominalis (EVERSMANN, 1852)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Andrena nigriceps (KIRBY, 1802)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Andrena nitidiuscula SCHENCK, 1853	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Anthidium byssinum (PANZER, 1798)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Anthidium manicatum (LINNAEUS, 1758)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Anthidium oblongatum (ILLIGER, 1806)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Anthophora furcata (PANZER, 1798)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Anthophora pubescens (FABRICIUS, 1781)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Biastes brevicornis (PANZER, 1798)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Coelioxys afra LEPELETIER, 1841	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Coelioxys alata FÖRSTER, 1853	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Coelioxys aurolimbata FÖRSTER, 1853	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Coelioxys brevis EVERSMANN, 1852	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Coelioxys conoidea (ILLIGER, 1806)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Coelioxys mandibularis NYLANDER, 1848	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Colletes impunctatus NYLANDER, 1852	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Colletes mlokossewiczi RADOSZKOWSKI, 1891	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Colletes nasutus SMITH, 1853	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Dufourea alpina MORAWITZ, 1865	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Epeolus schummeli SCHILLING, 1849	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Epeolus variegatus (LINNAEUS, 1758)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Eucera macroglossa ILLIGER, 1806	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Eucera salicariae (LEPELETIER, 1841)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Halictus simplex BLÜTHGEN, 1923	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus cardioscapus COCKERELL, 1924	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus cornutus CURTIS, 1831	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus difformis (EVERSMANN, 1852)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus gracilicornis (MORAWITZ, 1867)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus gredleri FÖRSTER, 1871	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus moricei (FRIESE, 1898)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus pictipes NYLANDER, 1852	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus rinki (GORSKI, 1852)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus sinuatus (SCHENCK, 1853)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Hylaeus styriacus FÖRSTER, 1871	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Megachile apicalis SPINOLA, 1808	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Megachile ericetorum LEPELETIER, 1841	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Megachile lagopoda (LINNAEUS, 1761)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Megachile lapponica THOMSON, 1872	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Megachile maritima (KIRBY, 1802)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Melitturga clavicornis (LATREILLE, 1806)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Nomada errans LEPELETIER, 1841	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Nomada pleurosticta HERRICH-SCHÄFFER, 1839	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Nomioides minutissimus (ROSSI, 1790)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Osmia acuticornis DUFOUR & PERRIS, 1840	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Osmia claviventris THOMSON, 1872	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Osmia lepeletieri PÉREZ, 1879	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Osmia leucomelana (KIRBY, 1802)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Osmia tridentata DUFOUR & PERRIS, 1840	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Panurginus herzi MORAWITZ, 1892	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Panurginus montanus GIRAUD, 1861	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Panurgus banksianus (KIRBY, 1802)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Rhophitoides canus (EVERSMANN, 1852)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Rophites quinquespinosus SPINOLA, 1808	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Stelis minima SCHENCK, 1861	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Stelis odontopyga NOSKIEWICZ, 1926	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Systropha curvicornis (SCOPOLI, 1770)	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Systropha planidens GIRAUD, 1861	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO	NO
Coelioxys lanceolata NYLANDER, 1852	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO
Epeolus alpinus FRIESE, 1893	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO
Osmia brevicornis (FABRICIUS, 1798)	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO
Osmia tuberculata NYLANDER, 1848	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO
Pseudapis femoralis (PALLAS, 1773)	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO
Rophites algirus PÉREZ, 1895	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO
Sphecodes cristatus VON HAGENS, 1882	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO	NO
Andrena angustior (KIRBY, 1802)	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Andrena marginata FABRICIUS, 1776	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Andrena simillima SMITH, 1851	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Colletes marginatus SMITH, 1846	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Eucera alticincta (LEPELETIER, 1841)	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Megachile pyrenaea PÉREZ, 1890	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Nomada argentata HERRICH-SCHÄFFER, 1839	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Nomada baccata SMITH, 1844	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Nomada roberjeotiana PANZER, 1799	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Nomada rufipes FABRICIUS, 1793	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO	NO
Andrena denticulata (KIRBY, 1802)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Andrena pallitarsis PÉREZ, 1903^	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Camptopoeum frontale (FABRICIUS, 1804)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Coelioxys echinata FÖRSTER, 1853	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Colletes fodiens (GEOFFROY, 1785)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Colletes hylaeiformis EVERSMANN, 1852^	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Dufourea dentiventris (NYLANDER, 1848)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Dufourea halictula (NYLANDER, 1852)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Dufourea inermis (NYLANDER, 1848)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Epeoloides coecutiens (FABRICIUS, 1775)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Epeolus cruciger (PANZER, 1799)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Melitta nigricans ALFKEN, 1905	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Nomada obtusifrons NYLANDER, 1848	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Thyreus histrionicus (ILLIGER, 1806)	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO	NO
Colletes collaris DOURS, 1872	NO	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO
Colletes halophilus VERHOEFF, 1944	NO	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO
Colletes hederae SCHMIDT & WESTRICH, 1993	NO	NO	NO	NO	NO	NO	NO	YES	YES	YES	NO	NO
Colletes succinctus (LINNAEUS, 1758)	NO	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO
Melitta tricincta KIRBY, 1802	NO	NO	NO	NO	NO	NO	NO	YES	YES	NO	NO	NO

Table S3: GenBank accession numbers for all species in the CO1 phylogeny.

Species	**GenBank Accession Number**	**Reference**
Ammobates punctatus	HM401141	Schmidt et al. 2015
Ammobatoides abdominalis	KJ83805	Schmidt et al. 2015
Andrena aberrans	KJ837129	Schmidt et al. 2015
Andrena agilissima	KT960836	Makkar et al. 2016
Andrena albofasciata	KJ837459	Schmidt et al. 2018
Andrena alfkenella	HM401243	Schmidt et al. 2015
Andrena allosa	KJ837196	Schmidt et al. 2015
Andrena alutacea	KJ836974	Schmidt et al. 2015
Andrena ampla	KJ836817	Schmidt et al. 2015
Andrena angustior	JQ909640	Magnacca and Brown 2012
Andrena apicata	JQ909642	Magnacca and Brown 2012
Andrena argentata	KJ838106	Schmidt et al. 2015
Andrena barbareae	KT164628	Tang et al. 2017
Andrena barbilabris	KJ836669	Schmidt et al. 2015
Andrena bicolor	GU706056	Schmidt et al. 2015
Andrena bimaculata	KJ837393	Schmidt et al. 2015
Andrena bucephala	KJ839574	Schmidt et al. 2015
Andrena carantonica	KT074022	Schmidt et al. 2015
Andrena chrysopus	GU705927	Schmidt et al. 2015
Andrena chrysopyga	HM376233	Schmidt et al. 2015
Andrena chrysosceles	HQ954749	Schmidt et al. 2015
Andrena cineraria	JQ909656	Magnacca and Brown 2012
Andrena clarkella	GU705928	Schmidt et al. 2015
Andrena coitana	KJ836599	Schmidt et al. 2015
Andrena combinata	KJ837482	Schmidt et al. 2015
Andrena confinis	HM401263	Schmidt et al. 2015
Andrena congruens	GU705940	Schmidt et al. 2015
Andrena curtula	KJ837178	Schmidt et al. 2015
Andrena curvungula	KJ837652	Schmidt et al. 2015
Andrena decipiens	KJ837637	Schmidt et al. 2015
Andrena denticulata	GU705953	Schmidt et al. 2015
Andrena distinguenda	KJ839472	Schmidt et al. 2015
Andrena dorsata	KJ837258	Schmidt et al. 2015
Andrena enslinella	KJ838020	Schmidt et al. 2015
Andrena falsifica	KJ838103	Schmidt et al. 2015
Andrena ferox	KJ839323	Schmidt et al. 2015
Andrena flavipes	KJ839275	Schmidt et al. 2015
Andrena florea	HM376235	Schmidt et al. 2015
Andrena floricola	KJ837140	Schmidt et al. 2015
Andrena florivaga	KJ837219	Schmidt et al. 2015
Andrena fucata	JQ909669	Magnacca and Brown 2012
Andrena fulva	GU705958	Schmidt et al. 2015

Andrena fulvago	KJ837292	Schmidt et al. 2015
Andrena fulvata	HM401059	Schmidt et al. 2015
Andrena fulvicornis	HM376237	Schmidt et al. 2015
Andrena fulvida	HM401047	Schmidt et al. 2015
Andrena fuscipes	HM401055	Schmidt et al. 2015
Andrena granulosa	HQ954767	Schmidt et al. 2015
Andrena gravida	KJ836450	Schmidt et al. 2015
Andrena haemorrhoa	KJ839483	Schmidt et al. 2015
Andrena hattorfiana	KJ837424	Schmidt et al. 2015
Andrena helvola	KJ837363	Schmidt et al. 2015
Andrena humilis	KJ838908	Schmidt et al. 2015
Andrena hypopolia	HM376239	Schmidt et al. 2015
Andrena intermedia	KJ836983	Schmidt et al. 2015
Andrena labialis	HM376240	Schmidt et al. 2015
Andrena labiata	HM401048	Schmidt et al. 2015
Andrena lagopus	HM376241	Schmidt et al. 2015
Andrena lapponica	KJ837558	Schmidt et al. 2015
Andrena lathyri	KJ839310	Schmidt et al. 2015
Andrena limata	KJ837654	Schmidt et al. 2015
Andrena marginata	KJ837896	Schmidt et al. 2015
Andrena minutula	KJ836685	Schmidt et al. 2015
Andrena minutuloides	HM401044	Schmidt et al. 2015
Andrena mitis	KJ838697	Schmidt et al. 2015
Andrena montana	GU705960	Schmidt et al. 2015
Andrena morio	HM376243	Schmidt et al. 2015
Andrena nana	KJ839631	Schmidt et al. 2015
Andrena nasuta	KJ839710	Schmidt et al. 2015
Andrena nigroaenea	KJ836732	Schmidt et al. 2015
Andrena nigrospina	KJ838255	Schmidt et al. 2015
Andrena nitida	KT074020	Schmidt et al. 2015
Andrena nitidiuscula	KJ838927	Schmidt et al. 2015
Andrena nitidula	KJ836688	Schmidt et al. 2015
Andrena niveata	KJ836650	Schmidt et al. 2015
Andrena nuptialis	KJ837325	Schmidt et al. 2015
Andrena nycthemera	KJ836417	Schmidt et al. 2015
Andrena ovatula	KJ838397	Schmidt et al. 2015
Andrena pallitarsis	HM401021	Schmidt et al. 2015
Andrena pandellei	KJ839079	Schmidt et al. 2015
Andrena pastellensis	HM401027	Schmidt et al. 2015
Andrena paucisquama	KJ839316	Schmidt et al. 2015
Andrena pilipes	KJ836606	Schmidt et al. 2015
Andrena polita	HM401023	Schmidt et al. 2015
Andrena potentillae	HM401024	Schmidt et al. 2015
Andrena praecox	HM376224	Schmidt et al. 2015

Andrena proxima	HM401052	Schmidt et al. 2015
Andrena pusilla	KJ839537	Schmidt et al. 2015
Andrena rhenana	KJ838999	Schmidt et al. 2015
Andrena rogenhoferi	KJ838541	Schmidt et al. 2015
Andrena rosae	EU374644	Schmidt et al. 2015
Andrena ruficrus	HM401042	Schmidt et al. 2015
Andrena rufizona	KJ836804	Schmidt et al. 2015
Andrena rufula	KJ838498	Schmidt et al. 2015
Andrena semilaevis	KJ839157	Schmidt et al. 2015
Andrena sericata	KJ836715	Schmidt et al. 2015
Andrena similis	KJ839751	Schmidt et al. 2015
Andrena spinigera	KJ837406	Schmidt et al. 2015
Andrena stragulata	KJ839175	Schmidt et al. 2015
Andrena strohmella	KJ839737	Schmidt et al. 2015
Andrena subopaca	KJ836638	Schmidt et al. 2015
Andrena suerinensis	KJ838205	Schmidt et al. 2015
Andrena susterai	KJ838537	Schmidt et al. 2015
Andrena symphyti	KJ837432	Schmidt et al. 2015
Andrena synadelpha	KT074024	Tang et al. 2017
Andrena taraxaci	KJ839582	Schmidt et al. 2015
Andrena tarsata	JQ909697	Magnacca and Brown 2012
Andrena thoracica	KJ839789	Schmidt et al. 2015
Andrena tibialis	KJ837901	Schmidt et al. 2015
Andrena trimmerana	KJ836680	Schmidt et al. 2015
Andrena tscheki	KJ836443	Schmidt et al. 2015
Andrena vaga	KJ837581	Schmidt et al. 2015
Andrena ventralis	KJ839138	Schmidt et al. 2015
Andrena viridescens	KJ836441	Schmidt et al. 2015
Andrena wilkella	KJ836402	Schmidt et al. 2015
Anthidiellum strigatum	KJ837946	Schmidt et al. 2015
Anthidium florentinum	KJ839553	Schmidt et al. 2015
Anthidium loti	KJ836898	Schmidt et al. 2015
Anthidium manicatum	KJ838277	Schmidt et al. 2015
Anthidium montanum	KJ837682	Schmidt et al. 2015
Anthidium oblongatum	GU706008	Schmidt et al. 2015
Anthidium punctatum	GU706009	Schmidt et al. 2015
Anthophora aestivalis	HM376217	Schmidt et al. 2015
Anthophora balneorum	KJ839342	Schmidt et al. 2015
Anthophora bimaculata	KJ837025	Schmidt et al. 2015
Anthophora furcata	KJ837165	Schmidt et al. 2015
Anthophora plagiata	KJ839757	Schmidt et al. 2015
Anthophora plumipes	HM376219	Schmidt et al. 2015
Anthophora pubescens	KJ836626	Schmidt et al. 2015
Anthophora quadrimaculata	KJ839773	Schmidt et al. 2015

Anthophora retusa	KJ837816	Schmidt et al. 2015
Apis mellifera	MG443154	Dewaard, BIOUG Archive GGBN Data Release
Biastes emarginatus	KJ839184	Schmidt et al. 2015
Biastes truncatus	KJ837962	Schmidt et al. 2015
Bombus alpinus	HQ948121	Schmidt et al. 2015
Bombus argillaceus	KJ837978	Schmidt et al. 2015
Bombus barbutellus	GU705885	Schmidt et al. 2015
Bombus bohemicus	GU705896	Schmidt et al. 2015
Bombus campestris	GU705893	Schmidt et al. 2015
Bombus confusus	KJ836795	Schmidt et al. 2015
Bombus cryptarum	JQ843394	williams et al. 2013
Bombus distinguendus	KJ837828	Schmidt et al. 2015
Bombus flavidus	AY181184	Pedersen 2002
Bombus gerstaeckeri	GU705902	Schmidt et al. 2015
Bombus hortorum	KT164676	Tang et al. 2017
Bombus humilis	KJ836557	Schmidt et al. 2015
Bombus hypnorum	KT074031	Tang et al. 2017
Bombus jonellus	KJ837105	Schmidt et al. 2015
Bombus lapidarius	GU705907	Schmidt et al. 2015
Bombus lucorum	KT164681	Tang et al. 2017
Bombus magnus	GU705915	Schmidt et al. 2015
Bombus mendax	HQ563801	Schmidt et al. 2015
Bombus mesomelas	HQ563803	Schmidt et al. 2015
Bombus monticola	GU705913	Schmidt et al. 2015
Bombus mucidus	KJ839017	Schmidt et al. 2015
Bombus muscorum	KJ838500	Schmidt et al. 2015
Bombus norvegicus	GU705916	Schmidt et al. 2015
Bombus pascuorum	KJ836788	Schmidt et al. 2015
Bombus pratorum	KT164684	Schmidt et al. 2015
Bombus pyrenaeus	KJ837876	Schmidt et al. 2015
Bombus quadricolor	HQ563807	Schmidt et al. 2015
Bombus ruderarius	GU705935	Schmidt et al. 2015
Bombus ruderatus	KX821204	Packer and Ruz 2016
Bombus rupestris	GU705932	Schmidt et al. 2015
Bombus semenoviellus	HQ563810	Schmidt et al. 2015
Bombus sichelii	HQ563811	Schmidt et al. 2015
Bombus soroeensis	GU705936	Schmidt et al. 2015
Bombus subterraneus	KJ837619	Schmidt et al. 2015
Bombus sylvarum	GU705942	Schmidt et al. 2015
Bombus sylvestris	GU705886	Schmidt et al. 2015
Bombus terrestris	JQ843625	Tang et al. 2017
Bombus vestalis	GU705952	Schmidt et al. 2015
Bombus veteranus	HQ563800	Schmidt et al. 2015
Bombus wurflenii	GU705917	Schmidt et al. 2015

Camptopoeum frontale	KJ837986	Schmidt et al. 2015
Ceratina chalybea	KJ836933	Schmidt et al. 2015
Ceratina cucurbitina	KJ836657	Schmidt et al. 2015
Ceratina cyanea	GU705965	Schmidt et al. 2015
Ceratina nigrolabiata	KJ836469	Schmidt et al. 2015
Chelostoma campanularum	KR792705	Schmidt et al. 2015
Chelostoma distinctum	KJ837112	Schmidt et al. 2015
Chelostoma emarginatum	KJ837355	Schmidt et al. 2015
Chelostoma grande	KJ836477	Schmidt et al. 2015
Chelostoma rapunculi	KR783170	Schmidt et al. 2015
Coelioxys afra	KJ837838	Schmidt et al. 2015
Coelioxys alatav	HM401246	Schmidt et al. 2015
Coelioxys argentea	KJ837998	Schmidt et al. 2015
Coelioxys aurolimbata	KJ838074	Schmidt et al. 2015
Coelioxys brevis	KJ837761	Schmidt et al. 2015
Coelioxys conica	HM401145	Schmidt et al. 2015
Coelioxys conoidea	KJ839589	Schmidt et al. 2015
Coelioxys echinata	HM401148	Schmidt et al. 2015
Coelioxys elongata	KJ837365	Schmidt et al. 2015
Coelioxys haemorrhoa	KJ839282	Schmidt et al. 2015
Coelioxys inermis	KJ839147	Schmidt et al. 2015
Coelioxys mandibularis	KJ839664	Schmidt et al. 2015
Coelioxys rufescens	KJ837496	Schmidt et al. 2015
Colletes brevigena	KJ839788	Schmidt et al. 2015
Colletes collaris	DQ085544	Kuhlmann et al. 2007
Colletes cunicularius	KJ837588	Schmidt et al. 2015
Colletes daviesanus	KJ837050	Schmidt et al. 2015
Colletes floralis	HQ948116	Schmidt et al. 2015
Colletes fodiens	HM401156	Schmidt et al. 2015
Colletes graeffei	KJ839614	Schmidt et al. 2015
Colletes halophilus	DQ085542	Kuhlmann et al. 2007
Colletes hederae	KJ839205	Schmidt et al. 2015
Colletes hylaeiformis	KJ837953	Schmidt et al. 2015
Colletes impunctatus	HM401265	Schmidt et al. 2015
Colletes marginatus	KJ837247	Schmidt et al. 2015
Colletes mlokossewiczi	KJ837366	Schmidt et al. 2015
Colletes nasutus	HM401158	Schmidt et al. 2015
Colletes similis	KJ838772	Schmidt et al. 2015
Colletes succinctus	KJ837472	Schmidt et al. 2015
Dasypoda argentata	KJ839763	Schmidt et al. 2015
Dasypoda hirtipes	KT074042	Schmidt et al. 2018
Dasypoda suripes	KJ838502	Schmidt et al. 2015
Dioxys cincta	KJ836409	Schmidt et al. 2015
Dioxys tridentata	KJ837073	Schmidt et al. 2015

Dufourea alpina	KJ839615	Schmidt et al. 2018
Dufourea dentiventris	HM401151	Schmidt et al. 2018
Dufourea halictula	HM401152	Schmidt et al. 2018
Dufourea inermis	KJ837444	Schmidt et al. 2018
Dufourea minuta	KJ838873	Schmidt et al. 2018
Dufourea paradoxa	KJ839493	Schmidt et al. 2018
Epeoloides coecutiens	GU706014	Schmidt et al. 2015
Epeolus alpinus	KJ837447	Schmidt et al. 2015
Epeolus cruciger	KJ836474	Schmidt et al. 2015
Epeolus marginatus	KJ838052	Schmidt et al. 2015
Epeolus schummeli	KJ837959	Schmidt et al. 2015
Epeolus variegatus	HM401155	Schmidt et al. 2015
Eucera chrysopyga	KJ836791	Schmidt et al. 2015
Eucera cineraria	KJ836627	Schmidt et al. 2015
Eucera interrupta	KJ836504	Schmidt et al. 2015
Eucera longicornis	KJ838283	Schmidt et al. 2015
Eucera nigrescens	KJ838368	Schmidt et al. 2015
Halictus cochlearitarsis	KJ836651	Schmidt et al. 2015
Halictus confusus	KJ839065	Schmidt et al. 2015
Halictus eurygnathus	KJ839238	Schmidt et al. 2015
Halictus gavarnicus	KJ839088	Schmidt et al. 2015
Halictus langobardicus	HM401091	Schmidt et al. 2015
Halictus leucaheneus	KJ838382	Schmidt et al. 2015
Halictus maculatus	KJ836478	Schmidt et al. 2015
Halictus pollinosus	KJ838192	Schmidt et al. 2015
Halictus quadricinctus	KJ836586	Schmidt et al. 2018
Halictus rubicundus	KJ837973	Schmidt et al. 2015
Halictus scabiosae	KJ839219	Schmidt et al. 2015
Halictus sexcinctus	KJ838845	Schmidt et al. 2015
Halictus simplex	KJ836612	Schmidt et al. 2015
Halictus smaragdulus	KJ837345	Schmidt et al. 2018
Halictus subauratus	KJ836879	Schmidt et al. 2018
Halictus tumulorum	KJ836913	Schmidt et al. 2015
Heriades crenulatus	KJ836538	Schmidt et al. 2015
Heriades truncorum	KJ836448	Schmidt et al. 2015
Hoplitis acuticornis	HM401195	Schmidt et al. 2015
Hoplitis adunca	HM401196	Schmidt et al. 2015
Hoplitis anthocopoides	KJ838067	Schmidt et al. 2015
Hoplitis claviventris	KJ837591	Schmidt et al. 2015
Hoplitis lepeletieri	KJ837451	Schmidt et al. 2015
Hoplitis leucomelana	HM401205	Schmidt et al. 2015
Hoplitis loti	HM401209	Schmidt et al. 2015
Hoplitis mitis	KJ838545	Schmidt et al. 2015
Hoplitis mucida	KJ837173	Schmidt et al. 2015

Hoplitis papaveris	KJ836470	Schmidt et al. 2015
Hoplitis ravouxi	KJ839378	Schmidt et al. 2015
Hoplitis tridentata	GU705987	Schmidt et al. 2015
Hoplitis tuberculata	HQ948088	Schmidt et al. 2015
Hoplitis villosa	HM401232	Schmidt et al. 2015
Hylaeus alpinus	HM401162	Schmidt et al. 2015
Hylaeus angustatus	KJ836545	Schmidt et al. 2015
Hylaeus annulatus	KJ839556	Schmidt et al. 2015
Hylaeus brevicornis	KJ839278	Schmidt et al. 2015
Hylaeus clypearis	HM401165	Schmidt et al. 2015
Hylaeus communis	KJ839696	Schmidt et al. 2015
Hylaeus confusus	GU705974	Schmidt et al. 2015
Hylaeus cornutus	KJ839471	Schmidt et al. 2015
Hylaeus difformis	HM401166	Schmidt et al. 2015
Hylaeus dilatatus	KJ839192	Schmidt et al. 2015
Hylaeus duckei	HM401169	Schmidt et al. 2015
Hylaeus gibbus	KJ837435	Schmidt et al. 2015
Hylaeus glacialis	KJ838093	Schmidt et al. 2015
Hylaeus gracilicornis	HM401171	Schmidt et al. 2015
Hylaeus gredleri	KJ837308	Schmidt et al. 2015
Hylaeus hyalinatus	KJ837179	Schmidt et al. 2015
Hylaeus incongruus	KJ837097	Schmidt et al. 2015
Hylaeus intermedius	KJ838687	Schmidt et al. 2015
Hylaeus kahri	KJ838978	Schmidt et al. 2015
Hylaeus leptocephalus	KJ838113	Schmidt et al. 2015
Hylaeus lineolatus	HM401173	Schmidt et al. 2015
Hylaeus moricei	HM401175	Schmidt et al. 2015
Hylaeus nigritus	KJ838096	Schmidt et al. 2015
Hylaeus nivalis	HM401179	Schmidt et al. 2015
Hylaeus paulus	KJ837780	Schmidt et al. 2015
Hylaeus pectoralis	KJ839242	Schmidt et al. 2015
Hylaeus pfankuchi	HM401182	Schmidt et al. 2015
Hylaeus pictipes	KJ838603	Schmidt et al. 2015
Hylaeus pilosulus	HQ948063	Schmidt et al. 2015
Hylaeus punctatus	KJ839293	Schmidt et al. 2015
Hylaeus punctulatissimus	HM401185	Schmidt et al. 2015
Hylaeus rinki	GU705973	Schmidt et al. 2015
Hylaeus signatus	KJ836815	Schmidt et al. 2015
Hylaeus sinuatus	KJ838509	Schmidt et al. 2015
Hylaeus styriacus	KJ837075	Schmidt et al. 2015
Hylaeus tyrolensis	KJ836565	Schmidt et al. 2015
Hylaeus variegatus	HM401187	Schmidt et al. 2015
Lasioglossum aeratum	KJ837299	Schmidt et al. 2015
Lasioglossum albipes	KJ838990	Schmidt et al. 2018

Lasioglossum albocinctum	KJ838953	Schmidt et al. 2018
Lasioglossum alpigenum	KJ837857	Schmidt et al. 2015
Lasioglossum angusticeps	HQ948051	Schmidt et al. 2015
Lasioglossum bavaricum	KJ838236	Schmidt et al. 2015
Lasioglossum bluethgeni	HM401099	Schmidt et al. 2015
Lasioglossum brevicorne	HQ948053	Schmidt et al. 2015
Lasioglossum breviventre	KJ836700	Schmidt et al. 2018
Lasioglossum calceatum	KT074051	Schmidt et al. 2018
Lasioglossum clypeare	KJ837961	Schmidt et al. 2015
Lasioglossum convexiusculum	KJ837411	Schmidt et al. 2015
Lasioglossum costulatum	KJ836497	Schmidt et al. 2015
Lasioglossum cupromicans	KJ837001	Schmidt et al. 2015
Lasioglossum discum	KJ839117	Schmidt et al. 2018
Lasioglossum euboeense	KJ838441	Schmidt et al. 2018
Lasioglossum fratellum	HQ954751	Schmidt et al. 2015
Lasioglossum fulvicorne	KJ838123	Schmidt et al. 2015
Lasioglossum glabriusculum	KJ836659	Schmidt et al. 2015
Lasioglossum griseolum	KJ838447	Schmidt et al. 2015
Lasioglossum intermedium	KJ838212	Schmidt et al. 2015
Lasioglossum interruptum	KJ839609	Schmidt et al. 2018
Lasioglossum laevigatum	HQ954752	Schmidt et al. 2018
Lasioglossum laticeps	KJ837829	Schmidt et al. 2018
Lasioglossum lativentre	KJ837839	Schmidt et al. 2015
Lasioglossum leucopus	KJ839703	Schmidt et al. 2015
Lasioglossum leucozonium	KT074054	Schmidt et al. 2018
Lasioglossum limbellum	KJ839645	Schmidt et al. 2015
Lasioglossum lineare	KJ837027	Schmidt et al. 2018
Lasioglossum lissonotum	KJ839702	Schmidt et al. 2015
Lasioglossum lucidulum	KJ836604	Schmidt et al. 2015
Lasioglossum majus	KJ839149	Schmidt et al. 2018
Lasioglossum malachurum	GU706051	Schmidt et al. 2018
Lasioglossum marginatum	HM401258	Schmidt et al. 2018
Lasioglossum marginellum	KJ838806	Schmidt et al. 2015
Lasioglossum minutissimum	KJ837045	Schmidt et al. 2015
Lasioglossum minutulum	KJ838016	Schmidt et al. 2015
Lasioglossum morio	GU706057	Schmidt et al. 2015
Lasioglossum nigripes	HM401251	Schmidt et al. 2018
Lasioglossum nitidiusculum	KT074055	Tang et al. 2017
Lasioglossum nitidulum	KJ837376	Schmidt et al. 2015
Lasioglossum pallens	KJ839719	Schmidt et al. 2015
Lasioglossum parvulum	HM376230	Schmidt et al. 2015
Lasioglossum pauperatum	HQ948112	Schmidt et al. 2015
Lasioglossum pauxillum	KT164647	Tang et al. 2017

Lasioglossum pleurospeculum	HQ948114	Schmidt et al. 2015
Lasioglossum politum	KJ838762	Schmidt et al. 2015
Lasioglossum punctatissimum	HM376229	Schmidt et al. 2015
Lasioglossum puncticolle	HM401255	Schmidt et al. 2015
Lasioglossum pygmaeum	KJ836931	Schmidt et al. 2015
Lasioglossum quadrinotatulum	KJ839622	Schmidt et al. 2015
Lasioglossum quadrinotatum	KX374818	unpublished
Lasioglossum rufitarse	JN272460	Schmidt et al. 2015
Lasioglossum sabulosum	KJ838136	Schmidt et al. 2015
Lasioglossum semilucens	KJ837659	Schmidt et al. 2015
Lasioglossum setulosum	KJ837830	Schmidt et al. 2015
Lasioglossum sexmaculatum	KJ839463	Schmidt et al. 2015
Lasioglossum sexnotatum	KJ838091	Schmidt et al. 2015
Lasioglossum sexstrigatum	HQ954761	Schmidt et al. 2015
Lasioglossum smeathmanellum	KT074061	Tang et al. 2017
Lasioglossum subfasciatum	KJ839824	Schmidt et al. 2015
Lasioglossum subfulvicorne	HQ948016	Schmidt et al. 2015
Lasioglossum tricinctum	KJ838157	Schmidt et al. 2015
Lasioglossum villosulum	GU705888	Schmidt et al. 2015
Lasioglossum virens	KJ839379	Schmidt et al. 2015
Lasioglossum xanthopus	KJ836625	Schmidt et al. 2015
Lasioglossum zonulum	KJ838322	Schmidt et al. 2018
Lithurgus chrysurus	KJ836731	Schmidt et al. 2015
Macropis europaea	GU706049	Schmidt et al. 2018
Macropis fulvipes	KJ838021	Schmidt et al. 2018
Megachile albisecta	KJ839743	Schmidt et al. 2015
Megachile alpicola	KJ838895	Schmidt et al. 2015
Megachile analis	M401190	Schmidt et al. 2015
Megachile apicalis	KJ837288	Schmidt et al. 2015
Megachile centuncularis	HM401192	Schmidt et al. 2015
Megachile circumcincta	GU705984	Schmidt et al. 2015
Megachile deceptoria	KJ836416	Schmidt et al. 2018
Megachile ericetorum	GU705988	Schmidt et al. 2015
Megachile flabellipes	KJ836765	schmidt et al. 2015
Megachile genalis	HM401106	Schmidt et al. 2015
Megachile lagopoda	HM401107	Schmidt et al. 2015
Megachile lapponica	HQ948055	Schmidt et al. 2015
Megachile leachella	HM401112	schmidt et al. 2015
Megachile ligniseca	GU705995	Schmidt et al. 2015
Megachile maritima	HM401117	Schmidt et al. 2015
Megachile melanopyga	HM401121	Schmidt et al. 2015
Megachile nigriventris	GU705992	Schmidt et al. 2015
Megachile opacifrons	KJ838937	schmidt et al. 2015

Megachile parietina	HM401125	Schmidt et al. 2015
Megachile pilidens	GU705996	Schmidt et al. 2015
Megachile pyrenaea	HM401130	Schmidt et al. 2015
Megachile pyrenaica	KJ838168	Schmidt et al. 2015
Megachile rotundata	GU706002	schmidt et al. 2015
Megachile rufescens	KJ838680	Schmidt et al. 2015
Megachile versicolor	KJ836926	Schmidt et al. 2015
Megachile willughbiella	GU706003	Schmidt et al. 2015
Melecta albifrons	KJ838618	Schmidt et al. 2015
Melecta luctuosa	KJ839507	Schmidt et al. 2015
Melitta dimidiata	KJ837102	Schmidt et al. 2015
Melitta haemorrhoidalis	GU706046	Schmidt et al. 2015
Melitta leporina	KJ837410	Schmidt et al. 2015
Melitta nigricans	KJ839607	Schmidt et al. 2015
Melitta tricincta	KJ838749	Schmidt et al. 2015
Melitturga clavicornis	KJ836607	Schmidt et al. 2015
Nomada alboguttata	KJ838522	Schmidt et al. 2015
Nomada argentata	KJ838360	Schmidt et al. 2015
Nomada armata	KJ836882	Schmidt et al. 2015
Nomada atroscutellaris	KJ838079	Schmidt et al. 2015
Nomada bifasciata	HM401039	Schmidt et al. 2015
Nomada bluethgeni	HQ948021	Schmidt et al. 2015
Nomada castellana	KJ837163	Schmidt et al. 2015
Nomada conjungens	KJ837916	Schmidt et al. 2015
Nomada distinguenda	KJ836592	Schmidt et al. 2015
Nomada emarginata	KJ836575	Schmidt et al. 2015
Nomada fabriciana	GU706016	Schmidt et al. 2015
Nomada facilis	HM401068	Schmidt et al. 2015
Nomada femoralis	HM401070	Schmidt et al. 2015
Nomada ferruginata	KJ836584	Schmidt et al. 2015
Nomada flava	GU706019	Schmidt et al. 2015
Nomada flavoguttata	KJ836513	Schmidt et al. 2015
Nomada flavopicta	HM401073	Schmidt et al. 2015
Nomada fucata	KT074069	Schmidt et al. 2015
Nomada fulvicornis	GU706024	Schmidt et al. 2015
Nomada furva	KJ837852	Schmidt et al. 2015
Nomada fuscicornis	HM401086	Schmidt et al. 2015
Nomada glabella	KJ837655	Schmidt et al. 2015
Nomada goodeniana	KT164660	Zheng et al. 2018
Nomada guttulata	HQ948030	Schmidt et al. 2015
Nomada hirtipes	GU706039	Schmidt et al. 2015
Nomada integra	KJ837492	Schmidt et al. 2015
Nomada kohli	HQ948035	Schmidt et al. 2015
Nomada lathburiana	KJ837412	Schmidt et al. 2015

Nomada leucophthalma	GU706027	Schmidt et al. 2015
Nomada marshamella	GU706032	Schmidt et al. 2015
Nomada melathoracica	HQ948037	Schmidt et al. 2015
Nomada meridionalis	KJ837880	Schmidt et al. 2015
Nomada minuscula	KJ837068	Schmidt et al. 2015
Nomada moeschleri	HM401079	Schmidt et al. 2015
Nomada mutabilis	KJ837610	Schmidt et al. 2015
Nomada mutica	KJ838713	Schmidt et al. 2015
Nomada nobilis	KJ836654	Schmidt et al. 2015
Nomada obscura	KJ837640	Schmidt et al. 2015
Nomada obtusifrons	KJ836639	Schmidt et al. 2015
Nomada opaca	HM401080	Schmidt et al. 2015
Nomada panzeri	KJ837799	Schmidt et al. 2015
Nomada pleurosticta	KJ836589	Schmidt et al. 2015
Nomada posthuma	KJ837409	Schmidt et al. 2015
Nomada rhenana	KJ838920	Schmidt et al. 2015
Nomada roberjeotiana	KJ837507	Schmidt et al. 2015
Nomada rostrata	KJ839808	Schmidt et al. 2015
Nomada ruficornis	KT164649	Schmidt et al. 2015
Nomada rufipes	KJ838388	Schmidt et al. 2015
Nomada sexfasciata	KJ837270	Schmidt et al. 2015
Nomada sheppardana	KJ83747	Schmidt et al. 2015
Nomada signata	HM401085	Schmidt et al. 2015
Nomada similis	HM401087	Schmidt et al. 2015
Nomada stigma	KJ837336	Schmidt et al. 2015
Nomada striata	KJ836473	Schmidt et al. 2015
Nomada succincta	GU706045	Schmidt et al. 2015
Nomada symphyti	KJ839448	Schmidt et al. 2015
Nomada tormentillae	HQ948039	Schmidt et al. 2015
Nomada villosa	KJ836467	Schmidt et al. 2015
Nomada zonata	HM401090	Schmidt et al. 2015
Nomia diversipes	KJ837536	Schmidt et al. 2015
Nomioides facilis	KJ838426	Schmidt et al. 2015
Nomioides minutissimus	KJ839479	Schmidt et al. 2015
Osmia alticola	KJ839450	Schmidt et al. 2015
Osmia andrenoides	HM401197	Schmidt et al. 2015
Osmia aurulenta	KJ837026	Schmidt et al. 2015
Osmia bicolor	KJ839576	Schmidt et al. 2015
Osmia bicornis	GU705983	Schmidt et al. 2015
Osmia brevicornis	HM401200	Schmidt et al. 2015
Osmia caerulescens	KT074074	Tang et al. 2017
Osmia cerinthidis	KC709832	Haider et al. 2013
Osmia cornuta	KJ836461	Schmidt et al. 2015
Osmia gallarum	KJ836777	Schmidt et al. 2015

Osmia inermis	HM401203	Schmidt et al. 2015
Osmia latreillei	KJ837570	Schmidt et al. 2015
Osmia leaiana	HM401204	Schmidt et al. 2015
Osmia melanogaster	HM401210	Schmidt et al. 2015
Osmia mustelina	KJ838242	Schmidt et al. 2015
Osmia nigriventris	KJ839628	Schmidt et al. 2015
Osmia niveata	KJ838274	Schmidt et al. 2015
Osmia parietina	HM401222	Schmidt et al. 2015
Osmia pilicornis	KJ839236	Schmidt et al. 2015
Osmia rufohirta	KJ836740	Schmidt et al. 2015
Osmia saxicola	KJ836508	Schmidt et al. 2015
Osmia spinulosa	HM376215	Schmidt et al. 2015
Osmia submicans	KJ836956	Schmidt et al. 2015
Osmia uncinata	HM401230	Schmidt et al. 2015
Osmia versicolor	KJ838819	Schmidt et al. 2015
Osmia viridana	KJ837269	Schmidt et al. 2015
Osmia xanthomelana	KJ836953	Schmidt et al. 2015
Panurginus herzi	KJ838943	Schmidt et al. 2015
Panurginus montanus	HQ948095	Schmidt et al. 2015
Panurginus sericatus	KJ837895	Schmidt et al. 2015
Panurgus banksianus	KJ837192	Schmidt et al. 2015
Panurgus calcaratus	GU705956	Schmidt et al. 2015
Panurgus dentipes	KJ836713	Schmidt et al. 2015
Pseudoanthidium melanurum	KJ838568	Schmidt et al. 2015
Pseudoanthidium scapulare	KJ836523	Schmidt et al. 2015
Rhodanthidium caturigense	KJ836719	Schmidt et al. 2015
Rhodanthidium septemdentatum	KJ838285	Schmidt et al. 2015
Rophites algirus	KJ839593	Schmidt et al. 2015
Rophites quinquespinosus	KJ839028	Schmidt et al. 2015
Sphecodes albilabris	GU705920	Schmidt et al. 2018
Sphecodes alternatus	KJ837938	Schmidt et al. 2018
Sphecodes crassanus	KJ838632	Schmidt et al. 2018
Sphecodes crassus	GU705945	Schmidt et al. 2018
Sphecodes cristatus	JX256667	Habermannová et al. 2013
Sphecodes croaticus	KJ836647	Schmidt et al. 2018
Sphecodes ephippius	KT074079	Schmidt et al. 2018
Sphecodes ferruginatus	KJ837622	Schmidt et al. 2018
Sphecodes geoffrellus	KJ837236	Schmidt et al. 2018
Sphecodes gibbus	KJ836803	Schmidt et al. 2018
Sphecodes hyalinatus	KJ837294	Schmidt et al. 2018
Sphecodes longulus	KJ836681	Schmidt et al. 2018
Sphecodes majalis	KJ837051	Schmidt et al. 2018
Sphecodes marginatus	KJ839540	Schmidt et al. 2018
Sphecodes miniatus	KJ836506	Schmidt et al. 2018

Sphecodes niger	KJ836693	Schmidt et al. 2018
Sphecodes pellucidus	KT074080	Tang et al. 2017
Sphecodes puncticeps	KT074081	Schmidt et al. 2018
Sphecodes reticulatus	KJ837577	Schmidt et al. 2018
Sphecodes rubicundus	HQ563095	Schmidt et al. 2018
Sphecodes ruficrus	KJ836476	Schmidt et al. 2018
Sphecodes rufiventris	KJ837280	Schmidt et al. 2018
Sphecodes scabricollis	KJ838552	Schmidt et al. 2015
Sphecodes schenckii	KJ836762	Schmidt et al. 2018
Sphecodes spinulosus	KJ839610	Schmidt et al. 2015
Stelis breviuscula	KJ838642	Schmidt et al. 2015
Stelis franconica	KJ838642	Schmidt et al. 2015
Stelis minima	HQ948107	Schmidt et al. 2015
Stelis minuta	KJ836896	Schmidt et al. 2015
Stelis nasuta	KJ839749	Schmidt et al. 2015
Stelis odontopyga	HM401240	Schmidt et al. 2015
Stelis ornatula	KJ836690	Schmidt et al. 2015
Stelis punctulatissima	HM401242	Schmidt et al. 2015
Stelis signata	KJ838629	Schmidt et al. 2015
Systropha curvicornis	KJ836819	Schmidt et al. 2018
Systropha planidens	KJ836726	Schmidt et al. 2018
Tetralonia malvae	KJ836698	Schmidt et al. 2015
Tetraloniella dentata	KJ836577	Schmidt et al. 2015
Tetraloniella salicariae	KJ836760	Schmidt et al. 2015
Thyreus histrionicus	HQ948099	Schmidt et al. 2015
Thyreus orbatus	HM401239	Schmidt et al. 2015
Trachusa byssina	KJ838247	Schmidt et al. 2015
Xylocopa iris	HM401103	Schmidt et al. 2015
Xylocopa violacea	KJ836969	Schmidt et al. 2015

References

Dewaard, J.R. BIOUG Archive GGBN Data Release.

Habermannová, J., Bogusch, P., and Straka, J. (2013). Flexible host choice and common host switches in the evolution of generalist and specialist cuckoo bees (Anthophila: *Sphecodes*). PLoS ONE 8: e64537.

Haider, M., Dorn, S., Sedivy, C., and Müller, A. (2013). Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (Megachilidae: Osmiini). Biological Journal of the Linnean Society 111: 78-91.

Kuhlmann, M., Else, G. R., Dawson, A., and Quicke, D. L. (2007). Molecular, biogeographical and phenological evidence for the existence of three western European sibling species in the *Colletes succinctus* group (Hymenoptera: Apidae). Organisms Diversity and Evolution 7: 155-165.

Magnacca, K. N., and Brown, M. J. (2012). DNA barcoding a regional fauna: Irish solitary bees. Molecular Ecology Resources 12: 990-998.

Makkar, G. S., Dey, D., and Chhuneja, P. K. (2016). Mining bee *Andrena (Agandrena) agilissima* (Hymenoptera: Andrenidae): A new record from India with morphological and molecular notes. Journal of Applied and Natural Science 8: 1775-1778.

Packer, L., and Ruz, L. (2016). DNA barcoding the bees (Hymenoptera: Apoidea) of Chile: species discovery in a reasonably well-known bee fauna with the description of a new species of *Lonchopria* (Colletidae). Genome 60: 414-430.

Pedersen, V. (2002). European bumblebees (Hymenoptera: Bombini)-phylogenetic relationships inferred from DNA sequences. Insect Systematics and Evolution 33: 361-386.

Schmidt, S., Schmid-Egger, C., Morinière, J., Haszprunar, G., and Hebert, P. D. (2015). DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Molecular Ecology Resources 15: 985-1000.

Tang, C.Q., Notton, D.G., Norman, H., and Vogler, A. P. (2017). Next generation pollinator identification using high throughput sequencing: Final summary report to the Department for Environment, Food and Rural Affairs (DEFRA): Project PH0521. The Natural History Museum and Defra. Pp 67.

Zheng, B.Y. et al. (2018). Gene arrangement and sequence of mitochondrial genomes yield insights into the phylogeny and evolution of bees and sphecid wasps (Hymenoptera: Apoidea). Molecular Phylogenetics and Evolution 124: 1-9.

Notes S1 R code for hierarchical Bayesian models estimating the effects of functional traits on extinction risk, fit via JAGS using the R2jags library.

```
#Inputs (all standardized) for binary and ordinal models
#specified in BUGS syntax:


#functional traits
size #(log) female body size
mean.flight.month #average month of flight activity
duration.of.activity #average duration of flight activity
pollen.specialisation #vector of 1=oligolectic 0=polylectic/mesolectic/cuckoo
nest.location #vector of 1=ground-nesting; 0=air nesting/cuckoo
sociality #vector of 1=solitary; 0=social/cuckoo

#habitat preferences
altitude #(log) mean altitudinal distribution
habitat.breadth #habitat breadth (number of occupied habitat types [1-6])
urban.areas #vector of 1=occurrence in urban areas; 0=no occurrence
hedgerows #vector of 1=occurrence in hedgerows and field edges; 0=no occurrence
wasteland #vector of 1=occurrence in wasteland and ruderal sites; 0=no occurrence
meadows #vector of 1=occurrence in meadows; 0=no occurrence
raw.soil #vector of 1=occurrence in raw-soil sites; 0=no occurrence
forest #vector of 1=occurrence in forests; 0=no occurrence

#taxonomic information
N.spp = 428 #number of species with information on Red List status
N.spp = 445 #number of species with information on abundance status
N.spp = 404 #number of species with information on population trends
N.genus = 37 #number of genera
N.family = 6 #number of families
genus #genus categories
family #family categories
```

```
#Binary model


#Additional input
response
#either extinction risk (Red List status) vector of 1=threatened; 0=not threatened
#population trend vector of 1=decrease; 0=no change or increase
#or abundance vector of 1=rare (occasional to extinct); 0=abundant to frequent

mod <- "model
{
#fixed effect components from Fig. S2, with corresponding betas (b)
  for(i in 1:N.spp) { #loop over observations (species)
  response[i] ~ dbern(p.binary[i])
  logit(p.binary[i]) <- b0 #intercept term
                    + b3*size[i] + b2*mean.flight.month[i]
                    + b1*duration.of.activity[i] + b4*pollen.specialisation[i]
                    + b6*nest.location[i] + b5*sociality[i] + b10*altitude[i]
                    + b7*habitat.breadth[i] + b8*urban.areas[i]
                    + b9*hedgerows[i] + b11*wasteland[i] + b12*meadows[i]
                    + b13*raw.soil[i] + b14*forest[i] #fixed effects
                    + b.genus[genus[i]] #genus random effect
                    + b.family[family[i]] } #family random effect

  #Genus random effect
  for(i in 1:N.genus) {
  b.genus[i] ~ dnorm(0, genus.tau)}

  #Family random effect
  for(i in 1:N.family) {
  b.family[i] ~ dnorm(0, family.tau)}

  ##Priors

  #Genus random effect priors
  genus.tau <- genus.sigma^-2
  genus.sigma ~ dunif(0, 100)

  #Family random effect priors
  family.tau <- family.sigma^-2
  family.sigma ~ dunif(0, 100)

  #prior for overall intercept
  b0 ~ dnorm(0,0.0001)
  #non-informative priors for fixed effects (mean=0, var=1000)
  for(i in 1:14) {b[i] ~ dnorm(0,0.0001)}

}" #end model
```

```
#Ordinal model


#Additional input:
response
#either ordinal vector of Red List status: 1=not threatened; 2=near-threatened;
                        #3=threatened; 4=highly threatened; 5=almost extinct; 6=extinct
#ordinal vector of population trend: 1=increase; 2=no change; 3=small decline;
                        #4=decline; 5=large decline; 6=extinct
#or ordinal vector of abundance: 1=abundant; 2=common; 3=frequent;
                        #4=occasional; 5=rare; 6=extremely rare; 7=extinct
M=6 #maximum value of ordinal classes for extinction risk and population trend
M=7 #maximum value of ordinal classes for abundance

mod <- "model
{
#fixed effect components from Figs. 2a and S4, with corresponding betas (b)
  for(i in 1:N.spp) { #loop over observations (species)
      mu[i] <- b3*size[i] + b2*mean.flight.month[i] + b1*duration.of.activity[i]
               + b4*pollen.specialisation[i] + b6*nest.location[i] + b5*sociality[i]
               + b10*altitude[i] + b7*habitat.breadth[i] + b8*urban.areas[i]
               + b9*hedgerows[i] + b11*wasteland[i] + b12*meadows[i] + b13*raw.soil[i]
               + b14*forest[i] #fixed effects
               + b.genus[genus[i]] + b.family[family[i]] #genus + family random effects

      ## cumulative logistic probabilities: ordinal logit part from Jackman 2009
         #M is the maximum value of classes(M=6)
          logit(Q[i,1]) <- tau[1]-mu[i]
          p[i,1] <- Q[i,1]
          for(j in 2:M){
          logit(Q[i,j]) <- tau[j]-mu[i]
          p[i,j] <- Q[i,j] - Q[i,j-1]
          }
          p[i,(M+1)] <- 1 - Q[i,M]
          response[i] ~ dcat(p[i,1:(M+1)]) ## p[i,] sums to 1 for each i
  }

  #genus random effect
  for(i in 1:N.genus) {
     b.genus[i] ~ dnorm(0, genus.tau)}

  #family random effect
  for(i in 1:N.family) {
     b.family[i] ~ dnorm(0, family.tau)}

  ## ordinal logit thresholds
  for(j in 1:M){
  tau0[j] ~ dnorm(0, .01)
  }
  tau[1:M] <- sort(tau0)

  ##Priors

  #genus random effect priors
  genus.tau <- genus.sigma^-2
  genus.sigma ~ dunif(0, 100)

  #family random effect priors
  family.tau <- family.sigma^-2
  family.sigma ~ dunif(0, 100)

  #non-informative priors for fixed effects (mean=0, var=1000)
  for(i in 1:14) {b[i] ~ dnorm(0,0.0001)}

}" #end model
```

Chapter 3

Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters

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and Renner, S. S.

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2018

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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters

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Abstract
Botanical gardens represent artificial, but stable environments. With this premise, we analyzed the Munich Botanical Garden's bee fauna in 1997/1999 and again in 2015/2017. The garden covers 20 ha, uses no bee-relevant insecticides, has a protected layout, and on three sides abuts protected areas. Outdoors, it cultivates some 10,871 species/subspecies, many suitable as pollen and nectar sources for bees. The first survey found 79 species, the second 106, or 55% of the 192 species recorded for Munich since 1990. A *Jackknife* estimate for the second survey suggests 115 expected species. Classifying bees according to their thermal preferences (warm habitats, cool habitats, broad preferences, or unknown) revealed that 15 warm-loving species were gained (newly found), two lost (no longer found), and 12 retained, but only one cool-loving species was gained, three lost, and none retained, which multinomial models show to be significant differences. Of the 62 retained species, 27 changed in abundance, with 18 less frequent and nine more frequent by 2017 than they had been in 1997/1999. Retention, gain, or loss were unconnected to pollen specialization and Red List status of bee species. Between 1997 and 2017, average temperatures in Munich have increased by 0.5 °C, and climate warming over the past century is the most plausible explanation for the directional increase in warm-loving and the decrease in cool-adapted species. These results highlight the potential of botanic gardens with their artificially diverse and near-pesticide-free floras as systems in which to investigate climate change per se as a possible factor in shifting insect diversity.

Keywords Botanic gardens · Bee fauna · Climate warming · Repeated monitoring · Stable habitat · Insect faunal change

Introduction

Bee diversity in the United States and Europe appears to be declining (Potts et al. 2010), with bumblebee losses especially well documented (Williams et al. 2007; Goulson et al. 2008). Reasons for the decline are manifold and include stress from parasites and pesticides, habitat loss and fragmentation (affecting nesting sites and food sources), a lack of suitable flowers for oligolectic bees, and climate warming (Williams et al. 2007; Potts et al. 2010; Goulson et al. 2015). Besides the causes, also the direction of faunal change remains poorly understood because few areas have been monitored with consistent methods over longer periods (Hallmann et al. 2017). Data on changes in regional bee faunas are therefore sparse, and where they exist, attribution to specific causes is difficult. Agricultural and urban habitats over the past 100 years have changed in many factors, relating to human construction projects and intensive agriculture. For some bees, urban parks and gardens are becoming refugia, but the relationships between bee diversity and parks are multifactorial, with floristic diversity playing a major role (Hall et al. 2016). By comparison to these habitats, botanic gardens, while also located in urban settings, have a persistent flora that always includes a rich mix of native and foreign species. The basic layout of many older gardens has not changed for the past 50 or even 100 years, and the use of

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insecticides in European public gardens and parks over the past 20 years has become increasingly restricted. Botanic gardens, therefore, provide a setting for not only studying plant responses to climate change (Primack and Miller-Rushing 2009; Zohner and Renner 2014) but also systems for monitoring insect faunas in which directional changes, such an increase or decrease in warm- or cool-loving species, can plausibly be attributed to a change in climate, rather than floristic change or other causes.

Here, we use two inventories, carried out 20 years apart, of the bees of the Munich Botanic Garden to investigate the possible impact of climate warming per se on an urban bee fauna. The garden's bees were inventoried in 1997–1999 (Bembé et al. 2001) and again in 2015–2017. The garden's paths and flower bed layout are protected; its seasonally changing flower displays over the past 20 years have not changed, hardly any pesticides have ever been used, and the flora and buildings surrounding the garden have essentially not changed, since it opened in May 1914 (details in "Methods"). Average temperatures during the vegetation season in Munich have increased by 0.5 °C over the past 20 years (compare Fig. 1), and winters have become shorter by almost 4 weeks (Zohner and Renner 2014). We, therefore, expected that bee diversity might have shifted to more warm-loving species.

Methods

Study area, bee monitoring and identification, and scoring of bee species traits

The Munich Botanic Garden opened in May 1914 and covers about 20 ha (Renner 2014). It is situated next to the Nymphenburg Palace Park at 48°09′45″N, 11° 30′06″E at an altitude of ca.500 m above sea level. On three of its sides, it borders on the 210-ha-large Palace Park and the orchard of a Catholic Nunnery; on its fourth side is a heavily travelled road that separates the garden from a hospital that opened at almost the same time as the garden. The garden currently cultivates 10,871 species and subspecies outdoors (data from the garden's living plant database, accessed by SSR on 1 Nov. 2017). The only pesticides used over the past 20 years are occasionally Neudorff Spruzit against molluscs and Neudorff Loxiran against ants (http://www.neudorff-handel.de, last accessed 3 Sep. 2017). Both have no known negative effects on bees. The layout of the garden and its visitor paths (Online Supporting Material Figure S1) are protected, as is the layout and all paths in the Nymphenburg Palace Park. Two large and several small nesting aids, consisting of bamboo, wood, and bricks, have long been used in the garden.

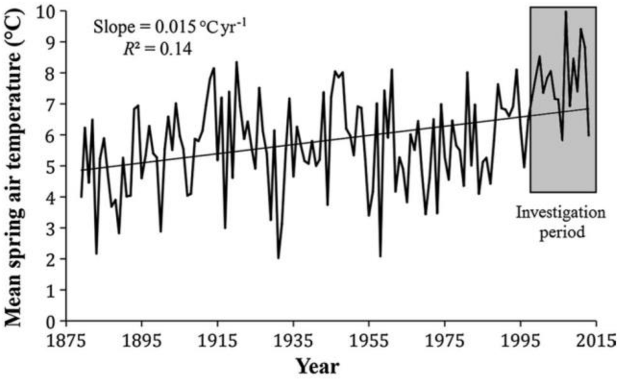

Fig. 1 Average spring (March and April) temperatures in Munich, with the slope revealing a mean temperature increase of 0.015 °C per year. Data from the weather stations Munich Botanical Garden (1879–1954), Munich-Nymphenburg (1955–1998), and Munich downtown (1999–2013) modified from Zohner and Renner (2014, Fig. S1)

Between spring and fall 1997, 1998, and 1999, Bembé et al. (2001) carried out 56 biweekly monitoring walks, mostly between 9:00 and 12:00, recording bees by hand-netting (with most netting effort in 1998). As customary in the 1990s, species identification was based on morphological features. Between spring and September 2015, 2016, and 2017, we carried out biweekly monitoring walks, resulting in 184 walks and 290 h of observation (2015: 38 walks, 59 h; 2016: 107 walks, 159 h; 2017: 72 walks, 72 h). Like Bembé et al. (2001), we did not follow a strict route, but instead focused on patches with numerous flowering plants (throughout the garden), and on the morning hours of warm and dry days rather than overcast or humid days. Depending on bee abundance and weather, our mapping walks lasted between half an hour and 4 h.

We recorded easily recognizable bee taxa, such as Megachilidae, by photography (in situ, but also close-ups of caught individuals chilled down to 4 °C for several hours and then released after photography), focusing on mandibles, coloration, hair and facial patterns, and tergite markings. For identification, we used keys by Dathe (1980), Amiet et al. (1999, 2001, 2004, 2007), Amiet and Krebs (2014), von Hagen and Aichhorn (2014), and Falk and Lewington (2015). Bees from genera that are difficult to identify were caught with a magnifying cup, chilled down to 4 °C for microscopic examination, and, in some cases, killed by storing them in a freezer at − 20 °C for later DNA isolation and barcoding, relying on the primers of Schmidt et al. (2015) who have barcoded 546 of the 571 bee species that occur in Germany; our lab procedure is described in the Online Supporting Materials, which also list GenBank accession numbers and details on vouchers deposited in the State Zoological Collection in Munich (ZSM; collecting permit StmUV Az.62 g-U8645.8-2014/1-2 v.10.11.2014). For the *Bombus lucorum* species complex, we used dead bees found below linden trees in large numbers in July and August (Baal et al. 1994); these partly damaged specimens were not deposited in the ZSM. Our bee taxonomy and nomenclature follow Scheuchl and Willner (2016).

To compare the 1997–1999 and 2015–2017 surveys, we assigned species to one of three categories, namely "lost", "retained", and "gained", with lost referring to species only found in the first survey, retained referring to species found in both surveys, and gained referring to species found only in the recent survey. Bee temperature preferences were scored based on habitat preferences in Switzerland (Amiet et al. 1999, 2001, 2004, 2007; Amiet and Krebs 2014) and Central Europe (Westrich 1989; Scheuchl and Willner 2016). Bee pollen foraging specialization was scored based on Scheuchl and Willner (2016), with oligolecty defined as pollen foraging restricted to closely related species and polylecty as pollen foraging on diverse (unrelated) species. Following Bembé et al. (2001), we scored abundance using the following categories: category 0 for species not seen; category I for species observed with fewer than 5 individuals; category II for 5–20 individuals, and category III for more than 20 individuals per year. Since the abundance estimates in the first (1997–1999) and second survey (2015–2017) were done by different people, we did not model the possible importance of abundance for 'predicting' extinction (Results). Red List categories follow Westrich et al. (2011), with 0 meaning extinct, 1 critically endangered, 2 endangered, 3 vulnerable, NT near threatened, G threat of unknown magnitude, and an asterisk for least concern. A list of all species and their traits can be found in the Online Supporting Materials (Table S1).

Correlations between bee species gain, loss, or retention and thermal habitat niche, pollen specialization, and Red List status were analyzed using multinomial models implemented in the R-package VGAM (Yee 2010), excluding all species with unknown thermal habitat niche. Since a first model with the independent variables "foraging preference" and "endangerment" indicated no significant influence of pollen specialization or Red List status on abundance changes, we excluded these factors and calculated a second model with only "temperature preference" as independent variable. In this model, the category "retained" was used as reference category. Due to low numbers of wild bees with preferences for cooler habitat, a third model without these species was calculated to check whether the coefficients of the other thermal preferences stay stable despite high variation for the factor "cooler habitats."

To assess our sampling success, we used the *Jackknife* method of Haeseler and Ritzau (1998), whereby the expected number of species for an area can be calculated using the formula $Sj = S + K \times \frac{n-1}{n}$, with S being the number of recorded species, K being the number of singletons, and n being the number of survey walks (we used the number of walks in 2016).

Results

Increase in warm-loving bees over the past 20 years and correlation with species traits

The 1997–1999 survey yielded 79 species, the more recent survey 106, in both cases including the honeybee (Table S1, Online Supporting Materials). The species number expected for the garden, using *Jackknife* estimation, is 115 ("Methods") for 2015–2017, which is close to the 106 so far found. A *Jackknife* estimation based on the 1997 monitoring efforts yields 97 expected species. The 106 species belong to 23 of the c. 45 genera of bees currently accepted for Germany (Schmidt et al. 2015; Scheuchl and Willner 2016).

Whether a species is warm-habitat preferring, cool-habitat preferring, or has broad habitat preferences significantly affected whether it was retained, lost, or newly gained: by 2017, we found 15 warm-loving species that were not present in 1997 (i.e., species that spread into the garden). The geographic ranges and habitat preferences of these 15 species are detailed in the "Discussion". In addition, 12 warm-preferring species were retained between the two surveys, and two lost. In comparison, three cool-preferring species were lost, one cool-loving species was gained, and none retained. For the geographic ranges and habitat preferences of the cool-adapted species, see the "Discussion".

Of the species with broad habitat preferences, 20 were gained, 7 lost, and 47 retained (Tables 1, S1; multinomial model including thermal habitat preferences, foraging specialization, and Red List status: $p = 0.010$; multinomial model including only thermal habitat preferences: $p = 0.022$; multinomial model excluding cool-loving species: $p = 0.022$). The 16 species recorded in 1997 and no longer found by 2017 (Table S1, online supporting material) mostly belong to *Hylaeus* and *Lasioglossum*, and are small-bodied bees.

We then tested for a correlation between pollen specialization and species persistence, gain, or loss (Tables 1, S1). Two of 17 species lost by 2017 were oligolectic, 12 were polylectic, and three were cuckoo bees. Of the species gained by 2017, 10 are oligolectic, 23 polylectic, and 11 kleptoparasitic. This does not argue for pollen specialization having contributed to bee species loss. Two oligolectic species decreased in abundance, two others increased, and 11 did not change in abundance (see Table 1). Of the 62 retained species, 27 changed in abundance, with 18 less frequent and nine more frequent by 2017 than they had been in 1997. Finally, of the species no longer found by 2017, 14 had the Red List status "least concern", two were

Table 1 Foraging specialization, thermal habitat preferences, Red List status, and abundance categories of bee species lost, retained, or gained in faunistic surveys of the Munich Botanical Garden in 1997/1999 and 2015/2017

	Lost ($n = 17$)	Retained ($n = 62$)	Gained ($n = 44$)
Foraging specialization			
Oligolectic	2	15	10
Polylectic	12	37	23
Parasitic	3	10	11
Thermal preferences			
Broad range	7	47	20
Cooler habitats	3	0	1
Thermophilic	2	12	15
Unknown	5	3	8
Red List status			
Least concern (*)	13	52	33
Threat of unknown magnitude (G)	0	1	1
Near threatened (NT)	2	4	3
Vulnerable (3)	0	4	5
Endangered (2)	1	1	1
N/A	1	0	1
Abundance categories			
I (< 5 individuals)	9		29
II (5–20 individuals)	6		12
III (> 20 individuals)	2		3
Increase in abundance		9	
Equal abundance		35	
Decrease in abundance		18	

	Increasing abundance ($n = 9$)	Equal abundance ($n = 35$)	Decreasing abundance ($n = 18$)
Foraging preferences			
Oligolectic	2	11	2
Polylectic	7	21	9
Parasitic	0	3	7
Thermal preferences			
Broad range	6	25	16
Thermophilic	3	7	2
Unknown	0	3	0
Red List status			
Least concern (*)	8	28	16
Threat of unknown magnitude (G)	1	0	0
Near threatened (NT)	0	2	2
Vulnerable (3)	0	4	0
Endangered (2)	0	1	0

"near threatened", and one was "endangered" (this species was already found only once in 1997–1999). Most of the species gained are categorized as "least concern" ($n = 33$), but, additionally, the garden gained three species that are "near threatened", five that are "vulnerable", and one that with the Red List status "endangered".

The 23 genera of bees recorded from the garden are distributed throughout the phylogeny of bees known from Germany that is shown in Appendix S6 of Schmidt et al. (2015), which includes 514 species from 45 genera. We refrained from testing for phylogenetic signal in the retention, gain, or loss of species from the Munich Botanical Garden over the past 20 years. Such a signal may well be present in a larger region, for example, southern Germany or the Alps, but is unlikely in a 21-ha garden, studied over 20 years.

Discussion

Of 515 species of bees known from Bavaria (Scheuchl and Schwenninger 2015), 192 have been recorded for Munich since 1990 (Bräu and Nützel 2010), so that the garden's 106 species represent some 55% of the city's species. Similar-sized gardens in Southern Germany and Switzerland have between 70 and 150 recorded species (Zurbuchen and Müller 2012).

The 15 warm-loving species first recorded by 2017 include (1) *Xylocopa violacea,* which has its main distribution in southern Europe. It has been documented north of the Alps in the Danube valley and other warm regions since 1850 (Hage 2005; Schmalz 2005; Bußler 2007), perhaps arriving with imported wood from the south or foehn winds from the Inn Valley (Knoerzer 1941). From the Munich area, including the botanic garden, *X. violacea* was recorded by 1980 (Burmeister in Bembé et al. 2001), but since 2000, it is becoming more frequent in Bavaria and other states, as far north as Hesse (Schmalz 2005; Bußler, 2007). (2) *Osmia cornuta* is a Mediterranean species that nests in sun-exposed loess and clay walls (Scheuchl and Willner 2016); in the Munich Botanic Garden, sun-exposed wooden nesting aids are intensely populated by *O. cornuta* (> 100 individuals). (3) *Eucera nigrescens* is a bee of Southern and Central Europe where it occurs mostly at elevations < 500 m (Westrich 1989; Falk and Lewington 2015; Scheuchl and Willner 2016). (4) The western Palearctic species *Anthophora bimaculata* may be a new record for the Munich area (http://www.buw-bayern.de/show.php?artid=601, last accessed: 3 Sep. 2017); it occurs in dry, warm locations with sand or clay, where it can dig nests. (5) *Anthidiellum strigatum* is restricted to sunny, warm forest edges (Scheuchl and Willner 2016). (6 and 7) *Halictus scabiosae* and *H. subauratus* both are distinctly thermophilic (Westrich 1989; Scheuchl and Willner 2016), and the former has rapidly expanded its range since 2000, most likely linked to climate warming (Frommer and Flügel 2005; Hopfenmüller 2014). (8) Another new arrival since 1997–1999, *Hoplitis adunca*, is strictly oligolectic on a thermophilic plant (*Echium vulgare*) that has become more abundant as winters have become shorter and temperatures warmer.

The three cool-habitat-adapted species no longer found are (1) *Andrena intermedia*, which has its main area of distribution in mountain regions and occurs north to the polar circle and south to Turkey and the Peloponnese (Scheuchl and Willner 2016); (2) *Megachile ligniseca,* which, in Southern Germany, occurs in cool habitats in forests up to the subalpine area (Westrich 1989; Scheuchl and Willner 2016); and (3) *M. nigriventris*, which is distributed in Northern Europe and the Alps, usually > 500 m a.s.l. (Dorn and Weber 1988; Westrich 1989). All three of these were already rare in 1997/1999 (Table S1), however, and over its 100 years of existence, the botanical garden may never have harbored many cool-habitat-adapted species.

What best explains the disappearance of three cool-loving species and the arrival of 15 thermophilic species over the past 20 years? Since the man-made flora of the botanical garden and the protected flora of its surroundings (namely, the 210 ha-large Nymphenburg Palace Park, the orchard of a Catholic nunnery, and a street and hospital) have not changed over the past 20 years, the loss of habitat and food plants for oligolectic bees seems an unlikely explanation for bee species disappearance, and this agrees with the absences of a statistical correlation between pollen specialization and retention or loss from the garden over the 20 years between the two surveys. We also found no significant difference in Red List status between the categories gained, lost, and retained ("Results").

Thus, over the past 20 years, plant diversity and availability of nesting sites in the garden and its adjacent areas have remained essentially identical, and the distinct increase in warm-loving species that we detected is, therefore, most likely due to climate warming (Fig. 1), with the novelty of our study being that we have used an artificial, but stable 'ecosystem' to link insect fauna changes to climate warming per se. No other environmental parameter in the Munich botanical garden matches the directional increase in warm-loving species documented in our study. This study thus highlights the potential of botanic gardens as systems in which to investigate the effects of climate on insect faunas, controlling for insecticides, habitat fragmentation, and other human-impact factors. Our findings also underscore the importance of urban gardens as bee habitat (Hernandez et al. 2009; Hall et al. 2016).

Author contribution statement MH, AF, and SSR designed the experiment, and MH and AF performed the fieldwork. MH and SSR analyzed the data, and all authors contributed to the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

References

Amiet F, Krebs A (eds) (2014) Bienen Mitteleuropas: Gattungen, Lebensweise, Beobachtung. 2., korrigierte Auflage. Haupt Verlag, Bern

Amiet F, Müller A, Neumeyer R (1999) Fauna Helvetica 9. Apidae 2: *Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha*. Centre Suisse de Cartographie de la Faune, Neuchatel

Amiet F, Herrmann M, Müller A, Neumeyer R (2001) Fauna Helvetica 9. Apidae 3: *Lasioglossum, Halictus*. Centre Suisse de Cartographie de la Faune, Neuchatel, Switzerland

Amiet F, Herrmann M, Müller A, Neumeyer R (2004) Fauna Helvetica 9. Apidae 4: *Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis*. Centre Suisse de Cartographie de la Faune, Neuchatel, Switzerland

Amiet F, Herrmann M, Müller A, Neumeyer R (2007) Fauna Helvetica 9. Apidae 5: *Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa*. Centre Suisse de Cartographie de la Faune, Neuchatel, Switzerland

Baal T, Denker B, Mühlen W, Surholt B (1994) Die Ursachen des Massensterbens von Hummeln unter spätblühenden Linden. Nat Landsch 69:412–418

Bembé B, Gerlach G, Schuberth J, Schönitzer K (2001) Die Wildbienen im Botanischen Garten München. Nachrichtenblatt der bayererischen Entomologen 50:30–41

Bräu M, Nützel R (2010) Bienen und Wespen in München. Bund Naturschutz in Bayern e.V, Munich

Bußler H (2007) Mediterrane Holzbienen entdecken Bayern. LWF Aktuell 58:50–51

Dathe HH (1980) Die Arten der Gattung *Hylaeus* F. in Europa (Hymenoptera: Apoidea, Colletidae). Mitteilungen aus dem Zoologischen Museum in Berlin 56:207–294

Dorn M, Weber D (1988) Die Luzerne-Blattschneiderbiene und ihre Verwandten in Mitteleuropa. A. Ziemsen Verlag, Wittenberg

Falk SJ, Lewington R (2015) Field guide to the bees of Great Britain and Ireland. Bloomsbury, London

Frommer U, Flügel H-J (2005) Zur ausbreitung der furchenbiene *Halictus scabiosae* (Rossi, 1790) in mitteleuropa unter besonderer berücksichtigung der situation in hessen (Hymenoptera: Apidae). Mitteilungen des Internationalen Entomologischen Vereins 30:51–79

Goulson D, Lye GC, Darvill B (2008) Decline and conservation of bumble bees. Annu Rev Entomol 53:191–208

Goulson D, Nicholls E, Botías C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347:1255957

Haeseler V, Ritzau C (1998) Zur Aussagekraft wirbelloser Tiere in Umwelt-und Naturschutzgutachten. Zeitschrift für Ökologie und Naturschutz 7:45–66

Hage HJ (2005) Die Holzbiene *Xylocopa violacea* (LINNAEUS 1758) in Bayern (Hymenoptera, Apidae). Nachrichtenblatt der Bayerischen Entomologen 54:39–46

Hall DM, Camilo GR, Tonietto RK, Ollerton J, Ahrné K, Arduser M, Ascher JS, Baldock KCR, Fowler R, Frankie G, Goulson D, Gunnarsson B, Hanley ME, Jackson JI, Langellotto G, Lowenstein D, Minor ES, Philpott SM, Potts SG, Sirohi MH, Spevak EM, Stone GN, Threlfall CG (2016) The city as a refuge for insect pollinators. Conserv Biol 31:24–29

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Goulson D (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12(10):e0185809

Hernandez JL, Frankie GW, Thorp RW (2009) Ecology of urban bees: a review of current knowledge and directions for future study. Cities Environ 2:1–15

Hopfenmüller S (2014) Folgt die Efeu-Seidenbiene Colletes hederae Schmidt & Westrich, 1993 dem Ausbreitungsweg der Furchenbiene Halictus scabiosae (Rossi, 1790) in Bayern? (Hymenoptera: Apoidea). Nachrichtenblatt der Bayerischen Entomologen 63:2–7

Knoerzer A (1941) Bemerkenswerte Hymenopterenfunde in Südbayern. Mitteilungen der Münchner Entomologischen Gesellschaft 31:934–937

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353

Primack RB, Miller-Rushing AJ (2009) The role of botanical gardens in climate change research. New Phytol 182:303–313

Renner SS (2014) 100 Jahre Botanischer Garten München-Nymphenburg. Berichte der Bayerischen Botanischen Gesellschaft 84:35–38

Scheuchl E, Schwenninger HR (2015) Kritisches Verzeichnis und aktuelle Checkliste der Wildbienen Deutschlands (Hymenoptera Anthophila) sowie Anmerkungen zur Gefährdung. Mitteilungen des Entomologischen Vereins Stuttgart 50:3–225

Scheuchl E, Willner W (2016) Taschenlexikon der Wildbienen Mitteleuropas: alle Arten im Porträt. Quelle & Meyer, Wiebelsheim

Schmalz K-H (2005) Erste Sichtnachweise der blauschwarzen Holzbiene *Xylocopa violacea* (Hymenoptera Apidae) in Osthessen. Beiträge zur Naturkunde in Osthessen 41:45–46

Schmidt S, Schmid-Egger C, Morinière J, Haszprunar G, Hebert PDN (2015) DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Mol Ecol Resour 15:985–1000

von Hagen E, Aichhorn A (2014) Hummeln: Bestimmen, Ansiedeln, Vermehren, Schützen, 6th edn. Fauna Verlag, Germany

Westrich P (1989) Die Wildbienen Baden-Württembergs. E. Ulmer, Stuttgart

Westrich P, Frommer U, Mandery K, Riemann H, Ruhnke H, Saure C, Voith J (2011) Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. Naturschutz und Biologische Vielfalt 70:373–416

Williams PH, Araújo MB, Rasmont P (2007) Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? Biol Cons 138:493–505

Yee TW (2010) The VGAM package for categorical data analysis. J Stat Softw 32:1–34

Zohner CM, Renner SS (2014) Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. Ecol Lett 17:1016–1025

Zurbuchen A, Müller A (2012) Wildbienenschutz: von der Wissenschaft zur Praxis. Haupt Verlag, Bern

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Map of the Botanical Garden Munich

DNA extraction, amplification and sequencing

For DNA extraction, the QIAGEN DNeasy®-Blood and Tissue Kit (Qiagen GmbH, Hilden, Germany) was used. DNA was extracted from one leg per bee, following the QIAGEN Quick-Start Protocol (January 2011) for tissue with two modifications: The legs were incubated in Lysis Buffer (ATL) and Proteinase K for at least 48 h at room temperature and 5 – 10 hours at 56°C. To increase DNA concentration elution was performed in 100 µL elution Buffer (PE; 5 mM Tris/HCL pH 8.5). The mitochondrial gene fragment of the cytochrome c oxidase (COI) with a 658 bp target region near the 5´terminus of COI was amplified using the primers described in Schmidt et al. (2015)[1], viz. COIfor (ATT CAA CCA ATC ATA AAG ATA TTG G) and COIrev (TAA ACT TCT GGA TGT CCA AAA AAT CA). For halictid bees, including *Lasioglossum*, we used COIrev and a forward primer Hym-COI-F (TAA GAA TAA TTA TTC GWA TAG AAT TAA G provided by Hanno Schäfer, Technical University Munich). *Lasioglossum* bees often are infested with *Wolbachia*, which can affect DNA-barcoding with standard primers (Smith et al. 2012)[2]. Polymerase chain reactions (PCR) were performed using standard conditions. Amplified products were sequenced on an ABI 3100

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[1] Schmidt S, Schmid-Egger C, Morinière J, Haszprunar G, Hebert PDN. 2015. DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Molecular Ecology Resources **15**:985–1000.

[2] Smith MA et al. 2012. Wolbachia and DNA Barcoding Insects: Patterns, Potential, and Problems. PLOS ONE **7**:e36514.

Avant capillary sequencer (Applied Biosystems), and forward and reverse sequences were manually edited and assembled, using Sequencher 5.1 (Gene Codes Corporation, Ann Arbor, Michigan, USA) and BLAST-search in GenBank. All bee species sequenced for this study have been previously barcoded for the GBOL-project, thus reference sequences were available in NCBI GenBank through the following DOIs: dx.doi.org/10.5883/DS-GBAPI and dx.doi.org/10.5883/DS-GBAPS. A total of 44 sequences were generated for this study. When several individuals of the same species were identified via barcoding, only a single reference sequence was deposited in GenBank (for Accession Numbers see Table S2). *Bombus* sequences were not deposited, because the bee voucher specimens were partly decayed and could not be deposited in the Munich zoological collections.

List of Apoidea voucher specimens with sample ID, location, date of collection, and GenBank accession number

Species	Sample ID	Location	Date of collection	Accession number
Halictus rubicundus	Hofmann BGM 10	At the lake	04.08.2016	KX904816
Halictus subauratus	Hofmann BGM 11	Gardeners' area	04.08.2016	KX904817
Lasioglossum calceatum	Hofmann BGM 8	Ornamentals	08.08.2016	KX904814
Lasioglossum laticeps	Hofmann BGM 5	Alpine collection	31.08.2016	KX904811
Lasioglossum morio	Hofmann BGM 4	Alpine collection	31.08.2016	KX904810
Lasioglossum villosulum	Hofmann BGM 9	Ornamentals	02.08.2016	KX904815
Nomada fabriciana	Hofmann BGM 1	Steppe	28.03.2016	KX904807
Nomada flavoguttata	Hofmann BGM 2	Steppe	01.04.2016	KX904808
Osmia cornuta	Hofmann BGM 3	Nesting aid at the Iris display	03.04.2016	KX904809
Sphecodes ephippius	Hofmann BGM 12	System	04.07.2016	KX904818
Sphecodes ferruginatus	Hofmann BGM 7	System	20.05.2016	KX904813
Sphecodes monilicornis	Hofmann BGM 6	Steppe	06.05.2016	KX904812

Chapter 4

Bee species persistence and increase in urban protected sites between 1990 and 2018

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Bee species persistence and increase between 1990 and 2018 in urban protected sites

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Abstract:	Previous work has shown that among 428 species of bees occurring in Germany, decline or extinction over the past 40 years have been correlated with late-season emergence and restricted habitats, while other factors, such as pollen specialization, body size, nesting sites, and sociality, played no role in models that included a phylogeny of these bees. Doing best are spring-flying, city-dwelling species. Building on these results, we here investigate changes in bee diversity from the 1990s to 2018 at three protected sites within the city perimeter of Munich, focusing on the effects of flight season (spring or summer), duration (in months), and number of habitats (one or two vs. three to six). Munich's total species pool against which the local pools were assessed is 324 species. Twenty years ago, 150 species were present at one or more of the sites, while in 2017/2018, this was true of 188 species, with the increase at two sites being of similar proportion. In all three areas, broad habitat use had a slight positive effect on persistence, while flight season or duration had no effect. These results underscore the function of urban protected sites in bee conservation and imply that food shortages, which negatively affect bees in agricultural areas, play less of a role in urbanized regions so that late-season flight is not an extinction handicap. That bee diversity has increased in similar proportion at two of the sites, with an influx of thermophilic species, implies climate warming as a likely explanation.

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Bee species persistence and increase between 1990 and 2018 in urban protected sites

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Running head: Urban bee species persistence and increase

Abstract.

Previous work has shown that among 428 species of bees occurring in Germany, decline or extinction over the past 40 years have been correlated with late-season emergence and restricted habitats, while other factors, such as pollen specialization, body size, nesting sites, and sociality, played no role in models that included a phylogeny of these bees. Doing best are spring-flying, city-dwelling species. Building on these results, we here investigate changes in bee diversity from the 1990s to 2018 at three protected sites within the city perimeter of Munich, focusing on the effects of flight season (spring or summer), duration (in months), and number of habitats (one or two vs. three to six). Munich's total species pool against which the local pools were assessed is 324 species. Twenty years ago, 150 species were present at one or more of the sites, while in 2017/2018, this was true of 188 species, with the increase at two sites being of similar proportion. In all three areas, broad habitat use had a slight positive effect on persistence, while flight season or duration had no effect. These results underscore the function of urban protected sites in bee conservation and imply that food shortages, which negatively affect bees in agricultural areas, play less of a role in urbanized regions so that late-season flight is not an extinction handicap. That bee diversity has increased in similar proportion at two of the sites, with an influx of thermophilic species, implies climate warming as a likely explanation.

Key words. Apidae, bee faunas, 20-year monitoring, seasonal flight time, urban nature conservation.

Introduction

Globally, over 40% of insect species, especially of lepidopterans, hymenopterans, and coleopterans, appear threatened with extinction (Sánchez-Bayo and Wyckhys, 2019), and drastic declines in diversity and biomass have been documented in German grassland and forests (Seibold et al., 2019) and even protected areas surrounded by agricultural fields (Hallmann et al., 2017). In Germany, sites embedded in landscapes with a higher cover of agricultural land show the strongest losses (Seibold et al., 2019). To make progress in our understanding of the factors driving the decline of insects, we here focus on protected sites *not* surrounded by agricultural land for which, based on these studies (Hallmann et al., 2017; Seibold et al., 2019), one would expect lower declines. We focus on bees, which are among the best-studied insects in Central Europe and whose decline has been linked to the combined stress from parasites, pesticides, and lack of flowers (Goulson et al., 2015). In Germany, 561 species of bees are red-listed, with 228 categorized threatened, and 39 already extinct (Westrich et al., 2011).

An analysis of the parameters that might predict the decline or extinction of those German bee species for which monitoring data have been gathered for Red Lists for 40+ years (namely 428 species) showed that of eight analysed traits (pollen specialization, body size, nesting sites, sociality, duration of flight activity [weeks or months], flight season [spring or summer], habitat breadth, and altitudinal range), only three predicted extinction risk (Hofmann et al., 2019). These were duration of flight activity, flight season, and habitat (with the six categories forests and heaths; meadows; hedgerows; wasteland and nutrient-poor sites; raw-soil sites with little vegetation, such as sand dunes, heathland, steppes, and sand or gravel pits; and urban areas, including gardens and parks). The results showed that species flying in late summer and not occurring in urban areas are about three times more likely to go extinct than spring-flying city-dwelling species. The study used a phylogeny of the German bee species as the background for Bayesian Hierarchical modelling, so that all predictors could be analysed simultaneously and with species relationships taken into account.

These German-wide findings need to be tested with more fine-grained data to tease out the effects of intensive agriculture. For example, one might test flight season as a predictor of persistence in bee faunas of urban areas because there one would not expect spring or summer emergence to determine long-term persistence. This is because the continued seasonal availability of floral resources in urban gardens, allotments, parks, and balconies may be higher than that in non-urban sites (Grimm et al., 2008) and the planting and mowing regime in cities is not determined by agricultural production patterns. By contrast, in European agricultural land, nectar availability tends to be low in August and September (Timberlake et al., 2019).

We here use a data set of bee species that have been monitored over at least 20 years in three protected greenspaces within the perimeter of the city of Munich (Bavaria, Germany; Fig. 1). The total species pool in Munich comprises 324 species (Appendix S1) and is a subset of the species included in an earlier German-wide study (Hofmann et al., 2019). The first of the sites is a remnant forest and heath, the second is an area that was long off-limits because of military use, and the third is the Munich Botanical Garden, which since 1914 has had an unchanging, albeit man-made (horticulturally-influenced) flora. Based on our finding for all German bees, we focused on flight season, flight duration, and habitat breadth as predictors based on the hypothesis that -- if agricultural intensification, including pesticide usage, year-round tillage, increased use of fertilizers and frequency of agronomic measures (Hallmann et al., 2017; Seibold et al., 2019) are key factor in bee decline -- bees in urban protected areas should have persisted regardless of their flight season or habitat breadth.

Material and methods

Study sites

The Allacher Lohe heath and forest area is located in Munich’s west at 48.202578°N, 11.481281°E. In 1988, the area of the Allacher Lohe was greatly reduced through the construction of the Munich marshalling yard, which has operated since 1991. On 1 April 2000, the remaining 150 ha area of the Allacher Lohe, became a nature reserve („Verordnung über das Naturschutzgebiet "Allacher Lohe" in der Landeshauptstadt München“, 28 Feb. 2000, Nr. 820-8622-13/82). The Virginia Depot lies west of the Schleißheimer Straße in the Munich-Lerchenau suburb (48.197325°N, 11.561308°E); it comprises about 20 hectares. From 1945 until 1957, the depot was owned by the US army, which used it as the *Virginia Area Storage Facility*. Between 1957 and the 1990s, the German army took it over, and since 2003, it has been managed by a regional nature conservation group and been transformed into a city biotope. Since the depot was off-limits between 1945 and 2003 due to its military use, it harbours rare plants and animals. Our third site, the Munich Botanical Garden (48°09′45″N, 11° 30′06″E), was opened in May 1914 and has a size of about 20 ha (Hofmann et al., 2018). The layout of the garden is protected (Denkmalliste für München, S. 554f.; Stand 27.05.2018; Bayerisches Landesamt für Denkmalpflege). The outdoor harbours about 10,000 species and subspecies (data from the garden’s living plant database, accessed by the second author), and it is flower-rich from late February to October. The location of the three study sites is shown in Figure 1.

Historic and 2017/2018 monitoring of the three sites

In 1980, Klaus Warncke and colleagues began inventorying the Allacher Lohe (Warncke, 1982), and over eight days from April to September 1980, they recorded 97 bee species. In 1997/1998, bees in the Allacher Lohe were monitored for the Upper Bavarian nature conservancy (https://www.regierung.oberbayern.bayern.de/aufgaben/umwelt/) by the entomologists F. Foeckler, H. Schmidt, and J. Schuberth. The first author transcribed their reports, which may not be copied and distributed, in the nature conservancy's office in Munich (all taxon names appear in our Appendix 1). In five mapping walks in 1997/1998, Schuberth found 44 species; he also monitored the area from 1990 to 1996, increasing the number to 71 species. Further observations from 1999 onwards resulted in a total of 135 species for the Allacher Lohe and adjoining areas. Twenty years later, during the bee flight seasons of 2009 and 2010, A. Dubitzky and J. Schuberth recorded 106 species for the area. To keep data comparable among the Allacher Lohe, Virginia Depot, and Botanical Garden, we focused on the assessment of J. Schuberth in the 1990s, because this allowed us to have similar time periods and comparable investigation efforts for the three sites. For the Virginia Depot, a bee inventory was conducted during the flight season of 1998 and 1999, again by J. Schuberth, and it, too, was studied by the first author in the Bavarian nature conservancy's office in Munich. The bees of the Munich Botanical Garden were surveyed in 1997/1999 by Bembé and colleagues (2001) and in 2015/2017 by Hofmann et al. (2018).

Between March 2017 and August 2018, the first author visited the Allacher Lohe and the Virginia Depot once a month (Appendix 2 shows the dates). For the Allach study site, the parts north and south of the marshalling yard were visited on consecutive days. Monitoring walks were conducted between 10 a.m. and 4 p.m. on sunny, warm days with little or no wind. The mapping did not follow a strict route; instead, bees were searched for on flowers and likely nesting sites. Where possible, species were identified directly in the field and were documented via macro-photography in a standardized setup: for close-up pictures, the bees were caught with an insect net and cooled down for 10 minutes in an Eppendorf cupped plastic vial stored on ice in a cooled box. When the bees fell into cold rigor, they were transferred onto scale paper (using a small box lined with millimetre paper on its bottom) and photographed from all sides (SLR camera: Pentax K-x; Lens: Sigma DG 17-70 mm, 1:2.8, macro). Within one to two minutes, they warmed up again and were released at the location where they had been caught. For species that are taxonomically difficult to distinguish by morphology alone, such as members of *Sphecodes*, *Lasioglossum* and *Halictus*, voucher specimens, preferably males (for morphological re-identification by genitalia preparations), were collected and identified morphologically and via DNA barcoding (methods and primers as described in Hofmann et al., 2018). Photo vouchers are accessible at the Diversity Workbench server (DWB; https://diversityworkbench.net/Portal/Diversity_Workbench), and DNA barcodes at NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/). Appendix S2 shows all GenBank and DWB accession numbers [they will work once this ms is accepted]. Voucher specimens were deposited in the Munich zoological collections, ZSM (https://www.zsm.mwn.de/?lang=en).

Statistical analyses and data structure

In an earlier German-wide study of predictors of changes in bee species diversity over the past 40 years, we relied on phylogenetically-informed models, but no phylogenetic signal in the prediction of species' vulnerability was detected (Hofmann et al., 2019: Fig. S5). We therefore here use simple logistic regression with two models applied to the 324 bee species ever recorded for Munich, scoring them as 0, if they were not present in one or more of the study areas, or as 1 if present (Appendix S1). Model 1 included duration of flight time in months (‘flight duration’) as a linear predictor while model 2 instead included flight season (‘seasonality’) as a categorical predictor, with the categories ‘early’, covering the months February to May (found in n = 19 of the 324 species), and ‘late’, covering June to September (n = 66). Species active in both seasons were categorized as ‘median’ (n = 239); the latter either fly from February to September or have shorter flight times that overlap the early and late season. Presence at time zero (T0) and habitat breadth, with the categories ‘narrow’ and ‘broad’ were included in both models. Narrow habitat breadth was defined as occurrence in one or two of the six habitats forests and heaths; meadows; hedgerows; wasteland and nutrient-poor sites; raw-soil sites with little vegetation, such as sand dunes, heathland, steppes, and sand or gravel pits; or urban areas, including gardens and park. Broad habitat use was defined as occurrence in three to six habitats. Species with unknown habitat preferences were excluded from further analysis.

Model 1 had the form:

$$Occurrence\_T_i1 \sim Bernoulli(p_i)$$

$$logit(p_i) = \alpha + \beta_1 * Occurrence\_T0 + \beta_2 * Habitat.breadth + \beta_3 * Flight.duration$$

Model 2 had the form:

$$Occurrence\_T_i1 \sim Bernoulli(p_i)$$

$$logit(p_i) = \alpha + \beta_1 * Occurrence\_T0 + \beta_2 * Habitat.breadth + \beta_3 * Seasonality$$

All scorings are shown in Appendix S1, which also lists each species’ foraging preferences, mode of pollen collection, nesting site, habitat preference, and the literature sources used. Predicted occurrence was defined as predicted probability >0.5. Model accuracy was calculated as (true positives + true negatives) / total pool. All statistical analyses were conducted in R 3.6.1 (R Core Team, 2019).

Results

Twenty years ago, 150 species were present at one or more of the sites, while in 2017/2018, this was true of 188 species, with the species increase at two sites being of similar proportion (Tables 1 and 2) and mostly due to thermophilic species, such as *Anthidiellum strigatum*, *Anthophora bimaculata*, *Eucera nigrescens*, *Halictus scabiosae, H. subauratus*, *Hoplitis adunca,Osmia cornuta*, and *Xylocopa violacea* (Appendix S1). Of the 150 species present 20 years ago (T0), 122 are able to breed in three or more habitat types (broad habitat preference; *Materials and Methods*), while 28 breed in only one or two habitats (narrow habitat preference); seven fly early (February to May), 32 late (June to September), and the remaining 111 have ‘median’ flight times spanning spring and summer. Of the 136 species seen at one or more of the study sites recently (T1), 111 have a broad and 27 a narrow habitat preference; eight fly early, 24 late, and 140 have a median flight time.

Based on these numbers, habitat breadth had a slight positive influence on species persistence when all three sites were taken together, while flight season never had a significant effect (Fig. 2a; Table S1 in Appendix 3), When the analysis was run separately for each site, abitat breadth no longer explained persistence of species at the Virginia Depot (Fig. 2a). Using flight season (early, median, late), instead of flight duration (in months), yielded similar results (Fig. 2b; Appendix 3: Table S1). The flight duration model correctly predicted the occurrence of 77% of the 319 species after 20 years (T1), while the flight season model had an accuracy of 76% (Table S2 in Appendix 3). The best ‘predictor’ of presence at T1 was presence at T0 (Figure 2).

Discussion

The occurrence of a species at any of the three areas was better predicted by its occurrence there 20 years ago than by its habitat breadth, flight season, or duration of flight activity (Fig. 2), although broad habitat preferences had a slightly positive effect on species persistence. The number of species at the Virginia Depot has increased from 32 to 44 and that in the Munich Botanical Garden from 78 to 105 over essentially the same 20-year period (Table 2), while in the Allacher Lohe, the number of bee species has decreased from 135 in the 1990s to 80 in 2018. These differences appear too large to be due purely to sampling artefacts. In 1988, a marshalling yard was built in the Allacher Lohe and has been in operation since 1991, which may have contributed to the decline in species at this site. A case in point is *Andrena rufizona*, which had one of its largest known populations in Germany in Allach before the marshalling yard opened, but declined from about 20 breeding females to one female and several males by 1999. The last sighting of this species was in 2002 (J. Schuberth, Munich, personal communication to the first author, 2019).

At the other two sites, species diversity over the past 20 years has increased in similar proportion (Table 2) pointing to a consistent cause for the increase. Winters in Munich have become shorter by four weeks over the past 100 years (Zohner and Renner, 2014), and warmer springs and summers have led to a significant increase in warm-loving species. In Munich, for example, some 15 thermophilic species are currently expanding their ranges (Hofmann et al., 2018; this study: Appendix S1), which is unlikely to be explained by an increase in the city's flower richness or bee habitat diversity. We therefore suspect that the increase in bee species detected at the Virginia Depot and in the Botanical Garden is due to climate warming.

The finding that flight season had no effect on bee persistence (at least over the past 20 years) probably implies that bees in urban areas have access to sufficient floral pollen and nectar sources throughout the season (cf. Grimm et al., 2008). This absence of any seasonal effects, however, needs to be interpreted with care. We used flight months for each species as given in the literature (Appendix S1 shows all sources), but bees' flight times vary between years and regions, depending on local conditions. Ideally, one would therefore use flight times from the Munich area and the particular period covered here. Such data, however, are not available for most of the 324 species.

Our results highlight the importance of protected urban sites for bee conservation, which is perhaps helped by most Central European bees being small, with correspondingly small foraging ranges. Thus, 92% of 436 species occurring in Germany are 4.5 to 13.5 mm long with foraging ranges in flower-rich sites of around 150 m (Hofmann et al., in review). Studies of 104 species with different body sizes in the centre and suburbs of the city of Poznan, Poland, found more small-bodied late-season bees in the centre than in the suburbs and a diversity in city parks comparable to that in natural areas (Banaszak-Cibicka and Zmihorski, 2012; Banaszak-Cibicka et al., 2018). This agrees with our finding that a late-flight season is not a handicap for species persistence in Munich, while it is in Germany overall (Hofmann et al., 2019). Similarly, a study in Northampton found that the city had more species of bees than do meadows and nature reserves surrounding it (Sirohi et al., 2015).

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Conflicts of interest

There are no conflicts of interest by any author.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Munich bee species, their Red List status, life-history parameters, and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Appendix S2: GenBank accession numbers and Diversity Work Bench accession numbers of the voucher specimen.

Appendix S3: Tables S1 and S2.

References

Banaszak-Cibicka, W., and Żmihorski, M. (2012). Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation* 16: 331-343.

Banaszak-Cibicka, W., Twerd, L., Fliszkiewicz, M., Giejdasz, K., Langowska, A. (2018). City parks vs. natural areas – is it possible to preserve a natural level of bee richness and abundance in a city park? *Urban Ecosystems* 21: 599-613.

Bembé B., Gerlach G., Schuberth J., Schönitzer K. (2001). Die Wildbienen im Botanischen Garten München. *Nachrichtenblatt der bayerischen Entomologen* 50: 30–41.

Goulson, D., Nicholls, E., Botías, C., Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347: 1435 and http://dx.doi.org/10.1126/science.1255957.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., and Briggs, J. M. (2008). Global change and the ecology of cities. *Science* 319: 756-760.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., ... and Goulson, D. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PloS One* 12: e0185809.

Hofmann, M. M., A. Fleischmann, S. S. Renner. Empirical foraging distances in six species of solitary bees with body lengths of 6 to 15 mm. (Ecology and Evolution, submitted 06 Nov. 2019).

Hofmann, M. M., Fleischmann, A., Renner, S. S. (2018). Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. *Oecologia* 187: 701–706.

Hofmann, M. M., Zohner, C. M., Renner, S. S. (2019). Narrow habitat breadth and late-summer emergence increases extinction vulnerability in Central European bees. *Proceedings of the Royal Society B* 286: 20190316.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Sánchez-Bayo, F., and Wyckhuys, K. A. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* 232: 8–27.

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., ... & Linsenmair, K. E. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574: 671-674.

Sirohi, M. H., Jackson, J., Edwards, M., and Ollerton, J. (2015). Diversity and abundance of solitary and primitively eusocial bees in an urban centre: a case study from Northampton (England). *Journal of Insect Conservation* 19: 487-500.

Timberlake, T. P., Vaughan, I. P., and Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology* 56: 1585-1596.

Warncke, K. (1982). Die Trockenrasen vor dem Südrand des Allacher Forstes (München), ein ausgefallender Biotop für seltene Wildbienenarten. *Nachrichtenblatt der Bayerischen Entomologen* 31: 1–3.

Westrich, P.; Frommer, U.; Mandery, K.; Riemann, H.; Ruhnke, H.; Saure, C. and Voith, J. (2011): Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. *Naturschutz und Biologische Vielfalt* 70: 373-416.

Zohner, C,M., Renner, S.S. (2014). Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. *Ecology Letters* 17:1016–1025.

Tables and Figures

Table 1: Flight season (early, late, median) and habitat breadth (narrow: one or habitats vs. broad: three to six) of 319 species of bees recorded at the protected urban areas Allacher Lohe, Virginia Depot, or Botanical Garden within the Munich city perimeters in the 1990s (time zero, T0) or 2017/2018 (T1). For details of study sites and years see *Material and Methods*, Fig. 1, and Appendix S1.

		Present at T1			Absent at T1		
		Early	Late	Median	Early	Late	Median
Present at T0	Broad	5	12	76	0	7	22
	Narrow	1	7	4	1	6	9
Absent at T0	Broad	2	3	11	2	9	51
	Narrow	0	2	13	8	19	49

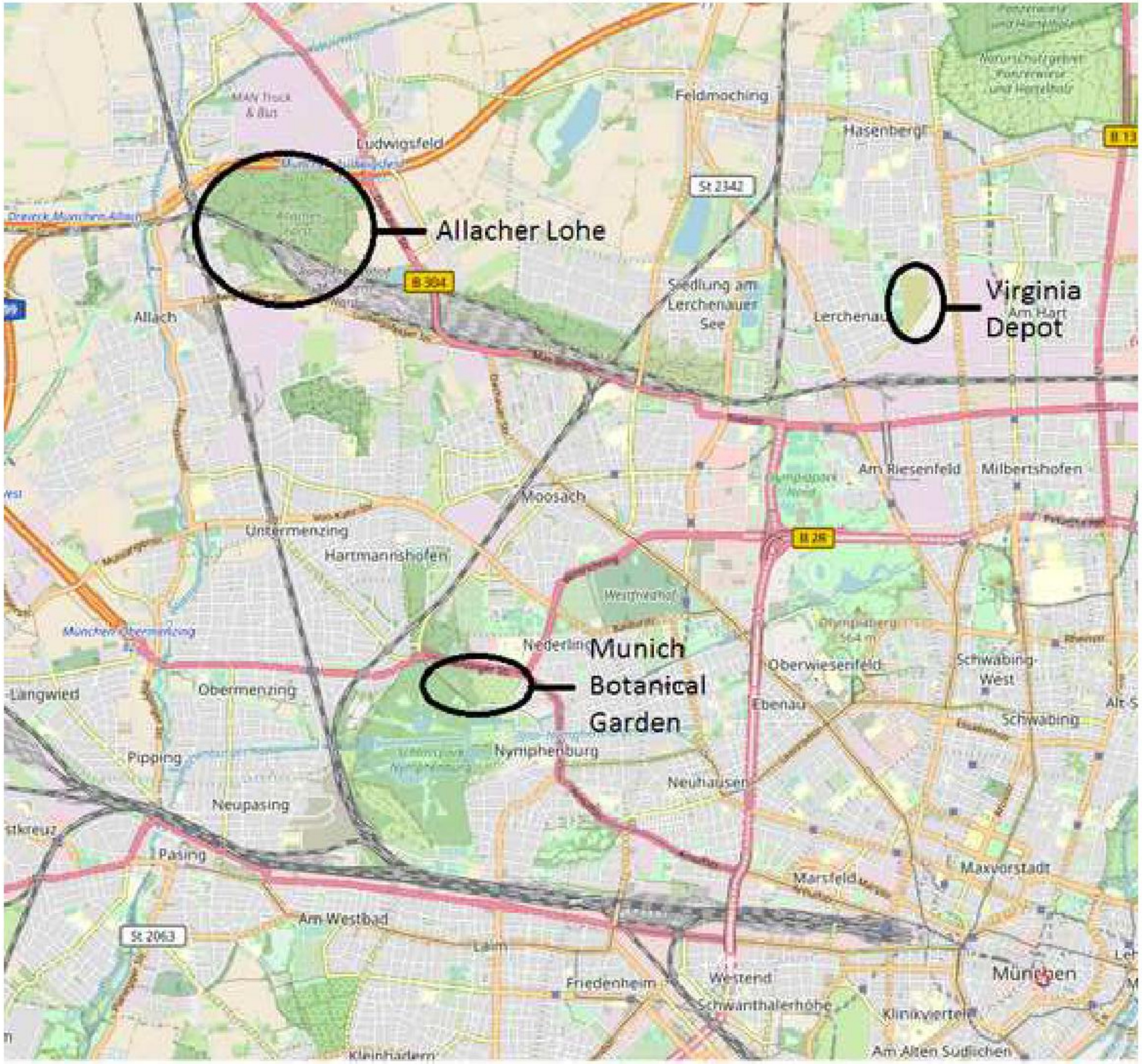
Table 2: Numbers of species recorded at the protected urban areas Allacher Lohe, Virginia Depot, or Botanical Garden within the Munich city perimeter in the 1990s (T0) or 2017/2018 (T1).

Number of species	**Allacher Lohe**	**Virginia Depot**	**Munich Botanical Garden**
Present at T0	135	32	78
Absent at T0	189	292	246
Present at T1	80	44	105
Absent at T1	244	280	219

Figure 1: The location of the three study sites within the Munich city perimeter.

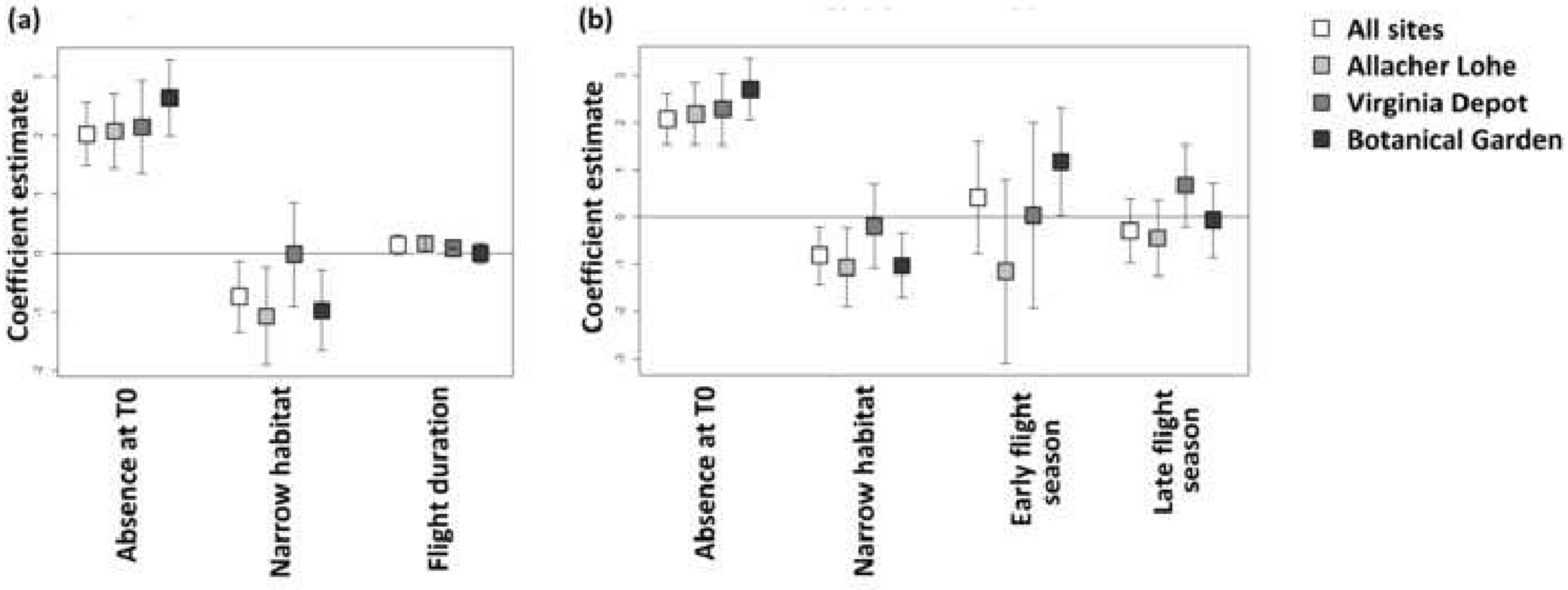
Figure 2: Coefficient estimates (beta estimate +95% confidence intervals) for the effects of (a) occurrence at time zero (T0), habitat breadth, and flight duration (in months) or (b) occurrence at T0, habitat breadth (one or two vs. three to six), and flight season (early, late, media) on species occurrence by 2017/2018 (T1). Positive estimates correspond to an increased occurrence probability at T1.

Figure 1



Karte hergestellt aus OpenStreetMap-Daten | Lizenz: Open Database License (ODbL)

Figure 2


(a)
Coefficient estimate
Absence at T0
Narrow habitat
Flight duration
(b)
Coefficient estimate
Absence at T0
Narrow habitat
Early flight season
Late flight season
□ All sites
▨ Allacher Lohe
▨ Virginia Depot
■ Botanical Garden

Supplementary material from

Bee species persistence and increase between 1990 and 2018 in urban protected sites

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Species		Family	Red List Statu	Foraging spec
Andrena agilissima	(Scopoli, 1770)	Andrenidae	3	oligolectic
Andrena alfkenella	Perkins, 1914	Andrenidae	V	polylectic
Andrena anthrisci	Blüthgen 1925	Andrenidae	N/A	polylectic
Andrena apicata	Smith, 1847	Andrenidae	G	oligolectic
Andrena barbilabris	(Kirby, 1802)	Andrenidae	V	polylectic
Andrena bicolor	Fabricius, 1775	Andrenidae	*	polylectic
Andrena bucephala	Stephens, 1846	Andrenidae	3	polylectic
Andrena chrysopyga	Schenck, 1853	Andrenidae	2	polylectic
Andrena chrysosceles	(Kirby, 1802)	Andrenidae	*	polylectic
Andrena cineraria	(Linnaeus, 1758)	Andrenidae	*	polylectic
Andrena clarkella	(Kirby, 1802)	Andrenidae	*	oligolectic
Andrena coitana	(Kirby, 1802)	Andrenidae	3	polylectic
Andrena combinata	(Christ, 1791)	Andrenidae	3	polylectic
Andrena congruens	Schmiedeknecht, 1883	Andrenidae	2	polylectic
Andrena curvungula	Thomson, 1870	Andrenidae	3	oligolectic
Andrena decipiens	Schenck, 1861	Andrenidae	2	polylectic
Andrena denticulata	(Kirby, 1802)	Andrenidae	V	oligolectic
Andrena dorsata	(Kirby, 1802)	Andrenidae	*	polylectic
Andrena falsifica	Perkins, 1915	Andrenidae	*	polylectic
Andrena ferox	Smith, 1847	Andrenidae	2	polylectic
Andrena flavipes	Panzer, 1799	Andrenidae	*	polylectic
Andrena florea	Fabricius, 1793	Andrenidae	*	oligolectic
Andrena floricola	Eversmann, 1852	Andrenidae	2	oligolectic
Andrena fucata	Smith, 1847	Andrenidae	*	polylectic
Andrena fulva	(Müller, 1766)	Andrenidae	*	polylectic
Andrena fulvago	(Christ, 1791)	Andrenidae	3	oligolectic
Andrena fulvata	Stöckhert, 1930	Andrenidae	*	polylectic
Andrena fulvida	Schenck, 1853	Andrenidae	3	polylectic
Andrena gelriae	Van Der Vecht, 1927	Andrenidae	3	oligolectic
Andrena gravida	Imhoff, 1832	Andrenidae	*	polylectic
Andrena haemorrhoa	(Fabricius, 1781)	Andrenidae	*	polylectic
Andrena hattorfiana	(Fabricius, 1775)	Andrenidae	3	oligolectic
Andrena helvola	(Linnaeus, 1758)	Andrenidae	*	polylectic
Andrena humilis	Imhoff, 1832	Andrenidae	V	oligolectic
Andrena intermedia	Thomson, 1870	Andrenidae	V	oligolectic
Andrena labialis	(Kirby, 1802)	Andrenidae	V	oligolectic
Andrena labiata	Fabricius, 1781	Andrenidae	*	polylectic
Andrena lathyri	Alfken, 1899	Andrenidae	*	oligolectic
Andrena minutula	(Kirby, 1802)	Andrenidae	*	polylectic
Andrena minutuloides	Perkins, 1914	Andrenidae	*	polylectic
Andrena mitis	Schmiedeknecht, 1883	Andrenidae	V	oligolectic
Andrena nigroaenea	(Kirby, 1802)	Andrenidae	*	polylectic
Andrena nitida	(Müller, 1776)	Andrenidae	*	polylectic
Andrena nitidiuscula	Schenck, 1853	Andrenidae	3	oligolectic
Andrena nycthemera	Imhoff, 1868	Andrenidae	3	oligolectic
Andrena ovatula	(Kirby, 1802)	Andrenidae	*	polylectic

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Pollen collecti	Nesting	Flight months	Flight season	Habitat	Habitat prefe	Altitudinal ra
leg	ground	V-VI	Median	4, 5, 3	broad	0-1600
leg	ground	V-VI, VII-VIII	Median	4, 6, 5	broad	0-1600
leg	ground	V-VI	Median	?	unknown	0-600
leg	ground	II-V	Early	1, 5, 2	broad	0-1600
leg	ground	III-V, VI-VII	Median	2, 5, 6	broad	0-800
leg	ground	III-V, VI-VIII	Median	7	broad	0-2100
leg	ground	IV-V	Early	5, 4	narrow	0-1600
leg	ground	IV-VI	Median	2, 4	narrow	0-1600
leg	ground	IV-VI	Median	5, 4, 6, 3	broad	0-800
leg	ground	III-V	Early	5, 4, 6, 3	broad	0-2100
leg	ground	III-V	Early	1, 5	narrow	0-2100
leg	ground	VI-IX	Late	1, 5	narrow	0-2100
leg	ground	V-VI	Median	4, 6	narrow	0-1600
leg	ground	IV-V, VII-VIII	Median	?	unknown	0-800
leg	ground	V-VII	Median	4, 5, 6	broad	0-1600
leg	ground	VI-IX	Late	2	narrow	0-800
leg	ground	VII-VIII	Late	6, 2, 1, 5	broad	0-1600
leg	ground	IV-V, VI-VIII	Median	2, 6, 5	broad	0-1600
leg	ground	III-V	Early	1, 5, 4, 6	broad	0-1600
leg	ground	V-VI	Median	1, 5	narrow	0-1600
leg	ground	III-VI, VII-IX	Median	7	broad	0-1600
leg	ground	V-VIII	Median	5, 6, 4,3	broad	0-1600
leg	ground	IV-V, VII-VIII	Median	6	narrow	0-1600
leg	ground	V-VII	Median	1	narrow	0-2100
leg	ground	III-V	Early	1, 5, 3	broad	0-1600
leg	ground	V-VII	Median	5, 4	narrow	0-2100
leg	ground	III-VI	Median	1, 4, 5	broad	0-1600
leg	ground	V-VII	Median	1, 5	narrow	0-800
leg	ground	V-VII	Median	4, 5	narrow	0-2100
leg	ground	III-VI	Median	7	broad	0-1600
leg	ground	III-VI	Median	7	broad	0-1600
leg	ground	V-VIII	Median	4, 5	narrow	0-800
leg	ground	IV-VI	Median	5, 4, 3	broad	0-2100
leg	ground	V-VII	Median	1, 5, 4, 2	broad	0-2100
leg	ground	V-VII	Median	2	narrow	?
leg	ground	V-VII	Median	4, 5	narrow	0-2100
leg	ground	IV-VII	Median	4, 5, 3	broad	0-2100
leg	ground	IV-VII	Median	4, 5, 3	broad	0-1600
leg	ground	I-VI, VI-VIII	Median	7	broad	0-2100
leg	ground	IV-VI, VI-IX	Median	7	broad	0-1600
leg	ground	III-VI	Median	1, 2, 4	broad	0-800
leg	ground	III-VII	Median	5, 4, 2, 3	broad	0-2100
leg	ground	III-VI	Median	7	broad	0-1600
leg	ground	VI-VIII	Late	5, 4, 6, 2, 3	broad	0-1600
leg	ground	III-VI	Median	2	narrow	0-800
leg	ground	III-VI, VII-VIII	Median	4, 6, 2, 5, 3	broad	0-2100

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Allacher Lohe 1980-89[1]	**Allacher Lohe 1997-99[2]**	Allacher Lohe 2009-10[3]	**Allacher Lohe 2017-18**	**Virginia Depot 1998-99[4]**	**Virginia Depot 2017-18**	**Botanical Garden 1997-99[5]**	**Botanical Garden 2015-17[6]**
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1
0	0	0	0	0	0	1	1
1	1	1	0	1	0	1	1
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	1	1	1	1	0	1	1
0	1	1	1	0	1	1	1
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0
0	1	1	0	0	0	1	1
1	1	1	1	1	0	0	0
0	0	0	0	0	0	0	0
1	1	1	1	0	0	1	1
0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
1	1	1	0	1	0	0	1
0	0	0	0	0	0	1	1
0	1	0	1	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	1
1	1	1	1	1	0	1	1
0	0	0	0	0	0	1	1
0	1	0	0	0	0	0	0
0	1	0	0	0	0	0	0
0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0
1	0	1	1	0	0	1	1
0	1	0	0	0	0	0	1
1	1	1	0	1	0	1	1
1	1	1	0	1	0	1	1
0	1	1	0	0	0	0	0
0	0	1	0	0	0	0	0
0	1	1	1	0	0	1	1
0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	1	0	0	0	1	1

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Andrena pandellei	Pérez, 1895	Andrenidae	3	oligolectic
Andrena pilipes	Fabricius, 1781	Andrenidae	3	polylectic
Andrena potentillae	Panzer, 1809	Andrenidae	2	oligolectic
Andrena praecox	(Scopoli, 1763)	Andrenidae	*	oligolectic
Andrena proxima	(Kirby, 1802)	Andrenidae	*	oligolectic
Andrena rosae	Panzer, 1801	Andrenidae	3	polylectic
Andrena ruficrus	Nylander, 1848	Andrenidae	G	oligolectic
Andrena rufizona	Imhoff, 1834	Andrenidae	1	oligolectic
Andrena schencki	Morawitz, 1866	Andrenidae	2	polylectic
Andrena scotica	Perkins, 1916	Andrenidae	*	polylectic
Andrena semilaevis	Pérez, 1903	Andrenidae	G	polylectic
Andrena sericata	Imhoff, 1868	Andrenidae	R	oligolectic
Andrena similis	(Smith, 1849)	Andrenidae	G	oligolectic
Andrena strohmella	Stöckhert, 1928	Andrenidae	*	polylectic
Andrena subopaca	Nylander, 1848	Andrenidae	*	polylectic
Andrena symphyti	Schmiedeknecht, 1883	Andrenidae	*	oligolectic
Andrena synadelpha	Perkins, 1914	Andrenidae	*	polylectic
Andrena tarsata	Nylander, 1848	Andrenidae	2	oligolectic
Andrena thoracica	(Fabricius, 1775)	Andrenidae	2	polylectic
Andrena tibialis	(Kirby, 1802)	Andrenidae	*	polylectic
Andrena vaga	Panzer, 1799	Andrenidae	*	oligolectic
Andrena varians	(Kirby, 1802)	Andrenidae	*	polylectic
Andrena ventralis	Imhoff, 1832	Andrenidae	*	oligolectic
Andrena viridescens	Viereck, 1916	Andrenidae	V	oligolectic
Andrena wilkella	(Kirby, 1802)	Andrenidae	*	oligolectic
Anthidium byssinum	(Panzer, 1798)	Megachilidae	3	oligolectic
Anthidium manicatum	(Linnaeus, 1758)	Megachilidae	*	polylectic
Anthidium montanum	Morawitz, 1864	Megachilidae	2	oligolectic
Anthidium nanum	Mocsáry, 1879	Megachilidae	3	oligolectic
Anthidium oblongatum	(Illiger, 1806)	Megachilidae	V	polylectic
Anthidium punctatum	Latreille, 1809	Megachilidae	V	polylectic
Anthidium strigatum	(Panzer, 1805)	Megachilidae	V	polylectic
Anthophora aestivalis	(Panzer, 1801)	Apidae	3	polylectic
Anthophora furcata	(Panzer, 1798)	Apidae	V	oligolectic
Anthophora plumipes	(Pallas, 1772)	Apidae	*	polylectic
Anthophora bimaculata	(Panzer, 1798)	Apidae	3	polylectic
Anthophora quadrimaculata	(Panzer, 1798)	Apidae	V	polylectic
Anthophora retusa	(Linnaeus, 1758)	Apidae	V	polylectic
Bombus barbutellus	(Kirby, 1802)	Apidae	*	cuckoo
Bombus bohemicus	Seidl, 1838	Apidae	*	cuckoo
Bombus campestris	(Panzer, 1801)	Apidae	*	cuckoo
Bombus confusus	Schenck, 1861	Apidae	1	polylectic
Bombus distinguendus	Morawitz, 1869	Apidae	2	polylectic
Bombus hortorum	(Linnaeus, 1761)	Apidae	*	polylectic
Bombus humilis	Illiger, 1806	Apidae	3	polylectic
Bombus hypnorum	(Linnaeus, 1758)	Apidae	*	polylectic
Bombus jonellus	(Kirby, 1802)	Apidae	3	polylectic
Bombus lapidarius	(Linnaeus, 1758)	Apidae	*	polylectic
Bombus lucorum	(Linnaeus, 1761)	Apidae	*	polylectic

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

leg	ground	V-VI	Median	4, 5, 6	broad	0-1600
leg	ground	IV-V, VII-IX	Median	2, 6, 4	broad	0-1600
leg	ground	III-V	Early	6, 2	narrow	0-800
leg	ground	III-V	Early	2, 5	narrow	0-1600
leg	ground	IV-VI	Median	4, 5, 6, 3	broad	0-2100
leg	ground	III-V, VII-VIII	Median	4, 6, 5	broad	0-1600
leg	ground	III-V	Early	1, 5. 2	broad	0-2100
leg	ground	V-VIII	Median	4, 6.2. 5	broad	300-3000
leg	ground	V-VII	Median	4, 6	narrow	0-800
leg	ground	IV-VI	Median	4, 5, 2, 3	broad	0-1600
leg	ground	V-VII	Median	5, 4, 6, 2	broad	0-2100
leg	ground	III-V	Early	5	narrow	0-1600
leg	ground	III-VII	Median	4, 5, 2	broad	0-800
leg	ground	III-V	Early	2, 4, 5, 6	broad	0-1600
leg	ground	III-VI, VII-VIII	Median	5, 1, 4, 6, 2, 3	broad	0-2100
leg	ground	IV-VI	Median	1, 2	narrow	0-800
leg	ground	V-VII	Median	1, 5, 6	narrow	0-800
leg	ground	VI-VIII	Late	1, 5, 2	broad	?
leg	ground	IV-VI, VII-IX	Median	2, 6	narrow	0-1600
leg	ground	I-VI, VI-VIII	Median	2, 5, 4, 6, 3	broad	0-1600
leg	ground	III-VI	Median	2	narrow	0-1600
leg	ground	III-V	Early	1, 5, 6, 4, 3	broad	0-1600
leg	ground	III-V	Early	2	narrow	0-800
leg	ground	IV-VI	Median	4, 5, 6, 2, 3	broad	0-1600
leg	ground	III-VII	Median	5, 4, 6, 2	broad	0-2100
pollen brush	ground	VI-VIII	Late	5, 4, 2	broad	0-2100
pollen brush	above	VI-VIII	Late	4, 5, 2, 3	broad	0-1600
pollen brush	above	VI-VIII	Late	?	unknown	800-3000
pollen brush	above	VI-IX	Late	6, 5	narrow	0-1600
pollen brush	above	VI-VIII	Late	6, 5, 3	broad	0-1600
pollen brush	above	V-IX	Median	6, 5, 3	broad	0-2100
pollen brush	above	IV-VIII	Median	5, 6, 2, 4, 3	broad	0-1600
leg	ground	IV-VII	Median	2, 6, 5	broad	0-2100
leg	above	VI-VIII	Late	1, 5, 4, 3	broad	0-1600
leg	ground	III-VI	Median	7	broad	0-1600
leg	g	V-IX	Median	2	narrow	0-1600
leg	ground	V-VIII	Median	2, 4, 3	broad	0-2100
leg	ground	IV-VII	Median	2, 4, 5	broad	0-1600
none	host nest	IV	Early	5, 4, 6, 3	broad	0-2100
none	host nest	IV-VIII	Median	5, 4, 6, 3	broad	0-2100
none	host nest	V	Early	5, 4, 6, 3	broad	0-2100
leg	ground and a	V	Early	6, 5	narrow	?
leg	ground	V-X	Median	4, 6, 5	broad	?
leg	ground and a	IV-VIII	Median	5, 4, 6, 3	broad	0-2100
leg	above	IV-X	Median	4, 5, 6	broad	0-2100
leg	above	III-VIII	Median	5, 1, 4, 6, 3	broad	0-2100
leg	ground and a	III_IX	Median	1, 2, 5, 6	broad	0-2100
leg	ground and a	III-X	Median	5, 4, 6, 3	broad	0-2100
leg	ground	II-VIII	Median	1, 5, 4, 6, 2, 3	broad	0-2100

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0
1	1	1	0	0	1	0	1
1	0	0	0	0	0	1	1
0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0
1	1	0	1	0	0	1	1
1	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
1	1	1	1	0	0	1	1
0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
1	1	0	0	1	0	0	1
0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0
1	1	0	0	1	0	0	0
1	1	1	0	0	0	0	0
1	1	0	0	0	0	0	0
0	1	0	0	1	1	1	1
0	0	0	0	0	0	0	0
1	1	1	1	0	0	0	0
1	1	1	0	0	1	1	1
1	1	1	1	0	1	1	0
1	0	0	0	0	0	0	1
0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	1
0	1	0	1	0	0	1	1
0	0	0	0	0	0	0	1
0	0	0	0	0	0	1	1
0	0	0	0	0	0	0	0
1	1	1	0	0	0	0	1
1	1	1	1	0	0	0	1
1	1	1	0	0	0	0	1
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
1	1	0	1	0	0	0	1
0	1	1	1	0	1	0	1
1	1	1	1	0	0	0	1
0	0	0	0	0	0	0	0
1	1	1	1	0	1	1	1
0	1	1	1	0	1	1	1

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Bombus mesomelas	Gerstäcker, 1869	Apidae	0	polylectic
Bombus muscorum	(Linnaeus, 1758)	Apidae	2	polylectic
Bombus norvegicus	(Sparre-Schneider, 1918)	Apidae	*	cuckoo
Bombus pascuorum	(Scopoli, 1763)	Apidae	*	polylectic
Bombus pomorum	(Panzer, 1805)	Apidae	2	polylectic
Bombus pratorum	(Linnaeus, 1761)	Apidae	*	polylectic
Bombus quadricolor	(Lepeletier, 1832)	Apidae	2	cuckoo
Bombus ruderarius	(Müller, 1776)	Apidae	3	polylectic
Bombus ruderatus	(Fabricius, 1775)^	Apidae	D	polylectic
Bombus rupestris	(Fabricius, 1793)	Apidae	*	cuckoo
Bombus soroeensis	(Fabricius, 1776)	Apidae	V	polylectic
Bombus subterraneus	(Linnaeus, 1758)	Apidae	2	polylectic
Bombus sylvarum	(Linnaeus, 1761)	Apidae	V	polylectic
Bombus sylvestris	(Lepeletier, 1832)	Apidae	*	cuckoo
Bombus terrestris	(Linnaeus, 1758)	Apidae	*	polylectic
Bombus vestalis	(Geoffroy, 1785)	Apidae	*	cuckoo
Bombus veteranus	(Fabricius, 1793)	Apidae	3	polylectic
Bombus wurflenii	Radoszkowski, 1859	Apidae	V	polylectic
Ceratina cyanea	(Kirby, 1802)	Apidae	*	polylectic
Coelioxys alata	Förster, 1853	Megachilidae	1	cuckoo
Coelioxys aurolimbata	Förster, 1853	Megachilidae	V	cuckoo
Coelioxys conica	(Linnaeus, 1758)	Megachilidae	V	cuckoo
Coelioxys elongata	Lepeletier, 1841	Megachilidae	*	cuckoo
Coelioxys inermis	(Kirby, 1802)	Megachilidae	*	cuckoo
Coelioxys lanceolata	Nylander, 1852	Megachilidae	2	cuckoo
Coelioxys mandibularis	Nylander, 1848	Megachilidae	*	cuckoo
Coelioxys rufescens	Lepeletier & Serville 1825	Megachilidae	V	cuckoo
Colletes cunicularius	(Linnaeus, 1761)	Colletidae	*	polylectic
Colletes daviesanus	Smith, 1846	Colletidae	*	oligolectic
Colletes fodiens	(Geoffroy, 1758)	Colletidae	3	oligolectic
Colletes similis	Schenck, 1853	Colletidae	V	oligolectic
Colletes succinctus	(Linnaeus, 1758)	Colletidae	V	oligolectic
Dufourea dentiventris	(Nylander, 1848)	Halictidae	3	oligolectic
Epeoloides coecutiens	(Fabricius, 1775)	Apidae	*	cuckoo
Epeolus variegatus	(Linnaeus, 1758)	Apidae	V	cuckoo
Eucera longicornis	(Linnaeus, 1758)	Apidae	V	oligolectic
Eucera nigrescens	Pérez, 1879	Apidae	*	oligolectic
Halictus confusus	Smith, 1853	Halictidae	*	polylectic
Halictus eurygnathus	Blüthgen, 1931	Halictidae	*	polylectic
Halictus gavarnicus	Pérez, 1903	Halictidae	1	polylectic
Halictus maculatus	Smith, 1848	Halictidae	*	polylectic
Halictus rubicundus	(Christ, 1791)	Halictidae	*	polylectic
Halictus scabiosae	(Rossi, 1790)	Halictidae	*	polylectic
Halictus sexcinctus	(Fabricius, 1775)	Halictidae	3	polylectic
Halictus simplex	Blüthgen, 1923	Halictidae	*	polylectic
Halictus subauratus	(Rossi, 1792)	Halictidae	*	polylectic
Halictus tumulorum	(Linnaeus, 1758)	Halictidae	*	polylectic
Hylaeus angustatus	(Schenck, 1861)	Colletidae	*	polylectic
Hylaeus brevicornis	Nylander, 1852	Colletidae	*	polylectic

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leg	ground	V-X	Median	?	narrow	800-3000
leg	above	V-IX	Median	2, 4	narrow	0-1600
none	host nest	IV-VIII	Median	5, 1, 4, 6	broad	0-2100
leg	ground and ab	IV-X	Median	5, 4, 6, 3	broad	0-2100
leg	ground	IV-VIII	Median	5, 4	narrow	0-1600
leg	ground and ab	III-VII	Median	5, 1, 4, 6, 3	broad	0-3000
none	host nest	IV-IX	Median	2, 5, 1, 4, 6	broad	0-3000
leg	above	IV-IX	Median	4	narrow	0-3000
leg	ground	V-X	Median	4	narrow	0-1600
none	host nest	IV-VIII	Median	5, 4, 6, 3	broad	0-2100
leg	ground	IV-IX	Median	2, 1, 5, 6	broad	0-3000
leg	ground	V-IX	Median	5, 4, 6	broad	?
leg	ground and ab	IV-X	Median	5, 4, 2, 6, 3	broad	0-2100
none	host nest	III-IX	Median	5, 1, 4, 6, 3	broad	0-3000
leg	ground	II-X	Median	5, 4, 6, 3	broad	0-2100
none	host nest	IV-VIII	Median	5, 4, 6, 3	broad	0-1600
leg	above	IV-IX	Median	4, 5	narrow	0-1600
leg	ground and ab	IV-X	Median	2, 1, 5	broad	0-3000
crop and leg	above	I-XII	Median	5, 4, 6, 3	broad	0-1600
none	host nest	VI-VIII	Late	2, 5	narrow	0-800
none	host nest	VI-VIII	Late	6, 5, 4, 2	broad	0-1600
none	host nest	V-VIII	Median	5, 4	narrow	0-2100
none	host nest	V-IX	Median	5, 6, 4, 2	broad	0-2100
none	host nest	V-X	Median	5, 4, 6, 3	broad	0-2100
none	host nest	VI-VII	Late	5, 2	narrow	800-1600
none	host nest	VI-VIII	Late	5, 6, 4, 2, 3	broad	0-2100
none	host nest	VI-IX	Late	5	narrow	0-2100
leg	ground	III-IV	Early	2	narrow	0-800
leg	ground	VI-IX	Late	2, 6, 4, 3	broad	0-2100
leg	ground	VII-VIII	Late	2, 6	narrow	0-1600
leg	ground	VI-IX	Late	6, 5, 2	broad	0-1600
leg	ground	VIII-IX	Late	5, 2	narrow	0-1600
leg	ground	VII-VIII	Late	5, 6	narrow	0-2100
none	host nest	VII-VIII	Late	2	narrow	0-1600
none	host nest	VI-VIII	Late	2, 6	narrow	0-1600
leg	ground	V-VII	Median	4, 6	narrow	0-800
leg	ground	IV-VI	Median	4, 5	narrow	0-800
leg	ground	III-IX	Median	2, 6	narrow	0-2100
leg	ground	IV-IX	Median	6, 2	narrow	0-1600
leg	ground	V-IX	Median	2, 6	narrow	800-2100
leg	ground	IV-IX	Median	6, 5, 2	broad	0-1600
leg	ground	IV-IX	Median	7	broad	0-2100
leg	ground	IV-IX	Median	5, 6, 2	broad	0-1600
leg	ground	V-IX	Median	2, 6	narrow	0-1600
leg	ground	VI-VIII	Late	2, 6	narrow	0-2100
leg	ground	III-VIII	Median	6, 2	narrow	0-1600
leg	ground	IV-IX	Median	7	broad	0-2100
crop	above	V-IX	Median	6, 2, 5	broad	?
crop	above	VI-IX	Late	5, 4, 6, 2, 3	broad	0-1600

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

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1	0	0	0	0	0	1	1
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0	1	0	1	0	1	0	1
1	1	1	1	0	1	1	1
1	0	0	0	0	0	0	0
1	1	1	0	0	0	0	1

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Hylaeus communis	Nylander, 1852	Colletidae	*	polylectic
Hylaeus confusus	Nylander, 1852	Colletidae	*	polylectic
Hylaeus cornutus	Curtis, 1831	Colletidae	*	polylectic
Hylaeus difformis	(Eversmann, 1852)	Colletidae	*	polylectic
Hylaeus dilatatus	(Kirby, 1802)	Colletidae	*	polylectic
Hylaeus gibbus	Saunders, 1850	Colletidae	*	polylectic
Hylaeus gracilicornis	(Morawitz, 1867)	Colletidae	*	polylectic
Hylaeus gredleri	Förster, 1871	Colletidae	*	polylectic
Hylaeus hyalinatus	Smith, 1842	Colletidae	*	polylectic
Hylaeus leptocephalus	(Morawitz, 1870)	Colletidae	*	polylectic
Hylaeus moricei	(Friese, 1898)	Colletidae	G	polylectic
Hylaeus nigritus	(Fabricius, 1798)	Colletidae	*	oligolectic
Hylaeus pectoralis	Förster, 1871	Colletidae	3	polylectic
Hylaeus pictipes	Nylander, 1852	Colletidae	*	polylectic
Hylaeus punctulatissimus	Smith, 1842	Colletidae	G	oligolectic
Hylaeus rinki	(Gorski, 1852)	Colletidae	*	polylectic
Hylaeus signatus	(Panzer, 1798)	Colletidae	*	oligolectic
Hylaeus sinuatus	(Schenck, 1853)	Colletidae	*	polylectic
Hylaeus styriacus	Förster, 1871	Colletidae	*	polylectic
Hylaeus variegatus	(Fabricius, 1798)	Colletidae	V	polylectic
Lasioglossum albipes	(Fabricius, 1781)	Halictidae	*	polylectic
Lasioglossum alpigenum	(Dalla Torre, 1877)	Halictidae	R	polylectic
Lasioglossum angusticeps	(Perkins, 1895)	Halictidae	G	polylectic
Lasioglossum bavaricum	(Blüthgen, 1930)	Halictidae	R	polylectic
Lasioglossum calceatum	(Scopoli, 1763)	Halictidae	*	polylectic
Lasioglossum costulatum	(Kriechbaumer, 1873)	Halictidae	3	oligolectic
Lasioglossum cupromicans	(Pérez, 1903)	Halictidae	G	polylectic
Lasioglossum fratellum	(Pérez, 1903)	Halictidae	*	polylectic
Lasioglossum fulvicorne	(Kirby, 1802)	Halictidae	*	polylectic
Lasioglossum intermedium	(Schenck, 1868)	Halictidae	3	polylectic
Lasioglossum laeve	(Kirby, 1802)	Halictidae	1	polylectic
Lasioglossum laevigatum	(Kirby, 1802)	Halictidae	3	polylectic
Lasioglossum laticeps	(Schenck, 1868)	Halictidae	*	polylectic
Lasioglossum lativentre	(Schenck, 1853)	Halictidae	V	polylectic
Lasioglossum leucopus	(Kirby, 1802)	Halictidae	*	polylectic
Lasioglossum leucozonium	(Schrank, 1781)	Halictidae	*	polylectic
Lasioglossum lineare	(Schenck, 1868)	Halictidae	3	polylectic
Lasioglossum lissonotum	(Noskiewicz, 1926)	Halictidae	2	polylectic
Lasioglossum lucidulum	(Schenck, 1861)	Halictidae	*	polylectic
Lasioglossum majus	(Nylander, 1852)	Halictidae	3	polylectic
Lasioglossum malachurum	(Kirby, 1802)	Halictidae	*	polylectic
Lasioglossum minutulum	(Schenck, 1853)	Halictidae	3	polylectic
Lasioglossum morio	(Fabricius, 1793)	Halictidae	*	polylectic
Lasioglossum nitidiusculum	(Kirby, 1802)	Halictidae	V	polylectic
Lasioglossum nitidulum	(Fabricius, 1804)	Halictidae	*	polylectic
Lasioglossum parvulum	(Schenck, 1853)	Halictidae	V	polylectic
Lasioglossum pauxillum	(Schenck, 1853)	Halictidae	*	polylectic
Lasioglossum punctatissimum	(Schenk, 1853)	Halictidae	*	polylectic
Lasioglossum politum	(Schenk, 1853)	Halictidae	*	polylectic

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

crop	above	V-X	Median	5, 2, 3	broad	0-2100
crop	above	IV-IX	Median	5, 2, 3	broad	0-2100
crop	above	VI-VIII	Late	5, 4, 6, 2	broad	0-1600
crop	above	VI-VIII	Late	1, 5	narrow	0-1600
crop	above	VI-IX	Late	2, 6, 5	narrow	0-1600
crop	above	V-IX	Median	5, 6, 2	narrow	0-2100
crop	above	VI-VIII	Late	1, 5, 2	narrow	0-800
crop	above	VI-VIII	Late	1, 5, 6, 3	broad	0-2100
crop	above	V-IX	Median	5, 4, 2, 6, 3	broad	0-1600
crop	above	V-IX	Median	5, 6, 3	broad	0-1600
crop	above	VI-VIII	Late	1, 6	narrow	0-800
crop	above	V-IX	Median	4, 6, 2, 3	broad	0-2100
crop	above	V-IX	Median	1, 4	narrow	0-800
crop	above	VI-VIII	Late	5, 6, 2	broad	0-1600
crop	above	V-VIII	Median	2, 6, 3	broad	0-1600
crop	above	VI-VIII	Late	1, 5	narrow	0-1600
crop	above	IV-IX	Median	6, 2, 3	broad	0-1600
crop	above	VI-VIII	Late	1, 5, 6	narrow	0-1600
crop	above	VI-VIII	Late	5, 6	narrow	0-1600
crop	ground	VI-IX	Late	2, 6	narrow	0-1600
leg	ground	IV-X	Median	5, 6, 3	narrow	0-3000
leg	ground	VI-X	Median	?	unknown	1600-3000
leg	ground	IV-VIII	Median	4, 6	narrow	0-800
leg	ground	V-IX	Median	?	unknown	300-800
leg	ground	III-X	Median	1, 6, 3	broad	0-3000
leg	ground	IV-IX	Median	6, 5, 4, 2	broad	0-2100
leg	ground	IV-IX	Median	2	narrow	800-3000
leg	ground	IV-X	Median	5, 1	narrow	0-3000
leg	ground	III-X	Median	6, 1, 3	broad	0-3000
leg	ground	IV-VIII	Median	2	narrow	0-3000
leg	ground	IV-IX	Median	6, 5	narrow	0-1600
leg	ground	III-X	Median	5, 4, 6, 2	broad	0-2100
leg	ground	III-X	Median	5, 4, 6, 2	broad	0-2100
leg	ground	IV-X	Median	5, 6, 4	broad	0-2100
leg	ground	IV-X	Median	5, 6, 4, 2	broad	0-2100
leg	ground	IV-X	Median	1, 3, 6	broad	0-2100
leg	ground	III-IX	Median	6, 2	narrow	0-1600
leg	ground	IV-VIII	Median	6, 2	narrow	0-1600
leg	ground	IV-X	Median	2, 6, 5, 4	broad	0-800
leg	ground	IV-IX	Median	5, 6, 4, 1	broad	0-1600
leg	ground	IV-X	Median	7	broad	0-1600
leg	ground	IV-IX	Median	6, 4	narrow	0-1600
leg	ground	III-X	Median	7	broad	0-2100
leg	ground	IV-IX	Median	5, 6, 2	broad	0-1600
leg	ground	III-X	Median	2, 3	narrow	0-1600
leg	ground	IV-X	Median	5, 4, 2	broad	0-2100
leg	ground	III-X	Median	7	broad	0-1600
leg	ground	IV-X	Median	2, 5, 6	broad	0-1600
leg	ground	III-X	Median	6, 4, 2, 3	broad	0-800

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

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1	1	0	0	0	0	0	0
1	1	1	1	1	0	1	0
0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Lasioglossum quadrinotatulum	(Schenck, 1861)	Halictidae	3	polylectic
Lasioglossum quadrinotatum	(Kirby, 1802)	Halictidae	3	polylectic
Lasioglossum rufitarse	(Zetterstedt, 1838)	Halictidae	*	polylectic
Lasioglossum sabulosum	(Warncke, 1986)	Halictidae	D	polylectic
Lasioglossum semilucens	(Alfken, 1914)	Halictidae	*	polylectic
Lasioglossum sexnotatum	(Kirby, 1802)	Halictidae	3	polylectic
Lasioglossum sexstrigatum	(Schenck, 1868)	Halictidae	*	polylectic
Lasioglossum villosulum	(Kirby, 1802)	Halictidae	*	polylectic
Lasioglossum xanthopus	(Kirby, 1802)	Halictidae	*	polylectic
Lasioglossum zonulum	(Smith, 1848)	Halictidae	*	polylectic
Macropis europaea	Warncke, 1973	Melittidae	*	oligolectic
Macropis fulvipes	(Fabricius, 1804)	Melittidae	*	oligolectic
Megachile apicalis	Spinola, 1808	Megachilidae	2	polylectic
Megachile centuncularis	(Linnaeus, 1758)	Megachilidae	V	polylectic
Megachile circumcincta	(Kirby, 1802)	Megachilidae	V	polylectic
Megachile ericetorum	Lepeletier, 1841	Megachilidae	*	oligolectic
Megachile lagopoda	(Linnaeus, 1761)	Megachilidae	2	polylectic
Megachile leachella	Curtis, 1828	Megachilidae	3	polylectic
Megachile ligniseca	(Kirby, 1802)	Megachilidae	2	polylectic
Megachile maritima	(Kirby, 1802)	Megachilidae	3	polylectic
Megachile nigriventris	Schenck, 1868	Megachilidae	*	polylectic
Megachile parietina	(Geoffroy, 1785)^	Megachilidae	1	polylectic
Megachile pilidens	Alfken, 1924	Megachilidae	3	polylectic
Megachile rotundata	(Fabricius, 1787)	Megachilidae	*	polylectic
Megachile versicolor	Smith, 1844	Megachilidae	*	polylectic
Megachile willughbiella	(Kirby, 1802)	Megachilidae	*	polylectic
Melecta albifrons	(Forster, 1771)	Apidae	*	cuckoo
Melecta luctuosa	(Scopoli, 1770)	Apidae	3	cuckoo
Melitta haemorrhoidalis	(Fabricius, 1775)	Melittidae	*	oligolectic
Melitta leporina	(Panzer, 1799)	Melittidae	*	oligolectic
Melitta nigricans	Alfken, 1905	Melittidae	*	oligolectic
Melitta tricincta	Kirby, 1802	Melittidae	V	oligolectic
Nomada alboguttata	Herrich-Schäffer, 1839	Apidae	*	cuckoo
Nomada armata	Herrich-Schäffer, 1839	Apidae	3	cuckoo
Nomada atroscutellaris	Strand, 1921	Apidae	V	cuckoo
Nomada bifasciata	Olivier, 1811	Apidae	*	cuckoo
Nomada braunsiana	Schmiedeknecht, 1882	Apidae	1	cuckoo
Nomada emarginata	Morawitz, 1877	Apidae	*	cuckoo
Nomada errans	Lepeletier, 1841	Apidae	2	cuckoo
Nomada fabriciana	(Linnaeus, 1767)	Apidae	*	cuckoo
Nomada facilis	Schwarz, 1967	Apidae	G	cuckoo
Nomada ferruginata	(Linnaeus, 1767)	Apidae	*	cuckoo
Nomada flava	Panzer, 1798	Apidae	*	cuckoo
Nomada flavoguttata	(Kirby, 1802)	Apidae	*	cuckoo
Nomada flavopicta	(Kirby, 1802)	Apidae	*	cuckoo
Nomada fucata	Panzer, 1798	Apidae	*	cuckoo
Nomada fulvicornis	Fabricius, 1793	Apidae	*	cuckoo
Nomada furva	Panzer, 1798	Apidae	D	cuckoo
Nomada fuscicornis	Nylander, 1848	Apidae	*	cuckoo

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

leg	ground	IV-X	Median	2, 6, 4	broad	0-800
leg	ground	IV-X	Median	6, 4	narrow	0-800
leg	ground	IV-X	Median	5, 2	narrow	0-2100
leg	ground	IV-IX	Median	2, 5, 6	broad	0-800
leg	ground	IV-VIII	Median	6, 2, 4	broad	0-1600
leg	ground	IV-X	Median	2, 6	narrow	0-1600
leg	ground	IV-X	Median	2, 5, 6, 3	broad	0-800
leg	ground	III-X	Median	5, 4, 6, 2	broad	0-1600
leg	ground	III-X	Median	4, 6, 5	broad	0-1600
leg	ground	IV-X	Median	4, 5, 6	broad	0-1600
leg	ground	VII-IX	Late	1	narrow	?
leg	ground	IV-VIII	Median	1	narrow	?
pollen brush	above	VI-VIII	Late	?	narrow	0-1600
pollen brush	above	V-X	Median	5, 4, 6, 3	broad	?
pollen brush	above	V-VIII	Median	5, 6, 4, 2	broad	?
pollen brush	above	VI-VIII	Late	6, 5, 4, 2, 3	broad	0-1600
pollen brush	ground and a	VI-VIII	Late	6, 2	narrow	0-1600
pollen brush	ground and a	V-IX	Median	2	narrow	0-1600
pollen brush	above	VI-IX	Late	5, 1	narrow	0-2100
pollen brush	ground	VI-VIII	Late	2, 6	narrow	0-1600
pollen brush	above	V-VIII	Median	5, 1	narrow	0-2100
pollen brush	above	III-VIII	Median	6, 2	narrow	0-2100
pollen brush	ground and a	V-IX	Median	2.6	narrow	0-1600
pollen brush	above	VI-IX	Late	6, 2, 5	broad	0-1600
pollen brush	above	V-IX	Median	5, 6, 4, 2, 3	broad	0-1600
pollen brush	above	V-IX	Median	5, 3, 4	broad	0-2100
none	host nest	III-VII	Median	2, 3	narrow	0-3000
none	host nest	IV-VII	Median	5, 2	narrow	0-1600
leg	ground	VI-IX	Late	5, 4, 6, 3	broad	0-2100
leg	ground	VI-IX	Late	4, 6, 3	broad	0-1600
leg	ground	VII-VIII	Late	5	narrow	0-800
leg	ground	VIII-IX	Late	6, 2, 4	broad	0-2100
none	host nest	IV-V	Early	2	narrow	0-800
none	host nest	V-VIII	Median	4, 5	narrow	0-1600
none	host nest	IV-VI	Median	4, 5, 6, 2, 3	broad	0-1600
none	host nest	III-VI	Median	3, 4, 5	broad	0-800
none	host nest	V-VIII	Median	6, 4, 5	broad	0-2100
none	host nest	V-IX	Median	5, 4, 6	broad	0-2100
none	host nest	VI-VIII	Late	5, 4, 6, 2, 3	broad	0-1600
none	host nest	III-VIII	Median	1, 2, 4, 5, 6, 3	broad	0-2100
none	host nest	V-VIII	Median	5, 4, 2	broad	0-2100
none	host nest	III-V	Early	2, 5	narrow	0-1600
none	host nest	III-VI	Median	1, 5, 4, 6, 2, 3	broad	0-1600
none	host nest	III-VIII	Median	5, 6, 4, 2, 3	broad	0-2100
none	host nest	V-X	Median	5, 4, 6, 3	broad	0-1600
none	host nest	III-VIII	Median	5, 6, 4, 2, 3	broad	0-1600
none	host nest	III-VIII	Median	1, 5, 4, 6, 2, 3	broad	0-1600
none	host nest	IV-IX	Median	5, 6, 4, 2	broad	0-800
none	host nest	VI-IX	Late	5, 6, 2	broad	0-1600

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0
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0	0	0	0	0	0	0	0
0	1	1	0	0	0	0	0
1	1	1	0	0	0	1	1
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0	1	1	0	0	0	0	0
0	1	0	0	0	0	1	1
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0	0	0	0	0	0	0	0
1	1	0	0	0	0	0	0
1	0	1	0	0	0	0	0
1	1	1	0	0	1	1	1
0	0	0	0	0	0	0	0
0	0	0	1	0	1	0	0
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0	0	0	1	0	0	0	1
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1	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0
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0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	1	1	1	0	0	1	1
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0	1	0	0	0	0	0	0
1	1	1	1	0	0	1	1
1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0
0	1	0	0	1	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Nomada goodeniana	(Kirby, 1802)	Apidae	*	cuckoo
Nomada hirtipes	Pérez, 1884	Apidae	3	cuckoo
Nomada integra	Brullé, 1832	Apidae	G	cuckoo
Nomada kohli	Schmiedeknecht, 1882	Apidae	2	cuckoo
Nomada lathburiana	(Kirby, 1802)	Apidae	*	cuckoo
Nomada leucophthalma	(Kirby, 1802)	Apidae	*	cuckoo
Nomada marshamella	(Kirby, 1802)	Apidae	*	cuckoo
Nomada moeschleri	Alfken, 1913	Apidae	*	cuckoo
Nomada obscura	Zetterstedt, 1838	Apidae	*	cuckoo
Nomada obtusifrons	Nylander, 1848	Apidae	2	cuckoo
Nomada opaca	Alfken, 1913	Apidae	2	cuckoo
Nomada panzeri	Lepeletier, 1841	Apidae	*	cuckoo
Nomada roberjeotiana	Panzer, 1799	Apidae	G	cuckoo
Nomada ruficornis	(Linnaeus, 1758)	Apidae	*	cuckoo
Nomada rufipes	Fabricius, 1793	Apidae	V	cuckoo
Nomada sexfasciata	Panzer, 1799	Apidae	*	cuckoo
Nomada signata	Jurine, 1807	Apidae	*	cuckoo
Nomada stigma	Fabricius, 1804	Apidae	*	cuckoo
Nomada striata	Fabricius, 1793	Apidae	*	cuckoo
Nomada succincta	Panzer, 1798	Apidae	*	cuckoo
Nomada villosa	Thomson, 1870	Apidae	G	cuckoo
Nomada zonata	Panzer, 1798	Apidae	V	cuckoo
Osmia adunca	(Panzer, 1798)	Megachilidae	*	oligolectic
Osmia anthocopoides	Schenck, 1853	Megachilidae	3	oligolectic
Osmia aurulenta	(Panzer, 1799)	Megachilidae	*	polylectic
Osmia bicolor	(Schrank, 1781)	Megachilidae	*	polylectic
Osmia bicornis	(Linnaeus, 1758)	Megachilidae	*	polylectic
Osmia caerulescens	(Linnaeus, 1758)	Megachilidae	*	polylectic
Osmia campanularum	(Kirby, 1802)	Megachilidae	*	oligolectic
Osmia cantabrica	(Benoist, 1935)	Megachilidae	*	oligolectic
Osmia cerinthidis	Morawitz, 1876	Megachilidae	1	oligolectic
Osmia claviventris	Thomson, 1872	Megachilidae	*	polylectic
Osmia cornuta	(Latreille, 1805)	Megachilidae	*	polylectic
Osmia florisomnis	(Linnaeus, 1758)	Megachilidae	*	oligolectic
Osmia leaiana	(Kirby, 1802)	Megachilidae	3	oligolectic
Osmia lepeletieri	Pérez, 1879	Megachilidae	0	oligolectic
Osmia leucomelana	(Kirby, 1802)	Megachilidae	*	polylectic
Osmia mitis	Nylander, 1852	Megachilidae	2	oligolectic
Osmia niveata	(Fabricius, 1804)	Megachilidae	3	oligolectic
Osmia parietina	Curtis, 1828	Megachilidae	3	polylectic
Osmia pilicornis	Smith, 1846	Megachilidae	G	polylectic
Osmia rapunculi	(Lepeletier, 1841)	Megachilidae	*	oligolectic
Osmia ravouxi	Pérez, 1902	Megachilidae	2	polylectic
Osmia rufohirta	Latreille, 1811	Megachilidae	3	polylectic
Osmia spinulosa	(Kirby, 1802)	Megachilidae	3	oligolectic
Osmia tridentata	Dufour & Perris, 1840	Megachilidae	3	oligolectic
Osmia truncorum	(Linnaeus, 1758)	Megachilidae	*	oligolectic
Osmia uncinata	Gerstäcker, 1869	Megachilidae	G	polylectic
Osmia villosa	(Schenck, 1853)	Megachilidae	2	oligolectic

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

none	host nest	IV-VI	Median	1, 5, 4, 6, 2, 3	broad	0-1600
none	host nest	IV-VI	Median	5, 4	narrow	0-1600
none	host nest	IV-VIII	Median	5, 4, 2	broad	0-2100
none	host nest	V-VIII	Median	2, 5, 6, 4	broad	0-800
none	host nest	III-VIII	Median	5, 4, 6, 2, 3	broad	0-2100
none	host nest	III-VI	Median	1, 5, 2	broad	0-2100
none	host nest	IV-VII	Median	4, 2, 1, 5, 6, 3	broad	0-1600
none	host nest	V-VII	Median	5, 4, 3	broad	0-1600
none	host nest	III-VI	Median	1, 5, 2	broad	0-2100
none	host nest	VII-VIII	Late	1, 5, 2	broad	0-2100
none	host nest	V-VI	Median	1, 5	narrow	0-800
none	host nest	III-VIII	Median	5, 4, 1, 2, 6, 3	broad	0-3000
none	host nest	VII-IX	Late	2	narrow	0-2100
none	host nest	III-VI	Median	5, 4, 3	broad	0-1600
none	host nest	VII-IX	Late	5, 2	narrow	0-2100
none	host nest	IV-VI	Median	6, 4, 5	broad	0-1600
none	host nest	III-VI	Median	3, 1, 5	broad	0-800
none	host nest	IV-VIII	Median	4, 5	narrow	0-1600
none	host nest	IV-VIII	Median	4, 5, 2	broad	0-2100
none	host nest	III-VI	Median	1, 5, 4, 6, 2, 3	broad	0-1600
none	host nest	IV-VII	Median	4, 5, 3	broad	0-1600
none	host nest	IV-VIII	Median	2, 6, 5	broad	0-800
pollen brush	above	VI-IX	Late	6, 2	narrow	0-1600
pollen brush	above	V-VIII	Median	2	narrow	0-2100
pollen brush	above	III-VI	Median	6, 4, 5, 2	broad	0-2100
pollen brush	above	III-VIII	Median	1, 5, 6	broad	0-2100
pollen brush	above	III-VIII	Median	5, 4, 6, 2, 3	broad	0-1600
pollen brush	above	III-X	Median	5, 6, 2, 3	broad	0-2100
pollen brush	above	VI-VIII	Late	5, 6, 4, 3	broad	?
pollen brush	above	V-VIII	Median	5, 6, 4, 3	broad	?
pollen brush	above	V-VI	Median	5, 6	narrow	0-1600
pollen brush	above	VI-VIII	Late	5, 6, 2	broad	0-2100
pollen brush	above	II-VI	Median	3, 2	narrow	0-1600
pollen brush	above	IV-VI	Median	5, 6, 4, 3	broad	?
pollen brush	above	IV-IX	Median	5, 4, 6	broad	0-2100
pollen brush	above	VI-VIII	Late	2	narrow	0-2100
pollen brush	above	VI-VIII	Late	5, 6, 2	broad	0-2100
pollen brush	above	VI-VIII	Late	6, 5, 2	broad	?
pollen brush	above	IV-VII	Median	5, 4, 6, 3	broad	0-2100
pollen brush	above	IV-VIII	Median	1, 5	narrow	0-2100
pollen brush	above	III-VI	Median	1, 5	narrow	0-1600
pollen brush	above	V-VIII	Median	5, 6, 4, 3	broad	0-2100
pollen brush	above	IV-VIII	Median	2, 6	narrow	0-1600
pollen brush	above	IV-VIII	Median	6, 2	narrow	0-1600
pollen brush	above	V-IX	Median	2, 5, 4	broad	0-2100
pollen brush	above	VI-VIII	Late	6, 5	narrow	0-1600
pollen brush	above	VI-IX	Late	5, 4	narrow	0-1600
pollen brush	above	III-VIII	Median	1, 5	narrow	0-2100
pollen brush	above	V-VII	Median	2	narrow	0-3000

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	0
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1	0	1	1	0	0	1	1
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
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1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0
1	1	1	1	0	1	1	1
0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	1

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

Osmia xanthomelana	(Kirby, 1802)	Megachilidae	2	oligolectic
Panurgus banksianus	(Kirby, 1802)	Andrenidae	*	oligolectic
Panurgus calcaratus	(Scopoli, 1763)	Andrenidae	*	oligolectic
Rophites algirus	Pérez, 1895	Halictidae	3	oligolectic
Sphecodes albilabris	(Fabricius, 1793)	Halictidae	*	cuckoo
Sphecodes crassus	Thomson, 1870	Halictidae	*	cuckoo
Sphecodes ephippius	(Linnaeus, 1767)	Halictidae	*	cuckoo
Sphecodes ferruginatus	Von Hagens, 1882	Halictidae	*	cuckoo
Sphecodes geoffrellus	(Kirby, 1802)	Halictidae	*	cuckoo
Sphecodes gibbus	(Linnaeus, 1758)	Halictidae	*	cuckoo
Sphecodes hyalinatus	Von Hagens, 1882	Halictidae	*	cuckoo
Sphecodes longulus	Von Hagens, 1882	Halictidae	*	cuckoo
Sphecodes marginatus	Von Hagens, 1882	Halictidae	*	cuckoo
Sphecodes miniatus	Von Hagens, 1882	Halictidae	*	cuckoo
Sphecodes monilicornis	(Kirby, 1802)	Halictidae	*	cuckoo
Sphecodes niger	(Hagens, 1874)	Halictidae	*	cuckoo
Sphecodes pellucidus	Smith, 1845	Halictidae	V	cuckoo
Sphecodes puncticeps	Thomson, 1870	Halictidae	*	cuckoo
Sphecodes reticulatus	Thomson, 1870	Halictidae	*	cuckoo
Sphecodes rubicundus	Von Hagens, 1875	Halictidae	3	cuckoo
Sphecodes rufiventris	(Panzer, 1798)	Halictidae	*	cuckoo
Sphecodes scabricollis	Wesmael, 1835	Halictidae	G	cuckoo
Sphecodes spinulosus	Von Hagens, 1875	Halictidae	G	cuckoo
Stelis minuta	Lepeletier & Serville 1825	Megachilidae	*	cuckoo
Stelis minima	Schenck, 1859	Megachilidae	*	cuckoo
Stelis breviuscula	(Nylander, 1848)	Megachilidae	*	cuckoo
Stelis ornatula	(Klug, 1807)	Megachilidae	*	cuckoo
Stelis phaeoptera	(Kirby, 1802)	Megachilidae	3	cuckoo
Stelis punctulatissima	(Kirby, 1802)	Megachilidae	*	cuckoo
Stelis signata	(Latreille, 1809)	Megachilidae	3	cuckoo
Thyreus histrionicus	(Illiger, 1806)	Apidae	0	cuckoo
Thyreus orbatus	(Lepeletier, 1841)	Apidae	2	cuckoo
Xylocopa violacea	(Linnaeus, 1758)	Apidae	*	polylectic

Scheuchl, E., & Willner, W. (2016). Taschenlexikon der Wildbienen Mitteleuropas: Alle Arten im Porträt . Quel

Westrich, P.; Frommer, U.; Mandery, K.; Riemann, H.; Ruhnke, H.; Saure, C. and Voith, J. (2011). Rote Liste un

1) Foeckler, F., & Schmidt, H. (1997). Schutzwürdigkeitsgutachten für das geplante Naturschutzgebiet "Allach

2) Schuberth, J. 2000. Artenhilfsprogramm Andrena rufizona. Im Auftrag des Bayerischen Landesamtes für U

3) Dubitzky, A. 2010. Rangierbahnhof Allach – Pflege- und Entwicklungsplan für den Zuständigkeitsbereich de

4) Schuberth, J., personal communication to the first author, MMH, 2019

5) Bembé B, Gerlach G, Schuberth J, Schönitzer K (2001) Die Wildbienen im Botanischen Garten München. Na

6) Hofmann, M. M., Fleischmann, A., & Renner, S. S. (2018). Changes in the bee fauna of a German botanical

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

pollen brush	above	V-VI	Median	5, 6	narrow	?
leg	ground	VI-VIII	Late	1, 5, 6, 4, 2	broad	0-2100
leg	ground	VI-IX	Late	5, 6, 2	broad	0-2100
leg	ground	VI-VII	Late	6, 2	narrow	0-1600
none	host nest	III-X	Median	2, 6	narrow	0-1600
none	host nest	IV-X	Median	7	broad	0-2100
none	host nest	III-X	Median	7	broad	0-2100
none	host nest	IV-X	Median	7	broad	0-3000
none	host nest	IV-X	Median	7	broad	0-3000
none	host nest	IV-X	Median	7	broad	0-3000
none	host nest	IV-X	Median	7	broad	0-2100
none	host nest	III-IX	Median	7	broad	0-1600
none	host nest	V-VIII	Median	?	narrow	0-1600
none	host nest	IV-IX	Median	7	broad	0-3000
none	host nest	III-X	Median	7	broad	0-1600
none	host nest	IV-IX	Median	7	broad	0-2100
none	host nest	IV-IX	Median	2, 5, 6	broad	0-2100
none	host nest	IV-IX	Median	2, 6	narrow	0-1600
none	host nest	IV-X	Median	2, 5, 6	broad	0-1600
none	host nest	V-VII	Median	4, 5	narrow	0-800
none	host nest	IV-IX	Median	6, 5, 2	broad	0-1600
none	host nest	V-IX	Median	4, 5, 6	broad	0-1600
none	host nest	V-VII	Median	4, 6, 5	broad	0-2100
none	host nest	VI-IX	Late	5, 6, 2	broad	0-1600
none	host nest	VI-VIII	Late	5, 6, 4, 3	broad	0-1600
none	host nest	V-IX	Median	5, 4	narrow	0-1600
none	host nest	IV-VIII	Median	5, 6, 2	broad	0-2100
none	host nest	IV-IX	Median	5, 4, 6	broad	0-2100
none	host nest	V-IX	Median	5, 2, 6, 3	broad	0-1600
none	host nest	V-VIII	Median	5, 6, 2, 3	broad	0-1600
none	host nest	VII-VIII	Late	2	narrow	0-1600
none	host nest	V-IX	Median	2, 4	narrow	0-2100
leg	above	III-X	Median	4, 3	narrow	0-1600

lle et Meyer Verlag. Wiebelsheim, Germany.

d Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. Naturschutz und Biologische

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r Landeshauptstadt München. Teil C. Teilbeitrag: Wildbienenfauna. Im Auftrag der Landeshauptstadt

chrichtenblatt der bayererischen Entomologen 50:30–41.

garden between 1997 and 2017, attributable to climate warming, not other parameters. Oecologia,

Appendix S1: Munich bee species, their Red List status (Westrich et al,. 2011), life-history parameters (Scheuchl Willner, 2016), and historic and modern (2017/2018) records in the Allacher Lohe, Virginia Depot, or Botanical Garden.

0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0
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München Baureferat Gartenbau GR.

187(3), 701-706.

Appendix S2: Diversity Work Bench accession numbers start with ALS or ALN; the remaining numbers are GenBank accessions of DNA barcodes. Physical vouchers were deposited in the Zoologische Staatssammlung Munich.

Species	**Accession numbers**	**Observation date (German date format)**
Andrena chrysosceles	ALS-00021	16.06.2017
Andrena cineraria	ALS-00060	30.04.2017
	ALN-00063	24.04.2017
	ALN-00098	24.04.2017
Andrena falsifica	MK268693	
Andrena flavipes	ALS-00140	26.07.2018
	ALS-00074	30.04.2017
Andrena fulvata	MG845943	
Andrena gravida	MG845945	
Andrena haemorrhoa	ALS-00073	30.04.2017
	ALS-00075	30.04.2017
	ALS-00086	21.04.2018
	MG845952	
Andrena labiata	ALN-00121	19.04.2018
Andrena nitida	ALS-00064	30.04.2017
	MG845934	
Andrena scotica	ALS-00062	30.04.2017
	ALN-00006	26.05.2017
Andrena subopaca	MG845935	
	MG845936	
	MG845940	
Anthidium nanum	ALS-00006	16.06.2017
Anthidium punctatum	ALS-00122	28.05.2018
	ALN-00163	21.05.2018
Anthophora plumipes	ALN-00134	19.04.2018
Bombus bohemicus	ALS-00148	02.07.2018
Bombus hortorum	ALS-00011	16.06.2017
	ALS-00024	16.06.2017
	ALN-00175	02.07.2018
	ALS-00050	01.08.2017
	ALS-00098	28.05.2018
Bombus humilis	ALN-00211	02.07.2018
Bombus hypnorum	ALN-00060	24.04.2017
Bombus lapidarius	ALS-00018	16.06.2017
	ALN-00059	24.04.2017
	ALN-00205	02.07.2018
Bombus lucorum	ALS-00055	30.04.2017
	ALN-00182	02.07.2018
Bombus pascuorum	ALS-00066	30.04.2017
	ALS-00084	21.04.2018
	ALN-00012	26.05.2017
	ALN-00076	24.04.2017
	ALN-00097	24.04.2017
	ALN-00133	19.04.2018
Bombus pratorum	ALS-00067	30.04.2017
	ALN-00096	24.04.2017
Bombus rupestris	ALN-00077	24.04.2017
Bombus sylvarum	ALS-00104	28.05.2018

Appendix S2: Diversity Work Bench accession numbers start with ALS or ALN; the remaining numbers are GenBank accessions of DNA barcodes. Physical vouchers were deposited in the Zoologische Staatssammlung Munich.

	ALN-00038	31.07.2017
Bombus terrestris	ALS-00157	02.07.2018
	ALN-00056	13.03.2017
	ALS-00012	16.06.2017
Bombus vestalis	ALN-00135	19.04.2018
Coelioxys elongata	ALS-00116	28.05.2018
Coelioxys mandibularis	ALS-00129	28.05.2018
Colletes daviesanus	ALS-00038	01.08.2017
Colletes similis	ALS-00141	26.07.2018
	ALN-00108	17.08.2017
	MG845962	
Halictus rubicundus	ALS-00032	01.08.2017
	ALS-00040	01.08.2017
	MK442006	
	MG792000	
Halictus scabiosae	ALS-00142	26.07.2018
	ALN-00042	31.07.2017
	ALN-00043	31.07.2017
	ALN-00145	21.05.2018
Halictus simplex	Not uploaded to GenBank due to low Sequence quality	
Halictus subauratus	MK442007	
	MG792005	
	MG792006	
	MG792007	
	ALS-00042	01.08.2017
	ALS-00043	01.08.2017
	ALS-00099	28.05.2018
	ALS-00132	26.07.2018
	ALN-00030	31.07.2017
	ALN-00111	17.08.2017
	ALN-00156	21.05.2018
	ALN-00161	21.05.2018
	ALN-00186	02.07.2018
Halictus tumulorum	MG792010	
Hylaeus confusus	ALN-00013	26.05.2017
Hylaeus communis	ALS-00165	02.07.2018
	ALN-00113	17.08.2017
	ALN-00173	21.05.2018
	ALN-00216	02.08.2018
Hylaeus gredleri	ALS-00133	26.07.2018
Hylaeus nigritus	ALS-00002	16.06.2017
	ALS-00035	01.08.2017
	ALS-00114	28.05.2018
	ALS-00139	26.07.2018
	ALN-00174	21.05.2018
Hylaeus signatus	ALS-00123	28.05.2018
Hylaeus sinuatus	MK268704	
Lasioglossum calceatum	MG791989	
	MG791988	

Appendix S2: Diversity Work Bench accession numbers start with ALS or ALN; the remaining numbers are GenBank accessions of DNA barcodes. Physical vouchers were deposited in the Zoologische Staatssammlung Munich.

	MG791987	
Lasioglossum fulvicorne	MG791994	
	MG791995	
	MG791996	
	MG791997	
Lasioglossum laevigatum	MG791998	
Lasioglossum laticeps	not uploaded to GenBank due to low Sequence quality	
Lasioglossum morio	MG791973	
	MG791974	
	MG791975	
	MG791976	
	MG791977	
	MG791978	
	MG791979	
Lasioglossum pauxillum	MG791983	
Lasioglossum politum	not uploaded to GenBank due to low Sequence quality	
Megachile leachella	ALS-00119	28.05.2018
Megachile maritima	ALN-00139	21.05.2018
Megachile versicolor	ALS-00025	16.06.2017
Megachile willughbiella	ALS-00020	16.06.2017
	ALS-00128	28.05.2018
	ALN-00138	21.05.2018
	ALN-00147	21.05.2018
	ALN-00201	02.07.2018
Melecta albifrons	ALN-00130	19.04.2018
Nomada flavoguttata	ALN-00088	24.04.2017
	ALN-00016	26.05.2017
	MK268694	
	MG845944	
	MG845937	
	MG845938	
	MG845951	
	MG845939	
Nomada fabriciana	ALN-00105	24.04.2017
Nomada flava	ALS-00053	24.04.2017
	ALN-00025	26.05.2017
	ALN-00094	24.04.2017
Nomada goodeniana	ALS-00057	30.04.2017
	ALS-00063	30.04.2017
	ALN-00064	24.04.2017
	ALN-00123	19.04.2018
Nomada lathburiana	ALN-00119	19.04.2018
Nomada marshamella	ALN-00066	24.04.2017
	ALN-00141	21.05.2018
Nomada panzeri	ALS-00090	21.04.2018
Nomada ruficornis	ALN-00091	24.04.2017
Nomada striata	ALN-00070	24.04.2017
	ALN-00075	24.04.2017
Osmia adunca	ALS-00017	16.06.2017

Appendix S2: Diversity Work Bench accession numbers start with ALS or ALN; the remaining numbers are GenBank accessions of DNA barcodes. Physical vouchers were deposited in the Zoologische Staatssammlung Munich.

	ALS-00023	16.06.2017
	ALS-00101	28.05.2018
	ALN-00023	26.05.2017
	ALN-00191	02.07.2018
Osmia aurulenta	ALS-00091	21.04.2018
	ALS-00102	28.05.2018
	ALN-00014	26.05.2017
	ALN-00018	26.05.2017
	ALN-00142	21.05.2018
	ALN-00148	21.05.2018
	ALN-00159	21.05.2018
Osmia bicolor	ALS-00052	24.04.2017
	ALN-00131	19.04.2018
	ALN-00175	21.05.2018
Osmia bicornis	ALS-00070	30.04.2017
	ALN-00067	24.04.2017
Osmia caerulescens	ALS-00092	21.04.2018
	ALN-00157	21.05.2018
Osmia campanularum	observation only	
Osmia florisomnis	MG845942	
Osmia leucomelana	ALS-00014	16.06.2017
	ALS-00016	16.06.2017
	Not uploaded to GenBank due to low Sequence quality	
Osmia mitis	ALN-00165	21.05.2018
Osmia spinulosa	ALS-00037	01.08.2017
	ALS-00127	28.05.2018
	ALS-00130	28.05.2018
	ALN-00166	21.05.2018
	ALN-00194	02.07.2018
Osmia truncorum	ALS-00049	01.08.2017
	ALS-00109	28.05.2018
	ALN-00112	17.08.2017
Sphecodes albilabris	MG845950	
Sphecodes ephippius	MK268696	
	MG845941	
Sphecodes gibbus	MK268700	
Sphecodes hyalinatus	MK268705	
Sphecodes monilicornis	MK268695	
	MK268706	
Stelis punctulatissima	ALS-00131	28.05.2018
Stelis signata	ALN-00045	31.07.2017
Group-level deterimination		
Andrena ovatula group	ALN-00169	21.05.2018
Andrena ovatula group	ALS-00169	02.07.2018
Andrena ovatula group	ALN-00144	21.05.2018
Andrena ovatula group	ALN-00168	21.05.2018
Andrena ovatula group	ALN-00150	21.05.2018
Andrena minutula/subopaca group	ALN-00015	26.05.2017

Appendix S2: Diversity Work Bench accession numbers start with ALS or ALN; the remaining numbers are GenBank accessions of DNA barcodes. Physical vouchers were deposited in the Zoologische Staatssammlung Munich.

	ALN-00099	24.04.2017
	ALN-00101	24.04.2017
	ALN-00167	21.05.2018
	ALS-00088	21.04.2018
	ALN-00193	02.07.2018
Halictus tumulorum group	ALS-00034	01.08.2017
	ALN-00007	26.05.2017
	ALN-00164	21.05.2018
Lasioglossum calceatum group	ALS-00136	26.07.2018
	ALS-00013	16.06.2017
	ALS-00076	30.04.2017
	ALN-00122	19.04.2018
	ALN-00009	26.05.2017
	ALN-00026	31.07.2017
	ALN-00031	31.07.2017
Lasioglossum leucozonium group	ALN-00149	21.05.2018
	ALS-00126	28.05.2018
Lasioglossum morio group	ALN-00034	31.07.2017
	ALS-00036	01.08.2017

M. M. Hofmann and S. S. Renner: **Bee species persistence and increase between 1990 and 2018 in urban protected sites - Appendix S3:** Tables S1 and S2.

Table S1: Coefficient estimates and beta estimate +95% confidence intervals for the effects of the predictor variables in the flight duration (in months) and flight season models (early, late, medium), with presence at T0 (1990s), habitat breadth (narrow: one or habitats vs. broad: three to six), and median flight duration being the reference variables. Confidence intervals were calculated using the "Confint"-function of the package "car" (Fox and Weisberg, 2019). Intervals not overlapping 0 are printed **bold**.

Predictor variable	**Flight duration**	**Flight season**
All sites		
Absence at T0	**2.10 (1.56; 2.65)**	**2.16 (1.62; 2.72)**
Narrow habitat preference	**- 0.71 (- 0.12; - 1.31)**	**- 0.78 (- 1.38; - 0.18)**
Flight duration	0.14 (- 0.02; 0.30)	---
Early flight season	---	0.34 (- 0.82; 1.46)
Late flight season	---	- 0.29 (- 0.98; 0.38)
Allach		
Absence at T0	**2.13 (1.50; 2.83)**	**2.24 (1.60; 2.95)**
Narrow habitat preference	**- 1.06 (- 1.88; - 0.31)**	**- 1.04 (- 1.88; - 0.28)**
Flight duration	0.15 (- 0.13; 0.32)	---
Early flight season	---	- 1.17 (- 3.11; 0.29)
Late flight season	---	- 0.44 (- 1.25; - 0.32)
Virginia Depot		
Absence at T0	**2.18 (1.39; 3.00)**	**2.3 (1.55; 3.12)**
Narrow habitat preference	- 0.011 (- 0.89; 0.84)	- 0.20 (- 1.10; 0.66)
Flight duration	0.095 (- 0.10; 0.30)	---
Early flight season	---	0.015 (- 1.95; 1.48)
Late flight season	---	0.66 (- 0.22; 1.50)
Botanical Garden		
Absence at T0	**2.68 (2.04; 3.38)**	**2.76 (2.11; 3.45)**
Narrow habitat preference	**- 0.97 (- 1.65; - 0.32)**	**- 1.00 (- 1-67; - 0.35)**
Flight duration	- 0.012 (- 0.18; 0.16)	---
Early flight season	---	1.08 (-0.05; 2.14)
Late flight season	---	- 0.060 (- 0.84; 0.69)

Fox J, Weisberg S (2019). An R companion to applied regression, Third edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Table S2: Accuracy of predictions of the presence and absence of species (n = 319) at the investigated sites at T1 (2017/2018) using the predictors presence/absence at T0 (1990s), habitat breadth, flight duration, and flight season, and pairwise interaction terms among them. Model accuracy was calculated as (true positives + true negatives) / total pool.

Models	Classification rate	Incorrect prediction "present" (type I error)	Incorrect prediction "absent" (type II error)
All sites			
Flight duration	245 (77 %)	43 (13 %)	31 (10 %)
Flight season	242 (76 %)	39 (12 %)	38 (12 %)
Allach			
Flight duration	224 (70 %)	12 (4 %)	83 (26 %)
Flight season	229 (72 %)	21 (7 %)	69 (22 %)
Virginia Depot			
Flight duration	193 (61 %)	0 (0%)	126 (39 %)
Flight season	188 (59 %)	1 (0.3 %)	130 (41 %)
Botanical Garden			
Flight duration	243 (76 %)	9 (3 %)	67 (21 %)
Flight season	243 (76 %)	9 (3 %)	67 (21 %)

Chapter 5

Empirical foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, using individual tagging

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Empirical foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, using individual tagging

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Abstract:	Bees require suitably close foraging and nesting sites to minimize travel time and energy expenditure for brood provisioning. Knowing foraging distances in persistent (‘healthy’) populations is therefore crucial for assessing harmful levels of habitat fragmentation. For small bees, such distances are poorly known because of the difficulty of individual tagging and problems with mark-recapture approaches. Using apiarist’s tags and color codes, we individually marked 2689 males and females of four oligolectic and two polylectic species of Osmiini (Megachilidae, genera Chelostoma, Heriades, Hoplitis, Osmia) with body lengths of 6 to 15 mm and long-term stable populations at our study site and then monitored their foraging distances in a 21 ha-large urban garden, where we relied on students and citizen scientists to detect marked bees. Based on 1045 re-sightings, including some by citizen scientists, mean female flight distances ranged from 73 to 121 m and male distances from 59 to 100 m, with maximal distances up to seven times larger. There was a strong correlation between body size and flight distance. The foraging distances observed here by individually tagging small solitary bees suggest that as a rule of thumb, flower strips for supporting such bees should be no further than 150 m apart. Our study also shows that apiarist’s tags applied to wild bees work well in citizen scientists projects and help provide much-needed data on insect traveling distances.

Empirical foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, using individual tagging

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Author declaration: MMH, AF, and SSR designed the experiment, and MH and AF performed the fieldwork. MMH and SSR analyzed the data; MMH and SSR co-wrote the manuscript, and all authors checked the final version.

Abstract Bees require suitably close foraging and nesting sites to minimize travel time and energy expenditure for brood provisioning. Knowing foraging distances in persistent ('healthy') populations is therefore crucial for assessing harmful levels of habitat fragmentation. For small bees, such distances are poorly known because of the difficulty of individual tagging and problems with mark-recapture approaches. Using apiarist's tags and color codes, we individually marked 2689 males and females of four oligolectic and two polylectic species of Osmiini (Megachilidae, genera *Chelostoma, Heriades, Hoplitis, Osmia*) with body lengths of 6 to 15 mm and long-term stable populations at our study site and then monitored their foraging distances in a 21 ha-large urban garden, where we relied on students and citizen scientists to detect marked bees. Based on 1045 re-sightings, including some by citizen scientists, mean female flight distances ranged from 73 to 121 m and male distances from 59 to 100 m, with maximal distances up to seven times larger. There was a strong correlation between body size and flight distance. The foraging distances observed here by individually tagging small solitary bees suggest that as a rule of thumb, flower strips for supporting such bees should be no further than 150 m apart. Our study also shows that apiarist's tags applied to wild bees work well in citizen scientists projects and help provide much-needed data on insect traveling distances.

Key-words: Foraging distances; individual tagging; Anthophila; body size; urban garden; solitary bees; Megachilidae

Introduction

Wild bees are pollinators of high conservation concern. One reason is the relatively small spatial and temporal scale of their life cycles, habitat ranges, and nesting behaviors (Westrich 1996, Gathmann and Tscharntke 2002, Greenleaf et al. 2007, Franzén et al. 2009, Zurbuchen et al. 2010a, Wood et al. 2016), traits that make them vulnerable to landscape fragmentation. Bees are central-place foragers, with females shuttling between foraging sites and nests to provide brood cells with pollen and nectar, and the distance between these resources largely determines bees' reproductive success (Zurbuchen et al. 2010b). The further nest and food sources are apart, the higher bees' energetic and reproductive costs (Williams and Tepedino 2003, Zurbuchen et al. 2010b). Thus, in the European solitary species *Hoplitis adunca* and *Chelostoma rapunculi* (Megachilidae), the number of brood cells provisioned per time decreased by a third to almost half (31% or 46%) when foraging flight distances were experimentally increased by 200 or 500 m (Zurbuchen et al. 2010b). In the solitary *Megachile rotundata*, 74% fewer offspring were produced when flight distances increased by 150 m (Peterson and Roithberg 2006). Increased flight requirements reduce adult lifespan (Schmid-Hempel and Wolf 1988), and absences from the nest increase brood cell parasitism, as most parasites enter the nest while the nest owner is away (Seidelmann 2006). Proximity of nesting and foraging sites is therefore crucial for the reproductive success of bees, and to predict the effects of habitat enhancements for conservation purposes (Nicholson et al. 2019), we need data on suitable distances that would help a maximum number of wild bees.

Bee foraging distances have been investigated with a range of methods, including microsatellite DNA markers to determine to which colony a bumblebee worker belongs (Chapman et al. 2003, Knight et al. 2005), pollen analysis to check the content of pollen loads or brood cells for plants occurring at known distances (Williams and Tepedino 2003, Beil et al. 2008), and radio tracking for species large enough for carrying a transmitter (Carreck et al. 1999). The two most widely used methods are translocation experiments (e.g., Gathmann and Tscharntke 2002) and mark-recapture studies (e.g., Osborne et al. 2008, Wolf and Moritz 2008, Franzén et al. 2009, Zurbuchen et al. 2010a). In translocation experiments, bees are removed from their nest and released at increasing distances until no more returnees are recorded at the nesting sites. Such experiments assume that bees will only be able to find the way back to their nests as long as they know the foraging area. Mark-recapture studies involve marking, releasing, and recapturing bees.

All these approaches aim to find maximal foraging distances, which are key to inferring body size/distance relationships. A linear regression model that included body length and maximum foraging distance in 17 European solitary bees showed that distance roughly triples as body length doubles (Gathmann and Tscharntke 2002), with the smallest species studied being *Chelostoma florisomne,* the largest the European carpenter bee *Xylocopa violacea.* A non-linear regression analysis of the maximum foraging distances of 62 species worldwide instead regressed intertegular distance on distance and found that larger bees had disproportionately larger foraging distances than smaller bees (Greenleaf et al. 2007).

Maximum foraging distances can be treated as a species-level trait, i.e., the result of the averaged physiological and mechanical capacities of a species. In the present study, we instead focus on mean foraging distances in stable populations, using a mark-release-resighting approach on large numbers of individuals. Such data are needed to help conservation measures, such as the planting of flower strips or islands. Of 436 Central European species, 92% are between 4.5 and 13.5 mm long (Hofmann et al. 2019). We therefore selected six small species to test how their *average* foraging distances in a flower-rich setting would compare to the maximum foraging distances of 150–600 m for 5.5 to 12 mm-long bees predicted from the above regression analysis (Gathmann and Tscharntke 2002). The population sizes of the six species at our study site have either not changed since 1997–1999 or, in the case of two thermophilic species (*Hoplitis adunca, Osmia cornuta*), increased (Hofmann et al. 2018: Table S1). Stable or increasing populations over 20 years suggest that foraging distances required at the study site are optimal, allowing a test of the suggested 150–600 m rule.

Materials and methods

STUDY SITE AND SPECIES

The study took place in the Munich Botanic Garden during the 2017 and 2018 bee foraging seasons (March and August). The garden opened in May 1914, covers about 21 ha, and borders on the 210-ha-large Nymphenburg Palace Park at 48° 09′45′′N, 11° 30′ 06′′E and 500 m above sea level. It is home to 106 bee species whose abundances have been recorded in 1997–1999 and again in 2016/2017 by repeated monitoring walks (Hofmann et al. 2018). Several cavity nest boxes for Megachilidae are located in the garden, with the larger ones harboring well-established populations. The botanical garden provides a flower-rich habitat with both flower beds and near-natural meadows blooming throughout the year.

We investigated six above-ground nesting species of Osmiini (Megachilidae) with different flight times (Table 1), namely *Chelostoma florisomne*. *C. rapunculi*, *Heriades truncorum*, *Hoplitis adunca*, *Osmia cornuta*, and *O. bicornis*. All Megachilidae are solitary bees, and the species we investigated are widespread in Europe, Northern Africa and Asia (Scheuchl and Willner 2016). While the two *Osmia* species are polylectic (meaning they forage on a taxonomic variety of plants; Cane and Sipes 2006), the others are oligolectic (they collect pollen at only a few plant families), with *Chelostoma florisomne* specialized on *Ranunculus* (Ranunculaceae), *C. rapunculi* on Campanulaceae, *Heriades truncorum* on Asteraceae, and *Hoplitis adunca* on *Echium* (Boraginaceae). *Heriades adunca* was tagged in 2017, *Chelostoma florisomne*, *C. rapunculi*, *Heriades truncorum*, and *Osmia bicornis* in 2018, and *O. cornuta* in both 2017 and 2018.

BEE MARKING AND TRACKING

Bees were captured with an insect net at the cavity nest boxes (shown on the garden map in Fig. S1), and the larger species *Osmia cornuta, O. bicornis,* and *Hoplitis adunca* were marked using apiarist's tags (Fig. 1). Female bees were mechanically immobilized in a queen marking tube (Fig. S2); male bees were held between the experimenter's fingers such that legs and antennae were hidden from the glue and the mesonotum was freely accessible (Fig. S3). A small amount of nontoxic shellac glue (Liebert 1986) was placed on the bee's thorax with a fine metal stylus and the colored, consecutively-numbered and slightly concave circular apiarist plastic plates (Opalith Classic from Holtermann, Brockel, Germany) were then attached. Each plate had an average weight of 1.3 mg and a diameter of 2.5 mm. For each species, several colors were used (allowing identification of sex and marking location). As the flight times of the species only partly overlap (Table 1), the same colors were used for *O. cornuta* and *H. adunca*, but different colors were used for the two *Osmia* species. Each individual was identifiable by its number/color combination.

The smaller species *Chelostoma florisomne*, *C. rapunculi* and *Heriades truncorum* with an intertegular distance < 2.5 mm were marked with paint, as apiarists' tags were too big for them (Fig. 1). They were cold anesthetized and then marked with two dots of paint. One dot coded for the cavity nest box, one for species and sex. Bees of the same species and sex marked at the same nesting site were therefore indistinguishable in the field. Bees were released directly after being marked, which took two to three minutes per individual.

We searched the garden for bees during two to three hours per day when the weather was warm and dry, and used photography (usually by smartphone) for documenting labeled bees during floral visits. For the oligolectic species, surveys targeted the relevant food plants. For the polylectic species, the entire garden was searched, and we used a citizen science approach involving garden visitors to increase sighting probability. During the outdoor season (April to October), the Munich Botanical Garden has about 2000 visitors/day. We used paper hand-outs, posters near the Garden's two public entrances, and the Garden's webpage to inform visitors about our project, and visitors were then given three options for informing us about bee sightings, paper forms available at the entrance, a dedicated email account (wildbienen@bio.lmu.de), and oral reports. Visitors only needed to report the color of the tag, its number and where the bee was seen; no special knowledge of bee species or the individual bee's sex was necessary for a 'successful' sighting. For the smartphone pictures, GPS tracking was usually available, for oral reports we were able to ask the visitors to show us the location directly if it was unclear, and for the reports via form we only used unambiguous location records, where the position of the bee was marked in the garden plan included on the sighting form.

STATISTICAL ANALYSES

Since the nest locations for all individuals included in the analysis were known, we were able to measure the beeline from the respective cavity next box to the most distant site where the respective bee was sighted on a flower using the measuring tool of Google Earth. One sighting of a tagged *Osmia cornuta* female from outside the garden was an outlier, and we therefore ran analyses with and without this record. Since we could not number-tag the individuals of smallest species (*Chelostoma florisomne, C. rapunculi* and *Heriades truncorum*), we cannot exclude the repeated observation of single individuals of these species. We applied a generalized mixed effect model, using the ´glmer´ function in the Package 'lme4' (Bates et al. 2015), and compared its results with a normal linear regression model ('lm'). All statistical calculations were made in R 3.4.3 (R Core Team 2017). The code we used is appended to Table S1.

Results

RECOVERY RATES OF TAGGED BEES; COMPARISON OF 2017 AND 2018

Male and female body lengths, flight periods, and foraging preferences of the six investigated species are shown in Table 1. We individually marked a total of 2689 bees, including 1808 females and 881 males, of which 1045 were re-sighted, some many times (Table 2; Table S1 shows all flight distance records). The small *Chelostoma* species were the most difficult to re-observe, with only 5.4% of *C. florisomne* females, 4% *C. rapunculi* females, and 4.8% *C. rapunculi* males sighted at flowers after marking. By contrast, we sighted 22% of the tagged *Heriades truncorum* females on flowers (Fig. 1), 56% of tagged *Hoplitis adunca* females (but only 6.5% of the males) at their *Echium* food plants, and 86.8% of the *Osmia bicornis* females and 55.2% of the males at the cavity nest boxes. In all species, recovery rates for males were lower than for females.

Observation rates for *Osmia cornuta*, the only species investigated in both years, at nest boxes for females were 80% in 2017 and 87.2% in 2018 and for males 67.1% in 2017 and 67.3% in 2018, and at flowers for females, 23.5% in 2017 and 9.7% in 2018 and for males 14.4% in 2017 and 10.6% in 2018. For *Osmia bicornis*, 24 of 37 tagged females were observed not only on flowers but also at a sand pile at 138 m distance from the nest boxes, where they collected earth for closing their nests. The nectar-foraging distances of *O. bicornis* males, which did not collect sand, were similar to those of the females (Table 2).

For the two *Osmia* species, we also had data from the citizen science approach. In 2017, 77 records of *O. cornuta* resulted from the citizen science approach (7 on a questionnaire, 14 sent in via emails, and 56 via personal communication), and 72 of these could be used for the distance analysis. In 2018, there were 76 records for this species by citizen scientist (35 on a questionnaire, 2 sent in emails, and 39 via personal communication), of which 70 were usable. For *O. bicornis*, 49 records were made by the garden visitors (22 on the questionnaire, 2 via email, and 25 via personal communication).

FLIGHT DISTANCES AND BODY SIZE

Mean female flight distances were between 73 and 121 m (Fig. 2A; standard deviations and sample sizes in Table 2), and mean male flight distances between 59 and 100 m (Table 2), but sample sizes for males were low (e.g., n = 5 for *Chelostoma rapunculi*). The maximum female flight distances found were 174 m for *Chelostoma florisomne* and 724 m for an *Osmia cornuta* reported from outside the Botanical Garden by a citizen scientist (Table 2). We found a positive correlation between flight distance and body length with both a generalized mixed-effects model (AIC = 2326.24) and the linear regression model (p<2e-16, AIC = 2325.13, Fig. 2B), using square-root transformed flight distance values (and with or without the *O. cornuta* 724 outlier). Square-root-transformed flight distances were normally distribution (Fig. S4A), but body size was not (Fig. S4B).

Discussion

To our knowledge, this is the largest tagging study of flight distances in solitary small bees in a natural setting with stable populations. Studies of foraging distances in solitary bees have generally been motivated by interest in crop pollination, while our study focused on gathering data on foraging distances in a setting on hundreds of non-crop flowering plants. The successful tracking of individually marked bees achieved in this study -- ‘tracking’ because marked bees were not recaptured, only re-observed -- was achieved through numerous search hours put in by students and citizen scientists. In this way, we obtained foraging distances for 1808 females and 881 males from six bee species of body lengths between 6 and 15 mm in a flower-rich environment and discovered that these bees foraged at average distances from the nest between 75 and 125 m. Maximum distances were up to seven times larger than mean flight distances (Table 2), similar to findings in other studies (Gathmann and Tscharntke 2002, Zurbuchen et al. 2010a,b). Even in the relatively large semi-social *Bombus terrestris*, 40% of the workers forage within a radius of 100 m around their nests (Wolf and Moritz 2008).

Bee foraging is highly context-dependent (e.g., Osborne et al. 2008, Pope and Jha 2018). For example, most of the tagged females of *Osmia bicornis* collected sand from a pile 138 m from their nesting site, and most tagged females of *Hoplitis adunca*, a species oligolectic on *Echium* pollen, were observed on exactly these plants in the garden. However, male flight distances in these species were similar even though males do not collect sand or pollen.

IMPLICATIONS

Our results support the correlation between body size and flight distance found in two previous studies (Gathmann and Tscharntke 2002: 16 Central European species; Greenleaf et al. 2007: 62 species worldwide), despite the many different methods used to infer flight distances, such as translocation experiments, genetic marker studies, and mark-recapture experiments. The body size/flight distance correlation implies that females of Central European bees, most of which are between 4.5 and 13.5 mm long (Hofmann et al. 2019), usually do not forage further than 125 to 150 meters from the nest (Gathmann and Tscharntke 2002: 150 to 600 m; our Table 2: 125 m). Despite the six or seven times larger flight distances that small bees can achieve (Gathmann and Tscharntke 2002, Zurbuchen et al. 2010a,b, this study), long flights between nests and floral resources have fitness costs in terms of lower offspring number and increased brood parasitism (Peterson and Roithberg 2006, Seidelmann 2006, Zurbuchen et al. 2010b). The persistence of populations therefore requires flower patches and nesting sites at suitable distances, for which we propose a rule-of-thumb of 150 m. This rule of thumb could be used by conservation practitioners planning urban greening measures. Implementing such simple habitat enhancements as flower strips with the appropriate spatial distribution, can greatly increase the connectivity of foraging sites and help bee conservation (Hofmann and Renner, in review).

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Conflict statement

The authors declare no conflict of interest.

Data Accessibility Statement

All data analysed in this study are shown in Table S1, namely the flight distances for males and females of the six species studied, with year of observation given for *Osmia cornuta* studied in 2017 and 2018.

References

Amiet, F., Herrmann, M., Müller, A., and Neumeyer, R. 2004. Fauna Helvetica 9. Apidae 4: *Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis*. Centre Suisse de Cartographie de la Faune (CSCF).

Bates, D., Maechler, M., Bolker, B., Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software 67*: 1- 48.

Beil, M., Horn, H., and Schwabe, A. 2008. Analysis of pollen loads in a wild bee community (Hymenoptera: Apidae) – a method for elucidating habitat use and foraging distances. *Apidologie 39*: 56-467.

Carreck, N. L., Osborne, J. L., Capaldi, E. A., and Riley, J. R. 1999. Tracking bees with radar. *Bee World 80*: 124-131.

Chapman, R. E., Wang, J., and Bourke, A. F. G. 2003. Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. *Molecular Ecology 12*: 2801-2808.

Cane, J. H. and Sipes, S. S. 2006. Characterizing floral specialization by bees: Analytical methods and a revised lexicon for oligolecty. PP. 99-122 in Plant–pollinator interactions: From specialization to generalization (eds. Waser, N. M. and Ollerton, J.). The University of Chicago Press, Chicago, USA.

Franzén, M., Larsson, M., and Nilsson, S. G. 2009. Small local population sizes and high habitat patch fidelity in a specialised solitary bee. *Journal of Insect Conservation 13*: 89-95.

Gathmann, A., and Tscharntke, T. 2002. Foraging ranges of solitary bees. *Journal of Animal Ecology 71*: 757-764.

Greenleaf, S. S., Williams, N. M., Winfree, R., and Kremen, C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia 153*: 589-596.

Hofmann, M. M., Fleischmann, A., and Renner, S. S. 2018. Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. *Oecologia 187*: 701–706.

Hofmann, M. M. and S. S. Renner. One year-old flower strips already support a quarter of a city's bee species. (Journal of Hymenoptera Research, submitted, 22 Oct.)

Hofmann, M. M., Zohner, C.M. and Renner, S.S. 2019. Narrow habitat breadth and late-summer emergence increase extinction vulnerability in Central European bees. *Proceedings of the Royal Society B*, https://doi.org/10.1098/rspb.2019.0316

Knight, M. E., Martin, A. P., Bishop, S., Osborne, J. L., Hale, R. J., Sanderson, R. A., and Goulson, D. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology 14*: 1811-1820.

Liebert, M. A. 1986. Final report on the safety assessment of shellac. *Journal of the American College of Toxicology* 5: 309-327.

Nicholson, C. C., Ricketts, T. H., Koh, I., Smith, H.G., Lonsdorf, E. V., and Olsson, O. 2019. Flowering resources distract pollinators from crops: Model predictions from landscape simulations. *Journal of Applied Ecology* 56: 618-628.

Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., ... and Sanderson, R. A. 2008. Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology 77*: 406-415.

Peterson, J. H., and Roitberg, B. D. 2006. Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee, *Megachile rotundata*. *Behavioral Ecology and Sociobiology* 59: 589-596.

Pope, N. S., and Jha, S. 2018. Seasonal food scarcity prompts long-distance foraging by a wild social bee. *The American Naturalist* 19: 45-57.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Scheuchl, E., and Willner, W. 2016. *Taschenlexikon der Wildbienen Mitteleuropas: Alle Arten im Porträt*. Quelle et Meyer Verlag, Wiebelsheim.

Schmid-Hempel, P., and Wolf, T. 1988. Foraging effort and life span of workers in a social insect. *Journal of Animal Ecology 57*: 509-521.

Seidelmann, K. 2006. Open-cell parasitism shapes maternal investment patterns in the Red Mason bee *Osmia rufa*. *Behavioral Ecology 17*: 839-848.

Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. In: Matheson, S., Buchmann, S.L., O'Toole, C., Westrich, P. and Williams, I.H. (eds.): The Conservation of Bees. *Linnean Society Symposium Series 18*: 1-16.

Williams, N. M., and Tepedino, V. J. 2003. Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee *Osmia lignaria*. *Behavioral Ecology 14*: 141-149.

Wolf, S., and Moritz, R. F. 2008. Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae). *Apidologie 39*: 419-427.

Wood, T. J., Holland, J. M., Goulson, D. 2016. Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology* 54: 323-333.

Zurbuchen, A., Bachofen, C., Müller, A., Hein, S., and Dorn, S. 2010a. Are landscape structures insurmountable barriers for foraging bees? A mark-recapture study with two solitary pollen specialist species. *Apidologie 41*: 497-508.

Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S., and Dorn, S. 2010b. Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology 79*: 674-681.

Tables and Figures

Table 1. The six studied species (tribe Osmiini, family Megachilidae), their male and female body sizes, flight periods, and foraging preferences (Amiet et al. 2004). The population abundance categories of these species in the 21 ha-large Munich Botanical Garden have either not changed since 1997-1999 or, in the case of *H. adunca* and *O. cornuta*, increased (Hofmann et al. 2018: Table S1).

Species	**Body size [mm]**	**Flight period**	**Foraging preference**
Chelostoma florisomne	♂: 7 - 9 mm ♀: 7 - 8 mm	April - June	Oligolectic on Ranunculaceae
Chelostoma rapunculi	♂: 8 – 10 mm ♀: 8 – 10 mm	May - September	Oligolectic on *Campanula*
Heriades truncorum	♂: 5 – 7 mm ♀: 6 – 7 mm	May - October	Oligolectic on Asteraceae
Hoplitis adunca	♂: 11 – 13 mm ♀: 11 – 13 mm	April - September	Oligolectic on *Echium*
Osmia cornuta	♂: 11 – 13 mm ♀: 12 – 15 mm	February - June	Polylectic
Osmia bicornis	♂: 8 – 12 mm ♀: 8 – 12 mm	March- July	Polylectic

Table 2. Mean and maximum foraging flight distances of individually tagged solitary bees in the Munich Botanical Garden in 2017 and 2018. N/A, not applicable, refers to small sample sizes. The 1045 re-sightings below include sightings of the same individual on different foraging flights; Table S1 shows maximum distances. The asterisk marks a single individual found by a citizen scientist outside the garden; we calculated regressions with and without this outlier.

Species	Number of marked individuals	Number of sightings at nesting site	Number of sightings at flowers	Mean flight distances	Standard deviation	Maximum flight distance
Chelostoma florisomne	♀: 221		♀: 12	82 m	58.7	174 m
	♂: 0	N/A		N/A	N/A	N/A
	total: 221					
Chelostoma rapunculi	♀: 248		♀: 10	104 m	45.2	178 m
	♂: 103	N/A	♂: 5	59 m	34.5	119 m
	total: 351					
Heriades truncorum	♀: 534		♀: 118	73 m	62.6	298 m
	♂: 0	N/A		N/A	N/A	N/A
	total: 534					
Hoplitis adunca	♀: 277	♀: 100	♀: 127	112 m	77.3	287 m
	♂: 92			N/A	N/A	N/A
	total: 369					
Osmia bicornis	♀: 136	♀: 118	♀: 42	121 m	44.6	250 m
	♂: 38	♂: 21	♂: 6	100 m	40.3	151 m
	total: 174					
Osmia cornuta	2017:					
	♀: 170	♀: 136	♀: 40	106 m	107.5	724* m
	♂: 201	♂: 135	♂: 29	96 m	39.0	225 m
	total: 371					
	2018:					
	♀: 320	♀: 279	♀: 31	107 m	67.9	226 m
	♂: 349	♂: 235	♂: 37	77 m	52.5	215 m
	total: 669					

Figure legends

Figure 1. Marked individuals of (A) *Chelostoma florisomne*, (B) *C. rapunculi*, (C) *Heriades truncorum*, (D) *Hoplitis adunca*, (E) *Osmia bicornis*, and (F) *Osmia cornuta*

Figure 2. (A) Mean flight distance and standard deviation for each species and body size. (B) Linear regression of flight distance on square-root transformed body sizes of (from left to right) *Heriades truncorum, Chelostoma florisomne, C. rapunculi, Osmia bicornis, Hoplitis adunca,* and *Osmica cornuta*.

Online enhancements:

Table S1. Flight distances for males and females of the six species, with year of observation given for *Osmia cornuta* studied in 2017 and 2018. Body sizes from Amiet et al. (2004) and Scheuchl and Willner (2016). The code used for analyzing the data in R is appended below the table.

Figure S1. Garden plan with the nesting sites of the tagged species (modified from http://www.botmuc.de/en/garden/garden_map.html)

Figure S2. Marking of an *Osmia cornuta* female (photos: J. Kirndorfer). (a-b) A female caught with an insect net is transferred to the queen-marking tube and (c-d) pushed with the plunger to immobilize it. (e-f) A stylus is used to put glue on the mesonotum. (g-h) The numbered color plate is attached and (i) the bee released.

Figure S3. Marking of an *Osmia cornuta* male (photos: J. Kirndorfer). (a) Application of the glue and (b, c) attaching of the apiarists' tag. (d) A labeled male ready to take off.

Figure S4. (A) Histogram of square-root transformed flight distances. (B) Histogram of body sizes (not normally distributed).

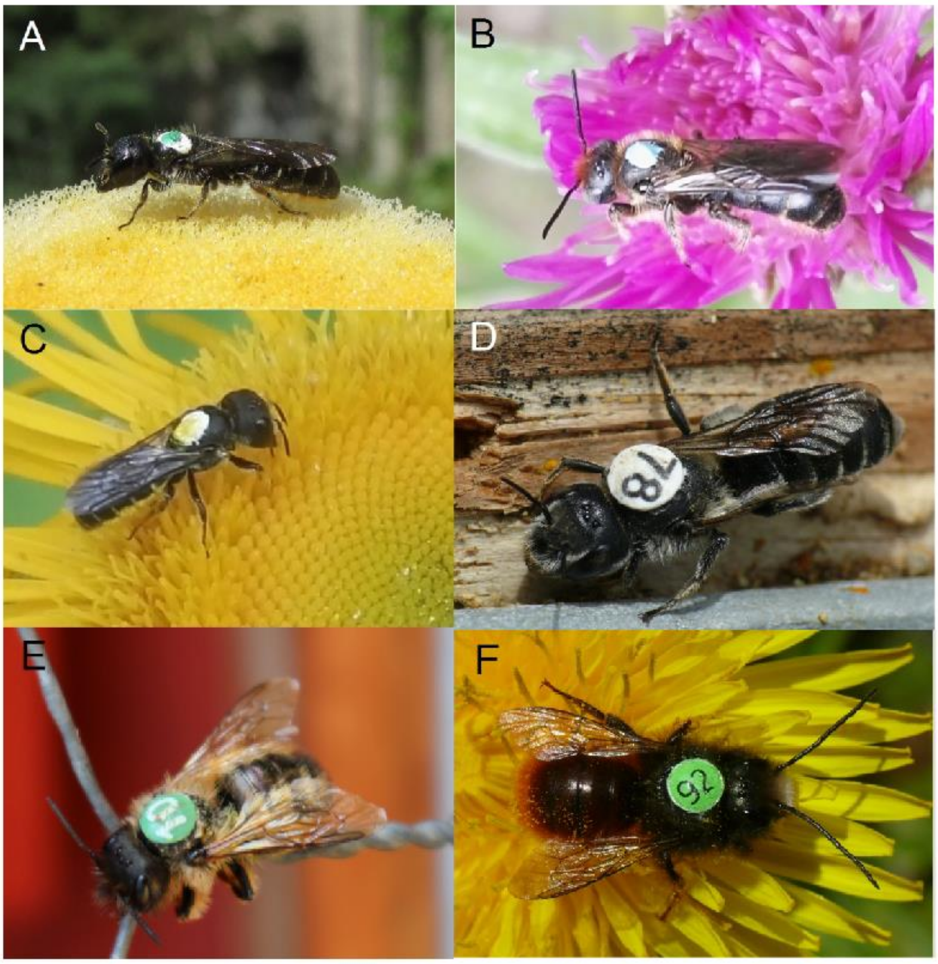


Figure 1

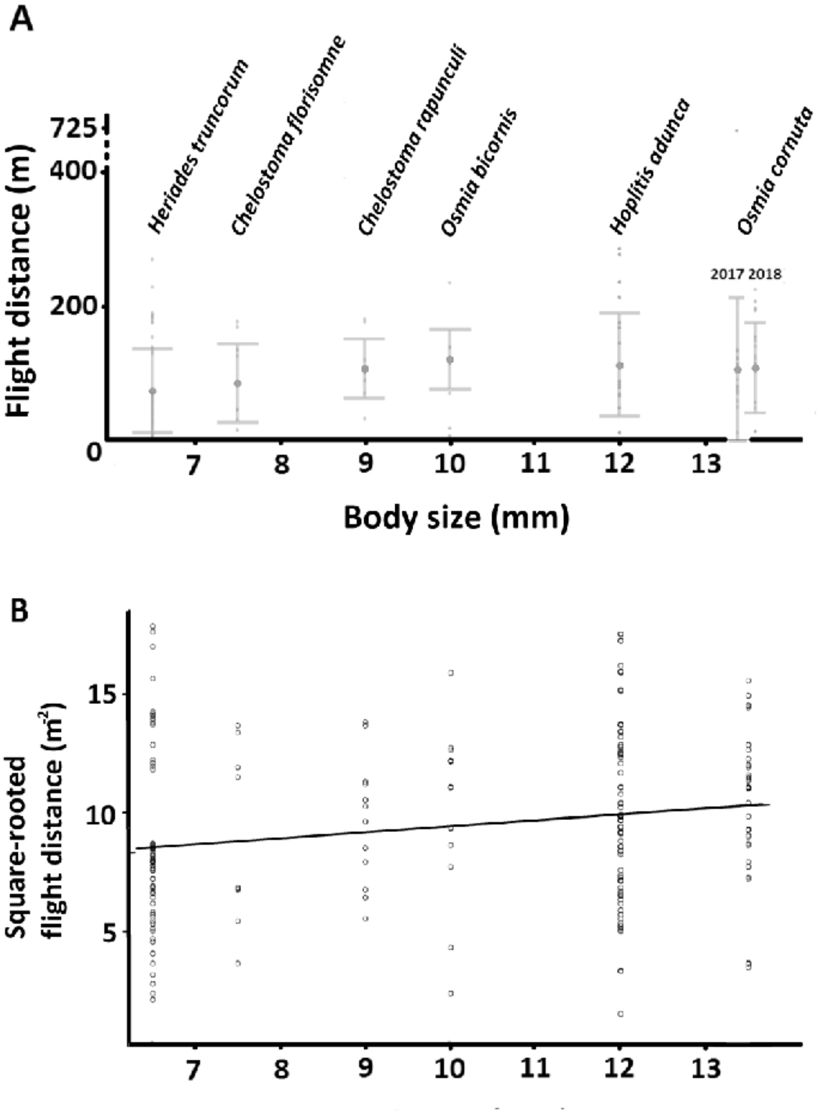


Figure 2

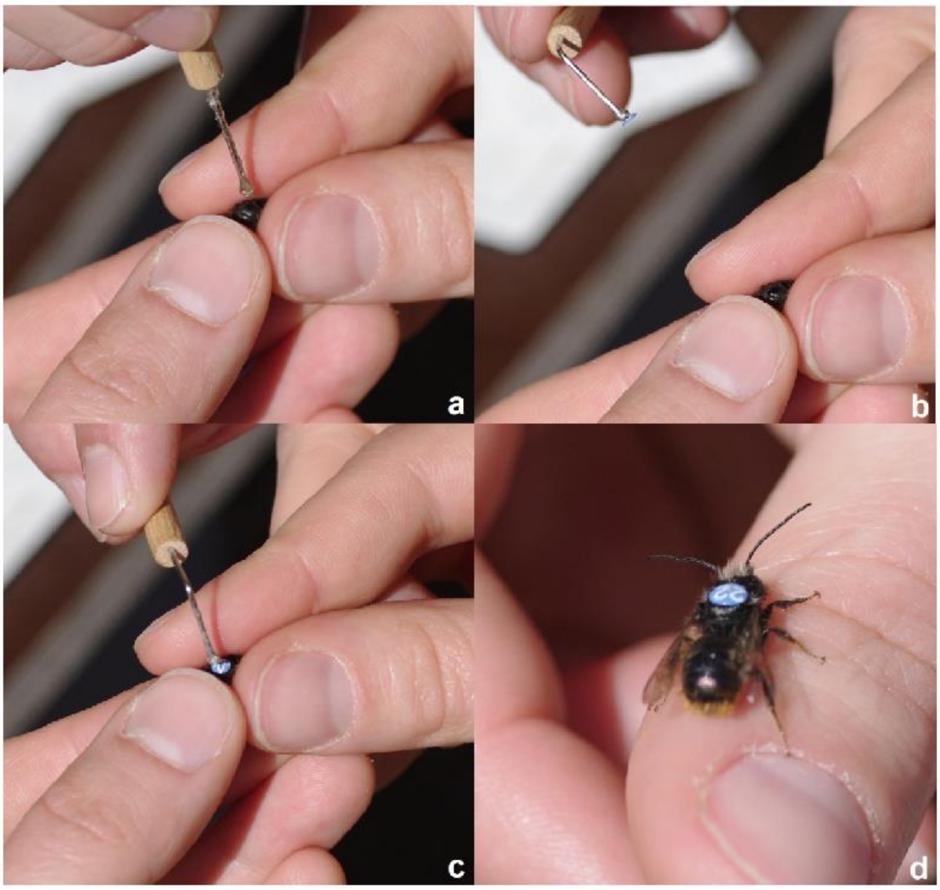
1134x1464mm (72 x 72 DPI)

Supplementary material from

Empirical foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, using individual tagging


Map
of the Botanical Garden
Munich-Nymphenburg
Way to the Nymphenburg Palace and Park
South entrance
Rhododendrons
Endangered flora
Systematic garden
Economic plants
WC
Ferns
Pump house from 1910
S
W
O
N
Roses
Cafeteria
Lake
Spring garden
Special habitats
Deciduous trees
Alpine plants
Moor
Hortus conclusus
Alpine house
Steppe
Heath
Ornamentals
Information on biotic interactions
Greenhouses
Iris garden
Conifers
Over-wintering hall
Botanical institute
Tickets, Shop
P
Main entrance: Menzinger Straße 65


a
b
c
d
e
f
g
h
i


a
b
c
d
6C

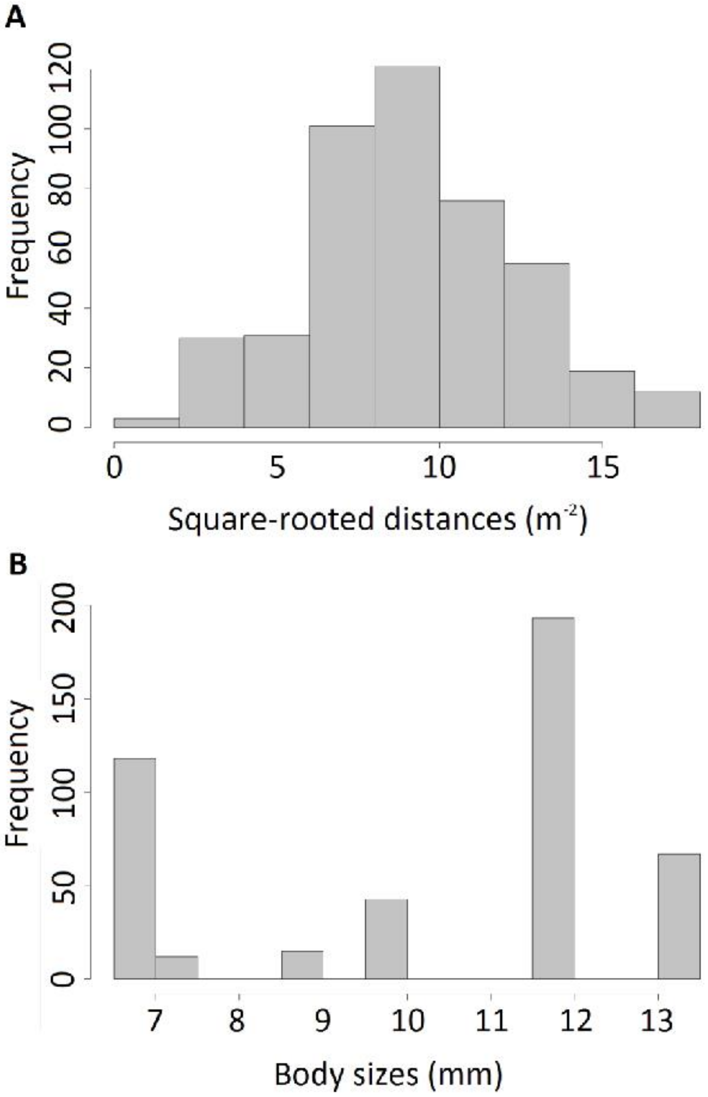

A
Frequency
0
20
40
60
80
100
120
0
5
10
15
Square-rooted distances (m-2)
B
Frequency
0
50
100
150
200
7
8
9
10
11
12
13
Body sizes (mm)

Table S1: Flight distances for males and females of the six species, with year of observation given for *Osmia cornuta* studied in 2017 and 2018. Body sizes from Amiet et al. (2004) and Scheuchl and Willner (2016). The code for analyzing these data in R is appended below the table.

Species	Sex	Flight distance*	Size range	Size mean
Chelostoma florisomne	W	12	7.0-8.0	7.5
Chelostoma florisomne	W	27	7.0-8.0	7.5
Chelostoma florisomne	W	42	7.0-8.0	7.5
Chelostoma florisomne	W	43	7.0-8.0	7.5
Chelostoma florisomne	W	174	7.0-8.0	7.5
Chelostoma florisomne	W	43	7.0-8.0	7.5
Chelostoma florisomne	W	43	7.0-8.0	7.5
Chelostoma florisomne	W	43	7.0-8.0	7.5
Chelostoma florisomne	W	123	7.0-8.0	7.5
Chelostoma florisomne	W	132	7.0-8.0	7.5
Chelostoma florisomne	W	132	7.0-8.0	7.5
Chelostoma florisomne	W	167	7.0-8.0	7.5
Chelostoma rapunculi	M	42	8.0-10.0	9
Chelostoma rapunculi	M	58	8.0-10.0	9
Chelostoma rapunculi	M	38	8.0-10.0	9
Chelostoma rapunculi	M	38	8.0-10.0	9
Chelostoma rapunculi	M	119	8.0-10.0	9
Chelostoma rapunculi	W	86	8.0-10.0	9
Chelostoma rapunculi	W	86	8.0-10.0	9
Chelostoma rapunculi	W	117	8.0-10.0	9
Chelostoma rapunculi	W	174	8.0-10.0	9
Chelostoma rapunculi	W	178	8.0-10.0	9
Chelostoma rapunculi	W	28	8.0-10.0	9
Chelostoma rapunculi	W	67	8.0-10.0	9
Chelostoma rapunculi	W	98	8.0-10.0	9
Chelostoma rapunculi	W	103	8.0-10.0	9
Chelostoma rapunculi	W	103	8.0-10.0	9
Heriades truncorum	W	4	6.0-7.0	6.5
Heriades truncorum	W	4	6.0-7.0	6.5
Heriades truncorum	W	5	6.0-7.0	6.5
Heriades truncorum	W	7	6.0-7.0	6.5
Heriades truncorum	W	7	6.0-7.0	6.5
Heriades truncorum	W	9	6.0-7.0	6.5
Heriades truncorum	W	9	6.0-7.0	6.5
Heriades truncorum	W	19	6.0-7.0	6.5
Heriades truncorum	W	12	6.0-7.0	6.5
Heriades truncorum	W	15	6.0-7.0	6.5
Heriades truncorum	W	15	6.0-7.0	6.5
Heriades truncorum	W	19	6.0-7.0	6.5
Heriades truncorum	W	19	6.0-7.0	6.5
Heriades truncorum	W	20	6.0-7.0	6.5

Heriades truncorum	W	23	6.0-7.0	6.5
Heriades truncorum	W	24	6.0-7.0	6.5
Heriades truncorum	W	26	6.0-7.0	6.5
Heriades truncorum	W	26	6.0-7.0	6.5
Heriades truncorum	W	27	6.0-7.0	6.5
Heriades truncorum	W	29	6.0-7.0	6.5
Heriades truncorum	W	30	6.0-7.0	6.5
Heriades truncorum	W	30	6.0-7.0	6.5
Heriades truncorum	W	30	6.0-7.0	6.5
Heriades truncorum	W	31	6.0-7.0	6.5
Heriades truncorum	W	35	6.0-7.0	6.5
Heriades truncorum	W	35	6.0-7.0	6.5
Heriades truncorum	W	38	6.0-7.0	6.5
Heriades truncorum	W	40	6.0-7.0	6.5
Heriades truncorum	W	40	6.0-7.0	6.5
Heriades truncorum	W	41	6.0-7.0	6.5
Heriades truncorum	W	41	6.0-7.0	6.5
Heriades truncorum	W	44	6.0-7.0	6.5
Heriades truncorum	W	44	6.0-7.0	6.5
Heriades truncorum	W	44	6.0-7.0	6.5
Heriades truncorum	W	59	6.0-7.0	6.5
Heriades truncorum	W	59	6.0-7.0	6.5
Heriades truncorum	W	48	6.0-7.0	6.5
Heriades truncorum	W	59	6.0-7.0	6.5
Heriades truncorum	W	59	6.0-7.0	6.5
Heriades truncorum	W	59	6.0-7.0	6.5
Heriades truncorum	W	48	6.0-7.0	6.5
Heriades truncorum	W	48	6.0-7.0	6.5
Heriades truncorum	W	48	6.0-7.0	6.5
Heriades truncorum	W	48	6.0-7.0	6.5
Heriades truncorum	W	53	6.0-7.0	6.5
Heriades truncorum	W	53	6.0-7.0	6.5
Heriades truncorum	W	53	6.0-7.0	6.5
Heriades truncorum	W	53	6.0-7.0	6.5
Heriades truncorum	W	54	6.0-7.0	6.5
Heriades truncorum	W	54	6.0-7.0	6.5
Heriades truncorum	W	56	6.0-7.0	6.5
Heriades truncorum	W	56	6.0-7.0	6.5
Heriades truncorum	W	56	6.0-7.0	6.5
Heriades truncorum	W	56	6.0-7.0	6.5
Heriades truncorum	W	56	6.0-7.0	6.5
Heriades truncorum	W	59	6.0-7.0	6.5
Heriades truncorum	W	59	6.0-7.0	6.5
Heriades truncorum	W	43	6.0-7.0	6.5
Heriades truncorum	W	43	6.0-7.0	6.5
Heriades truncorum	W	43	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5

Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	58	6.0-7.0	6.5
Heriades truncorum	W	60	6.0-7.0	6.5
Heriades truncorum	W	60	6.0-7.0	6.5
Heriades truncorum	W	62	6.0-7.0	6.5
Heriades truncorum	W	62	6.0-7.0	6.5
Heriades truncorum	W	62	6.0-7.0	6.5
Heriades truncorum	W	63	6.0-7.0	6.5
Heriades truncorum	W	63	6.0-7.0	6.5
Heriades truncorum	W	66	6.0-7.0	6.5
Heriades truncorum	W	66	6.0-7.0	6.5
Heriades truncorum	W	66	6.0-7.0	6.5
Heriades truncorum	W	66	6.0-7.0	6.5
Heriades truncorum	W	66	6.0-7.0	6.5
Heriades truncorum	W	70	6.0-7.0	6.5
Heriades truncorum	W	70	6.0-7.0	6.5
Heriades truncorum	W	70	6.0-7.0	6.5
Heriades truncorum	W	68	6.0-7.0	6.5
Heriades truncorum	W	68	6.0-7.0	6.5
Heriades truncorum	W	68	6.0-7.0	6.5
Heriades truncorum	W	66	6.0-7.0	6.5
Heriades truncorum	W	67	6.0-7.0	6.5
Heriades truncorum	W	67	6.0-7.0	6.5
Heriades truncorum	W	67	6.0-7.0	6.5
Heriades truncorum	W	67	6.0-7.0	6.5
Heriades truncorum	W	67	6.0-7.0	6.5
Heriades truncorum	W	69	6.0-7.0	6.5
Heriades truncorum	W	69	6.0-7.0	6.5
Heriades truncorum	W	69	6.0-7.0	6.5
Heriades truncorum	W	130	6.0-7.0	6.5
Heriades truncorum	W	133	6.0-7.0	6.5
Heriades truncorum	W	139	6.0-7.0	6.5
Heriades truncorum	W	136	6.0-7.0	6.5
Heriades truncorum	W	136	6.0-7.0	6.5
Heriades truncorum	W	154	6.0-7.0	6.5
Heriades truncorum	W	175	6.0-7.0	6.5
Heriades truncorum	W	177	6.0-7.0	6.5
Heriades truncorum	W	187	6.0-7.0	6.5
Heriades truncorum	W	187	6.0-7.0	6.5
Heriades truncorum	W	187	6.0-7.0	6.5

Heriades truncorum	W	185	6.0-7.0	6.5
Heriades truncorum	W	189	6.0-7.0	6.5
Heriades truncorum	W	181	6.0-7.0	6.5
Heriades truncorum	W	182	6.0-7.0	6.5
Heriades truncorum	W	187	6.0-7.0	6.5
Heriades truncorum	W	229	6.0-7.0	6.5
Heriades truncorum	W	270	6.0-7.0	6.5
Heriades truncorum	W	290	6.0-7.0	6.5
Heriades truncorum	W	298	6.0-7.0	6.5
Heriades truncorum	W	298	6.0-7.0	6.5
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	10	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	47	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12

Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	78	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	82	11.0-13.0	12
Hoplitis adunca	W	145	11.0-13.0	12
Hoplitis adunca	W	145	11.0-13.0	12
Hoplitis adunca	W	145	11.0-13.0	12
Hoplitis adunca	W	287	11.0-13.0	12
Hoplitis adunca	W	278	11.0-13.0	12
Hoplitis adunca	W	287	11.0-13.0	12
Hoplitis adunca	W	278	11.0-13.0	12
Hoplitis adunca	W	287	11.0-13.0	12
Hoplitis adunca	W	278	11.0-13.0	12
Hoplitis adunca	W	287	11.0-13.0	12
Hoplitis adunca	W	278	11.0-13.0	12
Hoplitis adunca	W	68	11.0-13.0	12
Hoplitis adunca	W	68	11.0-13.0	12
Hoplitis adunca	W	68	11.0-13.0	12
Hoplitis adunca	W	68	11.0-13.0	12
Hoplitis adunca	W	68	11.0-13.0	12
Hoplitis adunca	W	68	11.0-13.0	12
Hoplitis adunca	W	68	11.0-13.0	12
Hoplitis adunca	W	68	11.0-13.0	12
Hoplitis adunca	W	65	11.0-13.0	12
Hoplitis adunca	W	65	11.0-13.0	12
Hoplitis adunca	W	65	11.0-13.0	12
Hoplitis adunca	W	65	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12

Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	87	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	175	11.0-13.0	12
Hoplitis adunca	W	168	11.0-13.0	12
Hoplitis adunca	W	168	11.0-13.0	12
Hoplitis adunca	W	168	11.0-13.0	12
Hoplitis adunca	W	168	11.0-13.0	12
Hoplitis adunca	W	168	11.0-13.0	12
Hoplitis adunca	W	168	11.0-13.0	12
Hoplitis adunca	W	214	11.0-13.0	12
Hoplitis adunca	W	214	11.0-13.0	12
Hoplitis adunca	W	214	11.0-13.0	12
Hoplitis adunca	W	237	11.0-13.0	12
Hoplitis adunca	W	237	11.0-13.0	12
Hoplitis adunca	W	237	11.0-13.0	12
Hoplitis adunca	W	237	11.0-13.0	12
Hoplitis adunca	W	237	11.0-13.0	12
Hoplitis adunca	W	237	11.0-13.0	12
Hoplitis adunca	W	237	11.0-13.0	12
Hoplitis adunca	W	237	11.0-13.0	12
Osmia bicornis	M	55.1	8.0-12.0	10
Osmia bicornis	M	148.5	8.0-12.0	10
Osmia bicornis	M	151.3	8.0-12.0	10
Osmia bicornis	M	81	8.0-12.0	10

Osmia bicornis	M	81	8.0-12.0	10
Osmia bicornis	M	81	8.0-12.0	10
Osmia bicornis	W	114.1	8.0-12.0	10
Osmia bicornis	W	5	8.0-12.0	10
Osmia bicornis	W	114.1	8.0-12.0	10
Osmia bicornis	W	113.6	8.0-12.0	10
Osmia bicornis	W	16.5	8.0-12.0	10
Osmia bicornis	W	16.5	8.0-12.0	10
Osmia bicornis	W	114.1	8.0-12.0	10
Osmia bicornis	W	5	8.0-12.0	10
Osmia bicornis	W	114.1	8.0-12.0	10
Osmia bicornis	W	114.1	8.0-12.0	10
Osmia bicornis	W	114.1	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	68.5	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	236	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia bicornis	W	138.4	8.0-12.0	10
Osmia cornuta 2017	M	142	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	152	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12

Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	49	11.0-13.0	12
Osmia cornuta 2017	M	100	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	97	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	148	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	245	11.0-13.0	12
Osmia cornuta 2017	M	24	11.0-13.0	12
Osmia cornuta 2017	M	90	11.0-13.0	12
Osmia cornuta 2017	M	30	11.0-13.0	12
Osmia cornuta 2017	W	69	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	132	12.0-15.0	13.5
Osmia cornuta 2017	W	724	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	49	12.0-15.0	13.5
Osmia cornuta 2017	W	58	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	11	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	70	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	113	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	75	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	120	12.0-15.0	13.5
Osmia cornuta 2017	W	122	12.0-15.0	13.5
Osmia cornuta 2017	W	134	12.0-15.0	13.5
Osmia cornuta 2017	W	134	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	123	12.0-15.0	13.5

Osmia cornuta 2017	W	90	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	80	12.0-15.0	13.5
Osmia cornuta 2017	W	113	12.0-15.0	13.5
Osmia cornuta 2017	W	76	12.0-15.0	13.5
Osmia cornuta 2017	W	113	12.0-15.0	13.5
Osmia cornuta 2017	W	113	12.0-15.0	13.5
Osmia cornuta 2017	W	113	12.0-15.0	13.5
Osmia cornuta 2018	M	2	11.0-13.0	12
Osmia cornuta 2018	M	23	11.0-13.0	12
Osmia cornuta 2018	M	23	11.0-13.0	12
Osmia cornuta 2018	M	25	11.0-13.0	12
Osmia cornuta 2018	M	25	11.0-13.0	12
Osmia cornuta 2018	M	26	11.0-13.0	12
Osmia cornuta 2018	M	28	11.0-13.0	12
Osmia cornuta 2018	M	30	11.0-13.0	12
Osmia cornuta 2018	M	32	11.0-13.0	12
Osmia cornuta 2018	M	35	11.0-13.0	12
Osmia cornuta 2018	M	37	11.0-13.0	12
Osmia cornuta 2018	M	39	11.0-13.0	12
Osmia cornuta 2018	M	39	11.0-13.0	12
Osmia cornuta 2018	M	39	11.0-13.0	12
Osmia cornuta 2018	M	40	11.0-13.0	12
Osmia cornuta 2018	M	41	11.0-13.0	12
Osmia cornuta 2018	M	43	11.0-13.0	12
Osmia cornuta 2018	M	50	11.0-13.0	12
Osmia cornuta 2018	M	53	11.0-13.0	12
Osmia cornuta 2018	M	63	11.0-13.0	12
Osmia cornuta 2018	M	72	11.0-13.0	12
Osmia cornuta 2018	M	77	11.0-13.0	12
Osmia cornuta 2018	M	91	11.0-13.0	12
Osmia cornuta 2018	M	101	11.0-13.0	12
Osmia cornuta 2018	M	108	11.0-13.0	12
Osmia cornuta 2018	M	114	11.0-13.0	12
Osmia cornuta 2018	M	114	11.0-13.0	12
Osmia cornuta 2018	M	114	11.0-13.0	12
Osmia cornuta 2018	M	114	11.0-13.0	12
Osmia cornuta 2018	M	127	11.0-13.0	12
Osmia cornuta 2018	M	136	11.0-13.0	12
Osmia cornuta 2018	M	144	11.0-13.0	12
Osmia cornuta 2018	M	146	11.0-13.0	12
Osmia cornuta 2018	M	152	11.0-13.0	12
Osmia cornuta 2018	M	154	11.0-13.0	12
Osmia cornuta 2018	M	162	11.0-13.0	12

Osmia cornuta 2018	M	215	11.0-13.0	12
Osmia cornuta 2018	W	12	12.0-15.0	13.5
Osmia cornuta 2018	W	12	12.0-15.0	13.5
Osmia cornuta 2018	W	12	12.0-15.0	13.5
Osmia cornuta 2018	W	12	12.0-15.0	13.5
Osmia cornuta 2018	W	12	12.0-15.0	13.5
Osmia cornuta 2018	W	12	12.0-15.0	13.5
Osmia cornuta 2018	W	12	12.0-15.0	13.5
Osmia cornuta 2018	W	48	12.0-15.0	13.5
Osmia cornuta 2018	W	55	12.0-15.0	13.5
Osmia cornuta 2018	W	55	12.0-15.0	13.5
Osmia cornuta 2018	W	101	12.0-15.0	13.5
Osmia cornuta 2018	W	114	12.0-15.0	13.5
Osmia cornuta 2018	W	114	12.0-15.0	13.5
Osmia cornuta 2018	W	114	12.0-15.0	13.5
Osmia cornuta 2018	W	114	12.0-15.0	13.5
Osmia cornuta 2018	W	114	12.0-15.0	13.5
Osmia cornuta 2018	W	114	12.0-15.0	13.5
Osmia cornuta 2018	W	114	12.0-15.0	13.5
Osmia cornuta 2018	W	114	12.0-15.0	13.5
Osmia cornuta 2018	W	120	12.0-15.0	13.5
Osmia cornuta 2018	W	125	12.0-15.0	13.5
Osmia cornuta 2018	W	140	12.0-15.0	13.5
Osmia cornuta 2018	W	149	12.0-15.0	13.5
Osmia cornuta 2018	W	154	12.0-15.0	13.5
Osmia cornuta 2018	W	154	12.0-15.0	13.5
Osmia cornuta 2018	W	194	12.0-15.0	13.5
Osmia cornuta 2018	W	196	12.0-15.0	13.5
Osmia cornuta 2018	W	197	12.0-15.0	13.5
Osmia cornuta 2018	W	208	12.0-15.0	13.5
Osmia cornuta 2018	W	208	12.0-15.0	13.5
Osmia cornuta 2018	W	226	12.0-15.0	13.5

* Since we could not mark the smaller species *Chelostoma florisomne, C. rapunculi* and *Heriades truncorum* to an individual level, we cannot exclude the repeated observation of an individual for several times for these species.

R-code for a generalized mixed-effects model

```
dat    = read.table("Table_S1.csv", head=T, sep=";", dec=".")
require(lme4)

# Exclusion of the outlier
dat = dat[dat$Flightdistance<500,]

# Distribution of data
hist(sqrt(dat$Flightdistance))
hist((dat$size))

# fit the generalized mixed effects model

f1<-glmer(sqrt(Flightdistance)~size+(1|Species),data=dat)
summary(f1)
AIC(f1)

# predict the data, removing the grouping value
fix.pred<-predict(f1,re.form=NA)

# to remove the random effects term and view the original spread of the data
# with just the random noise added, add the residual error back onto the predicted values
y.adj<-fix.pred+resid(f1)

# Plot of the trend, with the random effects term removed
plot(y.adj~dat$size)
# add the trend line
lines(predict(f1,newdata=data.frame(size=seq(0,100,length(1000))),re.form=NA)~seq(0,100,l
ength(1000)),col="black",lwd=2)

#get summary statistics such as P value
summary(lm(y.adj~dat$size))

# fit the linear model without random effects

plot(sqrt(Flightdistance)~size, data=dat)
abline(lm(sqrt(Flightdistance)~size, data=dat), col="black", lwd=2)
#get summary statistics such as P value
summary(lm(sqrt(Flightdistance)~size, data=dat))
```

Chapter 6

One-year-old flower strips already support a quarter of a city´s bee species

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One year-old flower strips already support a quarter of a city's bee species

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Abstract. – To combat the loss of flower-rich meadows, many cities are supporting greening measures, including the creation of flower strips. To assess the effectiveness of these measures in supporting flower-visiting insects, their faunas need to be compared to the background fauna at various distances from the flower strips. To meet this goal, we quantified the bee faunas of nine 1000 m^2-large and newly established flower strips in the city of Munich, all planted with a regional seed mix, and compared them to the fauna recorded between 1997 and 2017 within 500, 1000, and 1500 m from the respective strip. The 68 species recorded during the flower strips' first season represent 21% of the 324 species ever recorded for Munich and 29% of the 232 species recorded between 1997 and 2017. Non-threatened species are statistically over-represented in the strips, but pollen generalists are not. These findings illustrate the conservation value of urban flower strips for common species that apparently quickly discover this food source. To our knowledge, this is the first quantitative assessment of the speed and distance over which urban flower strips attract wild bees.

Key words: Urban ecosystem; attraction effect; flower strips; wild bees

1. Introduction

Insects that rely on a mix of flowers for nectar or pollen for their survival, such as bees and many butterflies and flies, are rapidly decreasing in diversity and abundance (Mandery et al., 2003; Potts et al., 2010, Westrich et al., 2011). One reason for this is the loss of flower-rich meadows, which are becoming increasingly rare. In Germany, for example, meadows covered 5.3 Million hectares (Mio. ha) in 1991, but only 4.7 Mio. ha in 2019 (Statistisches Bundesamt, https://www.destatis.de/DE/Themen/Branchen-Unternehmen/Landwirtschaft-Forstwirtschaft-Fischerei/Feldfruechte-Gruenland/Tabellen/zeitreihe-dauergruenland-nach-nutzung.html). To address the loss of flower-rich areas, the European Union is supporting 'greening' measures, which include the creation of flower strips (European Commission, 2011). Flower strips are man-made patches of flowering plants that provide foraging resources for flower-visiting insects, especially bees, butterflies, and flies. Monitoring and experiments have shown that such strips enhance the local plant and insect diversity in agricultural landscapes (e.g. Scheper et al., 2015; Jönsson et al., 2015; Buhk et al., 2018; Dicks et al., 2017 review 80 studies of flower strips).

Despite the work demonstrating the diversity-enhancing effects of flower strips near crops, it is unclear what proportion of bee diversity these usually small, young, and artificial plantings may be 'capturing' and how strongly their faunas may be biased towards common insect species. From first principles, the success of flower strips in maintaining populations of solitary bees will depend on their floristic composition, distance from suitable nesting sites, and distance from other habitats that maintain stable populations. To study the attractiveness of flower strips in an urban landscape, we took advantage of nine 1000 m^2-large flower strips newly established in Munich, all with autochthonous seed mixtures selected by the Bavarian bird protection society (Landesbund für Vogelschutz, acronym LBV) and department of horticulture (Gartenbaureferat München). We identified and counted the bees visiting flowers on each strip and then related these numbers to the total diversity of Munich's bee fauna and to the diversity within 500, 1000, and 1500 m radii around the strips. Our expectation was that newly planted flowers strips would attract a small subset of mostly generalist, non-threatened species and that oligolectic species (species using pollen from a taxonomically restricted set of plants) would be underrepresented compared to the city's overall species pool.

2. Material and methods

Study sites and plant species inventories

In April 2017, the Regional Society for the Protection of Birds (LBV) and the Department of Horticulture of the city of Munich created eight 1000 m^2-large flower strips throughout Munich (Fig. 1). Besides these eight strips, we included one strip established in 2015. All strips were sown with regional seeds from the seed supplier Kirmer (http://www.krimmer-naturnahes-gruen.de), adapted either for nutrient-rich or nutrient-poor sites, and the LBV also provided man-made nesting sites for cavity-breeding bees at the sites. Flowering plant species were identified in randomly placed plots of one square-m per strip at the strips Fockensteinstraße (established in 2015), Willy-Brandt-Allee and Rathenaustraße (nutrient-poor sites established in 2017), and Pasing Stadtpark, and Werner-Seelenbinder-Weg (nutrient-rich sites established in 2017). Plant species found on each strip are listed in Table S1, along with information on herbarium voucher specimens deposited in the Munich herbarium (Botanische Staatssammlung, international acronym M).

Bee species inventories

From March to August in 2017 and 2018, each flower strip was visited four to five times. Visits were made between 10 a.m. and 4 p.m. on sunny, warm days with little or no wind. Where possible, bee species were identified directly in the field and were documented via macro-photography in a standardized setup: for close-up pictures, the bees were caught with an insect net and cooled down for 10 minutes in an Eppendorf cupped plastic vial stored on ice in a cooled box. When they fell into rigor of cold, they were transferred onto scale paper (using a small box lined with millimetre paper on its bottom) and photographed from all sides (SLR camera: Pentax K-x; Lens: Sigma DG 17-70 mm, 1:2.8, macro). Within one to two minutes, bees warmed up again and were released at the location where they had been caught. For species that are difficult to identify by morphology alone, such as species of *Sphecodes*, *Lasioglossum* or *Halictus*, voucher specimens, preferably males (for morphological re-identification by genitalia preparations), were collected and identified morphologically and via DNA barcoding (methods and primers as described in Hofmann et al., 2018). The voucher specimens are deposited in the Zoologische Staatssammlung Munich (ZSM). Photo vouchers are accessible at the Diversity Workbench server (DWB; https://diversityworkbench.net/Portal/Diversity_Workbench), and DNA barcodes at NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/). Table S2 in the Online Supporting Material shows all GenBank and DWB accession numbers [data will be accessible once this ms accepted]. Additionally, Table S2 shows each species' Red List status based on Westrich et al. (2011) as well as foraging and nesting preferences based on Scheuchl and Willner (2016).

To investigate the catchment area of each flower strip, we analysed 7589 Gauß-Krüger-referenced records, including sightings of single bees or populations made between 1997 and 2017 and assessed the species and individuals within a radius of 500, 1000, and 1500 m from each strip using QGIS 3.8.2. For species that were recorded on a flower strip, but not within the 1500 m radius from the strip, we measured the distance from the strip to the nearest sightings of the respective species (Table S3). For Fockensteinstraße and Willy-Brandt-Allee, we increased the radius to 1600 m, as there were too few records within the

1500 m radius, while a 1600 m radius yielded comparable numbers of records to those of the other sites.

3. Results

Oligolecty and Red List status of the species on the flower strips compared to the total Munich species pool

On the nine 1000 m^2-large flower strips, we found 83 species of flowering plants, 35 of them coming from the regional seed mix *(Materials and Methods*) and 17 self-sown at Fockensteinstraße (Fig. 2), 27 from the seed mix and 28 self-sown at Rathenaustraße and Willy-Brandt-Allee, and all 23 from the seed mix at Pasinger Stadtpark and Werner-Seelenbinder-Weg (see Table S1 for species lists for each site). The flowers of these plants were visited by honey bees and 68 species of wild bees, that is, 21% of the 324 species ever recorded for Munich and 29% of the 232 re-observed or newly observed species over the last twenty years (1997 – 2017).

Of the 68 species, 62 (91%) have the Red List category 'not threatened,' three (4%) are listed on the pre-warning-list, and three are 'threatened' (Table S2). The respective percentages for the 324-species-pool are 54% (n = 174) not threatened, 11% (n = 35) on the pre-warning list, and 27% (n = 89) threatened. Twenty-two of the 324 species are not Red-listed due to a lack of data or rareness of the species, and three are considered locally extinct. There are thus significantly more non-threatened species on the flower strips than in Munich overall (chi-square test with 2 df, χ^2=26.4, $P = 1.8 \times 10^{-6}$). Of the 232-species-pool recorded for 1997 - 2017, 156 (67%) species are non-threatened, 29 (13%) on the pre-warning list, 38 (16%) threatened, and 9 (4%) of unknown status. Also with these numbers, the flower strip fauna includes a disproportionate number of non-threatened species (chi-square test with 2 df, χ^2=12.5, $P = 0.002$).

Of the 68 species found on the strips, 63% (n = 43) are polylectic and 15% (n = 10) oligolectic. Some 22% (n = 15) parasitize other bee species (Table S2). The respective percentages for the 324 species pool are 51% (n = 165) polylectic, 22% (n = 72) oligolectic, and 27% (n = 87) parasitic (Hofmann and Renner, in review), while in the 232 species pool of the last 20 years, 50% (n = 118) of species are polylectic, 25% (n = 59) oligolectic, and 24% (n = 55) parasitic. Of the oligolectic flower strip visitors, seven specialized on Asteraceae, two on *Campanula*, one on *Echium*, and one on Fabaceae. There is thus no significant difference in the frequencies of polylectic, oligolectic, or parasitic species among the flower strips and the remainder of Munich either for the larger pool (chi-square test with 2 df, χ^2=3.62, $P = 0.164$) or the smaller 1997 – 2017 pool (2df, χ^2=4.19, $P = 0.123$).

'Catchment areas' of the flower strips

Our quantification of species recorded between 1997 and 2017 within a radius of 500, 1000, or 1500 m around each of the nine flower strips revealed that the strips at Altostraße (400 records of 105 different species) and Pasinger Stadtpark (329 records of 156 species) were richest in bees within a radius of 1500 m around them, while Weitlstraße and Willy-Brandt-Allee (19 records of 15 species each) have the fewest records within 1500/1600 m around them (Fig. 3; Table S3). At a distance of 1500 m from the strip, the percentages of bees found at the different strips become almost identical (Fig. 4).

4. Discussion

Bees need time to discover newly created habitat, but Munich's common species did so in just one year, so that the 1000 m^2-small and young flower strips studied here attracted 68 (21%) of the 324 species ever recorded for Munich and 29% of the 232 species recorded during 1997 - 2017. These percentages are similar to those found for much larger protected sites in Munich. Thus, 105 species (32% of the 324 species pool) were recorded in 2017/2018 in the 21 ha-large Munich botanical garden and 44 species (14% of 324) in a 20 ha-large protected city biotope called 'Virginia Depot' (Hofmann & Renner, in review). Surprisingly, the flower strips attracted a random subset of Munich's 324 bee species in terms of pollen specialization, although as expected, the first-year flower-strip visitors mostly belong to common, non-threatened species. To demonstrate positive effects of flower strips on pollinator populations it would be necessary to show increased abundances of pollinators at the urban landscape scale, which was not part of this study. Still, our data strongly support that flower strip planting in cities helps ensure the availability of foraging resources for pollinators and that this simple conservation measure is effective. We therefore agree with Buhk et al.'s (2018) call that flower strip networks should be implemented much more in the upcoming Common Agricultural Policy (CAP) reform in the European Union.

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Authors' contributions

MMH designed the experiment, performed the fieldwork, and analyzed the data; SSR and MMH co-wrote the manuscript.

Conflict statement

The authors declare no conflict of interest.

References

Buhk, C., Oppermann, R., Schanowski, A., Bleil, R., Lüdemann, J., & Maus, C. (2018). Flower strip networks offer promising long term effects on pollinator species richness in intensively cultivated agricultural areas. BMC Ecology 18: 55. https://doi.org/10.1186/s12898-018-0210-z

Dicks, L.V., Ashpole, J.E., Dänhardt, J., James, K., Jönsson, A., Randall, N., Showler, D.A., Smith, R.K., Turpie, S., Williams D.R. & Sutherland, W.J. (2017). Farmland Conservation. Pages 245-284 in: W.J. Sutherland, L.V. Dicks, N. Ockendon & R.K. Smith (eds.) What Works in Conservation 2017. Open Book Publishers, Cambridge, UK

European Commission (2011) CAP Reform - an explanation of the main elements MEMO/11/685. http://www.ala.org.uk/sites/default/files/ExplanatoryMemo.pdf

Hofmann, M. M., Fleischmann, A., & Renner, S. S. (2018). Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. Oecologia 187: 701-706.

Hofmann, M. M., & S. S. Renner. In review. Bee species persistence and increase over 20 years in urban protected sites. (Insect Conservation and Diversity, 15 Sep.)

Jönsson, A. M., Ekroos, J., Dänhardt, J., Andersson, G. K., Olsson, O., & Smith, H. G. (2015). Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the wider landscape. Biological Conservation 184: 51-58.

Mandery, K., Voith, J., Kraus, M., Weber, K., & Wickl, K. (2003). Rote Liste gefährdeter Bienen (Hymenoptera: Apidae) Bayerns. Bayerisches Landesamt für Umweltschutz 166: 198-207.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25: 345-353.

QGIS Development Team (2019). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

Scheper, J., Bommarco, R., Holzschuh, A., Potts, S. G., Riedinger, V., Roberts, S. P., ... & Wickens, V. J. (2015). Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. Journal of Applied Ecology 52: 1165-1175.

Scheuchl, E., & Willner, W. (2016). Taschenlexikon der Wildbienen Mitteleuropas: Alle Arten im Porträt. Quelle et Meyer Verlag. Wiebelsheim, Germany, 917 pages.

Westrich, P.; Frommer, U.; Mandery, K.; Riemann, H.; Ruhnke, H.; Saure, C. & Voith, J. (2011): Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. – In: Binot-Hafke, M.; Balzer, S.; Becker, N.; Gruttke, H.; Haupt, H.; Hofbauer, N.; Ludwig, G.; Matzke-Hajek, G. & Strauch, M. (Red.): Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 3: Wirbellose Tiere (Teil 1). – Münster (Landwirtschaftsverlag). Naturschutz und Biologische Vielfalt 70: 373-416.

Figures

Figure 1. The nine flower strips monitored for this study (modified from https://www.openstreetmap.org, using QGIS 3.8.2, (c) OpenStreetmap Contributors) and bee records (sightings and/or specimen) between 1997 and 2017.

Figure 2: The flower strip at Fockensteinstraße as an example of the urban context of the flower strips studied here.

Figure 3. Numbers of species and individuals recorded between 1997 and 2017 within a radius of 500, 1000, and 1500 m from the centre of the respective flower strip (compare Fig. 1). For details of how past recordings were made see Materials and Methods.

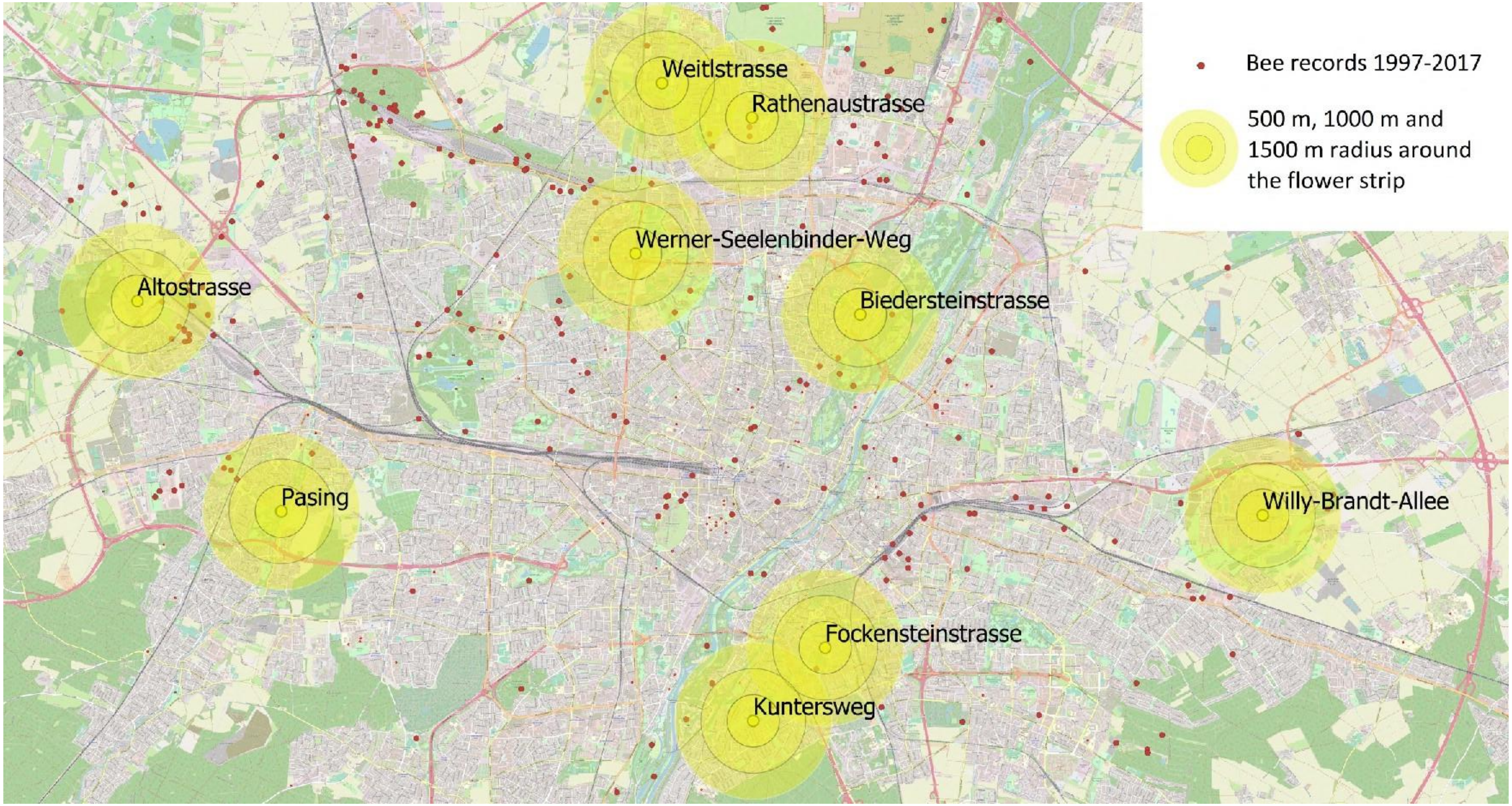
Figure 4. The percentage of bee species recorded at each flower strip that is also found in the surrounding area at distances of 500, 1000, and 1500 m.

Online Supporting Material

Table S1: Lists of plant species and voucher specimens for the nine flower strips.

Table S2: GenBank (https://www.ncbi.nlm.nih.gov/genbank/) accession numbers and Diversity Workbench (https://diversityworkbench.net/Portal/Diversity_Workbench) accession numbers of the bee voucher specimen. Diversity Work Bench accession numbers start with three letters referring to the respective flower strip site. The remaining numbers are GenBank accession numbers for the DNA barcode sequences. Physical vouchers have been deposited in the Zoologische Staatssammlung München.

Table S3: List of bee species records at different radii around the nine flower strips (1997-2017).



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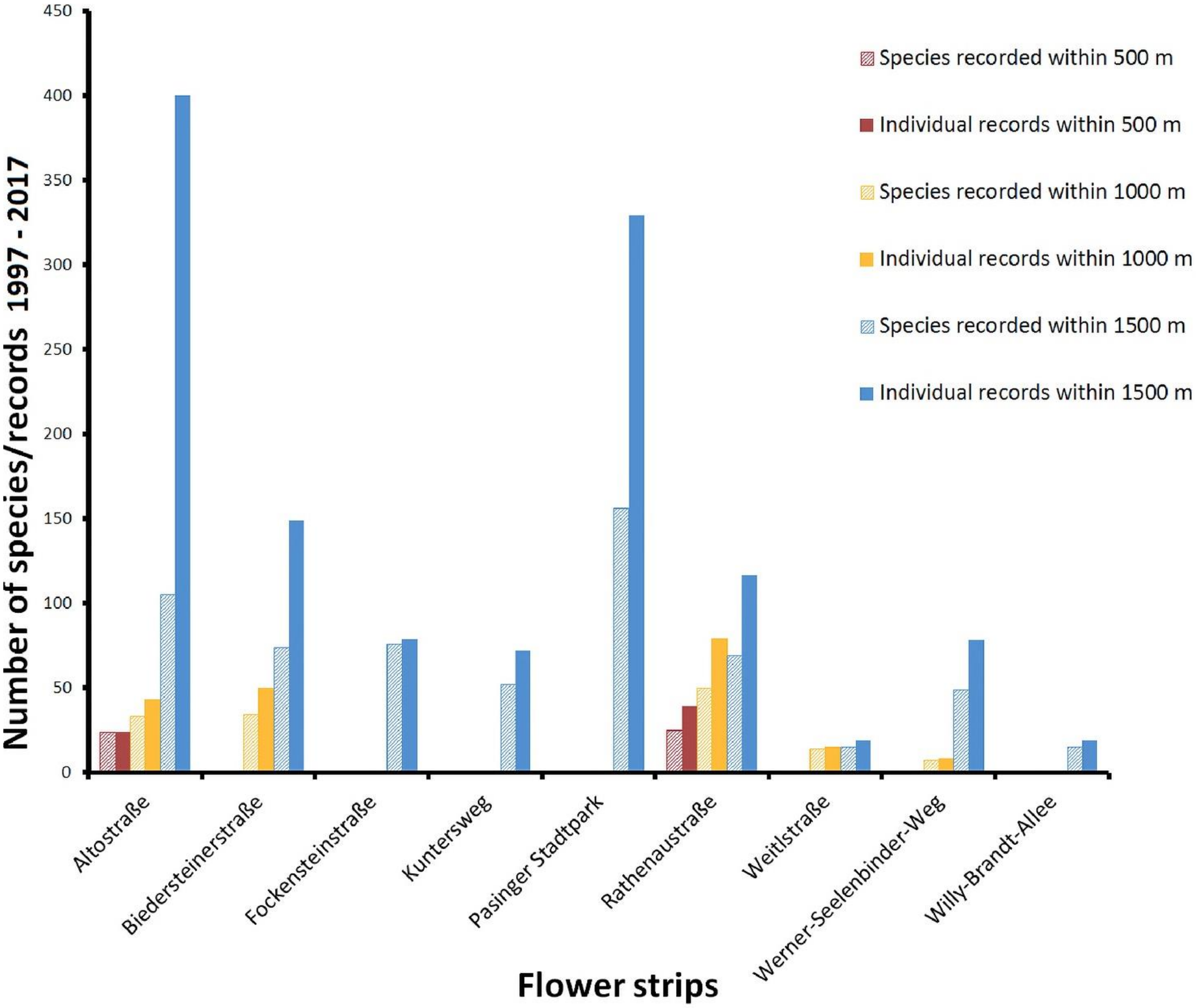

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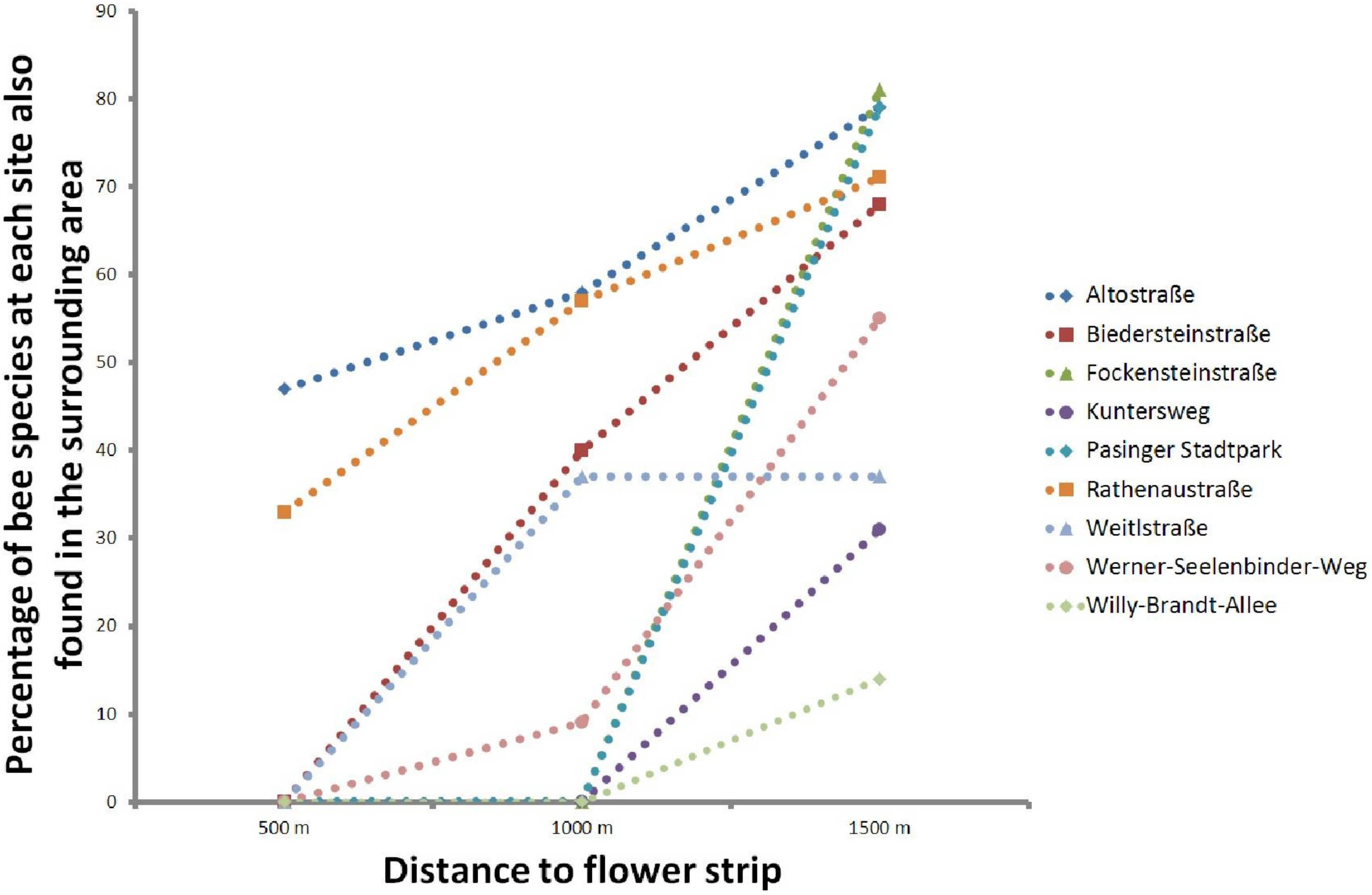

Figure 4. The percentage of bee species recorded at each flower strip that is also found in the surrounding area at distances of 500, 1000, and 1500 m.

Supplementary material from

One-year-old flower strips already support a quarter of a city´s bee species

Table S1. Plant species lists and voucher IDs for the investigated flower strips. Herbarium specimens are deposited at the Botanische Staatssammlung München.

Fockensteinstraße	Voucher ID
Achillea millefolium L.	Leg. Pia Schumann 1
Anthemis tinctoria L.	Leg. Pia Schumann 2
Bellis perennis L.	
Barbarea vulgaris W. T. Aiton	Leg. Pia Schumann 3
Camelina sativa L.	Leg. Pia Schumann 4
Campanula patula L.	Leg. Pia Schumann 5
Carum carvi L.	Leg. Pia Schumann 6
Centaurea cyanus L.	Leg. Pia Schumann 7
Centaurea jacea subspec. *jacea* L.	Leg. Pia Schumann 8
Cichorium intybus subspec. *intybus* L.	Leg. Pia Schumann 9
Crepis biennis L.	Leg. Pia Schumann 10
Daucus carota subspec. *carota* L.	Leg. Pia Schumann 11
Dianthus carthusianorum L.	
Echium vulgare L.	Leg. Pia Schumann 12
Erigeron annuus L.	Leg. Pia Schumann 36
Galium verum L.	Leg. Pia Schumann 13
Geranium pyrenaicum Burm.	Leg. Pia Schumann 38
Hypericum perforatum var. *perforatum* L.	Leg. Pia Schumann 14
Papaver rhoeas L.	Leg. Pia Schumann 15
Knautia arvensis L.	Leg. Pia Schumann 16
Leontodon autumnalis subspec. *autumnalis* L.	Leg. Pia Schumann 17
Leucanthemum vulgare Vaill.	Leg. Pia Schumann 18
Lotus corniculatus L.	Leg. Pia Schumann 19
Malva moschata L.	Leg. Pia Schumann 20
Malva sylvestris L.	
Medicago lupulina L.	
Melilotus officinalis L.	Leg. Pia Schumann 21
Onobrychis viciifolia Scop.	Leg. Pia Schumann 22
Origanum vulgare L.	Leg. Pia Schumann 23
Pastinaca sativa subspec. *sativa* L.	Leg. Pia Schumann 24
Plantago lanceolata L.	Leg. Pia Schumann 25
Potentilla anserina L.	
Reseda lutea L.	Leg. Pia Schumann 26
Rhinanthus alectorolophus (Scop.) Pollich	
Salvia pratensis L.	Leg. Pia Schumann 27
Saponaria officinalis L.	Leg. Pia Schumann 28
Securigera varia L.	Leg. Pia Schumann 37
Silene dioica L.	Leg. Pia Schumann 29
Silene flos-cuculi L.	Leg. Pia Schumann 30
Silene latifolia subspec. *alba* Mill.	Leg. Pia Schumann 31
Silene vulgaris (Moench) Garcke	Leg. Pia Schumann 32

Sisymbrium officinale (L.) Scop.	
Symphytum officinale L.	
Taraxacum officinale F.H.Wigg.	
Tragopogon pratensis L.	
Trifolium campestre Schreb.	
Trifolium incarnatum L.	Leg. Pia Schumann 35
Trifolium pratense subspec. *pratense* L.	Leg. Pia Schumann 33
Trifolium repens L.	
Verbascum nigrum L.	Leg. Pia Schumann 34
Veronica chamaedrys L.	

Rathenaustraße	**Voucher ID**
Agrimonia eupatoria L.	Leg.: N. Dasch 1
Achillea millefolium L.	
Anthemis tinctoria L.	Leg.: N. Dasch 2
Bellis perennis L.	
Centaurea jacea L.	
Cerastium arvense L.	
Cichorium intybus L.	
Crepis biennis L.	
Dianthus carthusianorum L.	
Dianthus deltoides L.	
Echium vulgare L.	Leg.: N. Dasch 12
Erigeron annuus (L.) Pers.	
Erysimum hieraciifolium L.	
Galium mollugo L.	
Geranium pyrenaicum Burm.f.	
Glechoma hederacea L.	
Hesperis matronalis L.	
Knautia arvensis (L.) Coulter	
Leontodon hispidus L.	Leg.: N. Dasch 29
Leucanthemum vulgare agg.	
Lotus corniculatus L.	
Malva moschata L.	
Oenothera suaveolens Pers.	
Papaver rhoeas L.	
Plantago lanceolata L.	
Plantago media L.	
Prunella vulgaris L.	
Ranunculus acris L.	
Reseda alba L.	
Rhinanthus alectorolophus (Scop.) Pollich	
Salvia pratensis L.	
Salvia verticillata L.	Leg.: N. Dasch 23
Securigera varia (L.) Lassen	
Silene dioica (L.) Clairv.	
Silene vulgaris (Moench) Garcke	
Taraxacum officinale (L.) Weber ex F.H.Wigg.	
Tragopogon pratensis L.	
Trifolium pratense L.	
Trifolium repens L.	
Verbascum densiflorum Bertol.	
Verbascum lychnitis L.	
Veronica chamaedrys L.	

Willy-Brandt-Allee	**Voucher ID**
Agrimonia eupatoria L.	
Achillea millefolium L.	
Anthemis tinctoria L.	
Barbarea vulgaris W. T. Aiton	
Bellis perennis L.	
Biscutella laevigata L.	Leg.: N. Dasch 3
Campanula rotundifolia L.	Leg.: N. Dasch 4
Carduus acanthoides L.	
Centaurea cyanus L.	Leg.: N. Dasch 5
Centaurea jacea L.	Leg.: N. Dasch 6
Centaurea scabiosa L.	Leg.: N. Dasch 27
Cichorium intybus L.	Leg.: N. Dasch 7
Cirsium arvense (L.) Scop.	
Crepis biennis L.	Leg.: N. Dasch 8
Daucus carota L.	Leg.: N. Dasch 9
Dianthus carthusianorum L.	Leg.: N. Dasch 10
Dianthus deltoides L.	Leg.: N. Dasch 11
Echium vulgare L.	
Erigeron annuus (L.) Pers.	
Erysimum hieraciifolium L.	Leg.: N. Dasch 13
Glechoma hederacea L.	
Hesperis matronalis L.	Leg.: N. Dasch 14
Hypericum perforatum L.	Leg.: N. Dasch 28
Knautia arvensis (L.) Coulter	Leg.: N. Dasch 15
Leucanthemum vulgare agg.	Leg.: N. Dasch 16
Lychnis flos-cuculi L.	
Malva moschata L.	Leg.: N. Dasch 17
Onobrychis viciifolia Scop.	Leg.: N. Dasch 18
Papaver rhoeas L.	Leg.: N. Dasch 19
Plantago lanceolata L.	
Plantago media L.	Leg.: N. Dasch 20
Prunella vulgaris L.	
Ranunculus acris L.	
Reseda alba L.	
Rhinanthus alectorolophus (Scop.) Pollich	
Rhinanthus minor Personnat	Leg.: N. Dasch 21
Salvia pratensis L.	Leg.: N. Dasch 22
Senecio jacobaea L.	
Silene dioica (L.) Clairv.	Leg.: N. Dasch 24
Silene nutans L.	Leg.: N. Dasch 25
Taraxacum officinale (L.) Weber ex F.H.Wigg.	
Thymus pulegioides L.	Leg.: N. Dasch 30
Tragopogon pratensis L.	Leg.: N. Dasch 26
Trifolium pratense L.	
Trifolium repens L.	
Veronica chamaedrys L.	

Pasinger Stadtpark	Voucher ID
Achillea millefolium L.	Leg. T. Greindl 4
Barbarea vulgaris W. T. Aiton	Leg. T. Greindl 7
Campanula patula L.	Leg. T. Greindl 8
Carum carvi L.	
Centaurea jacea L.	Leg. T. Greindl 1
Crepis biennis L.	Leg. T. Greindl 2
Dianthus superbus L.	Leg. T. Greindl 6
Galium verum L.	Leg. T. Greindl 16
Geranium pratense L.	
Knautia arvensis (L.) Coulter	
Lathyrus pratensis L.	Leg. T. Greindl 12
Leontodon autumnalis L.	
Leontodon hispidus L.	
Leucanthemum vulgare agg.	Leg. T. Greindl 3
Lotus corniculatus L.	Leg. T. Greindl 13
Salvia pratensis L.	
Silene dioica (L.) Clairv.	Leg. T. Greindl 9
Silene flos-cuculi L.	
Silene vulgaris (Moench) Garcke	Leg. T. Greindl 10
Trifolium pratense L.	Leg. T. Greindl 5
Rhinanthus minor L.	Leg. T. Greindl 14
Papaver rhoeas L.	
Ranunculus acris L.	Leg. T. Greindl 15
Ranunculus lanuginosus L.	

Werner-Seelenbinder-Weg	Voucher ID
Barbarea vulgaris W. T. Aiton	
Campanula glomerata L.	
Campanula patula L.	
Carum carvi L.	
Centaurea jacea L.	
Crepis biennis L.	
Dianthus superbus L.	
Galium verum L.	
Knautia arvensis (L.) Coulter	
Lathyrus pratensis L.	
Leontodon autumnalis L.	
Leontodon hispidus L.	
Leucanthemum vulgare agg.	
Lotus corniculatus L.	
Papaver rhoeas L.	
Ranunculus acris L.	
Ranunculus lanuginosus L.	
Rhinanthus minor L.	
Sanguisorba officinalis L.	
Scabiosa columbaria L.	
Silene dioica (L.) Clairv.	
Silene flos-cuculi L.	
Silene vulgaris (Moench) Garcke	

Table S2. Bee species lists at the investigated flower strips,
with Red List Status (Westrich et al. 2011),
foraging and nesting preferences (Scheuchl & Willner, 2016),
voucher ID (either GenBank or Diverstiy Workbench Accession number), and
distance of the nextclosest species records.

Site	**Species**	**Red List Status** [1]	**Foraging preference**
Altostraße	*Andrena chrysosceles*	*	polylectic
Altostraße	*Andrena gravida*	*	polylectic
Altostraße	*Andrena haemorrhoa*	*	polylectic
Altostraße	*Anthidium oblongatum*	V	polylectic
Altostraße	*Bombus hortorum*	*	polylectic
Altostraße	*Bombus lapidarius*	*	polylectic
Altostraße	*Bombus lucorum/terrestris*	*	polylectic
Altostraße	*Bombus pascuorum*	*	polylectic
Altostraße	*Bombus sylvarum*	V	polylectic
Altostraße	*Bombus vestalis*	*	parasitic
Altostraße	*Colletes similis*	V	oligolectic: Asteraceae
Altostraße	*Halictus erygnathus* group		
Altostraße	*Halictus rubicundus*	*	polylectic
	Halictus subauratus	*	polylectic
Altostraße	*Heriades truncorum*	*	oligolectic: Asteraceae
Altostraße	*Hylaeus communis*	*	polylectic
Altostraße	*Lasioglossum pauxillum*	*	polylectic
Altostraße	*Megachile willughbiella*	*	polylectic
Altostraße	*Nomada fabriciana*	*	parasitic
Altostraße	*Osmia aurentula*	*	polylectic
Biedersteinstraße	*Andrena bicolor*	*	polylectic
Biedersteinstraße	*Andrena cineraria*	*	polylectic
Biedersteinstraße	*Anthidium manicatum*	*	polylectic

Nesting location	ID[2]	100 m	250 m	500 m	1000 m	1500 m	
groundnesting	ALT-00025						3762 m
groundnesting	ALT-00026						1873 m
groundnesting	ALT-00006					x	
cavities above ground	ALT-00040			x	x	x	
above and below ground	ALT-00037					x	
above and below ground	observation only			x	x	x	
groundnesting	ALT-00014, ALT-00033, ALT-00046			x	x	x	
above and below ground	ALT-00015			x	x	x	
above and below ground	ALT-00011, ALT-00016, ALT-00035				x	x	
host nest	ALT-00032			x	x	x	
groundnesting	ALT-00048					x	
	ALT-00029					x	
groundnesting	ALT-00030			x	x	x	
groundnesting	ALT-00009, ALT-00031				x	x	
cavities above ground	ALT-00007, ALT-00019, ALT-00049					x	
cavities above ground	ALT-00028			x	x	x	
groundnesting	MK442002, MK442003			x	x	x	
cavities above ground	ALT-00027			x	x	x	
host nest	ALT-00004						1857 m
cavities above ground	ALT-00005						3320 m
groundnesting	BST-00042				x	x	
groundnesting	BST-00003				x	x	
cavities above ground	BST-00018				x	x	

Biedersteinstraße	*Anthidium oblongatum*	V	polylectic
Biedersteinstraße	*Bombus barbutellus*	*	parasitic
Biedersteinstraße	*Bombus hortorum*	*	polylectic
Biedersteinstraße	*Bombus lapidarius*	*	polylectic
Biedersteinstraße	*Bombus lucorum/terrestris*	*	polylectic
Biedersteinstraße	*Bombus pascuroum*	*	polylectic
Biedersteinstraße	*Halictus confusus* group		
Biedersteinstraße	*Halictus rubicundus*	*	polylectic
Biedersteinstraße	*Halictus tumulorum*	*	polylectic
Biedersteinstraße	*Heriades truncorum*	*	oligolectic: Asteraceae
Biedersteinstraße	*Hylaeus communis*	*	polylectic
Biedersteinstraße	*Hylaeus hyalinatus*	*	polylectic
Biedersteinstraße	*Hylaeus nigritus*	*	oligolectic: Asteraceae
Biedersteinstraße	*Hylaeus signatus*	*	
Biedersteinstraße	*Lasioglossum albipes*	*	polylectic
Biedersteinstraße	*Lasioglossum laticeps*	*	polylectic
Biedersteinstraße	*Lasioglossum morio*	*	polylectic
Biedersteinstraße	*Lasioglossum pauxillum*	*	polylectic
Biedersteinstraße	*Megachile ericetorum*	*	oligolectic: Fabaceae
Biedersteinstraße	*Megachile willughbiella*	*	polylectic
Biedersteinstraße	*Osmia bicornis*	*	polylectic
Biedersteinstraße	*Osmia cornuta*	*	polylectic
Biedersteinstraße	*Sphecodes monilicornis*	*	parasitic
Fockensteinstraße	*Andrena subopaca* group		
Fockensteinstraße	*Anthidium manicatum*	*	polylectic
Fockensteinstraße	*Anthidium oblongatum*	V	polylectic
Fockensteinstraße	*Bombus hypnorum*	*	polylectic
Fockensteinstraße	*Bombus lapidarius*	*	polylectic

cavities above ground	BST-00019, BST-00064			2613 m
host nest	BST-00023		x	
above and below ground	BST-00063			2536 m
above and below ground	BST-00061		x	
groundnesting	BST-00026		x	
above and below ground	BST-00008, BST-00048	x	x	
	BST-00062			
groundnesting	MK441993	x	x	
groundnesting	MG846690, MG846691	x	x	
cavities above ground	BST-00027			3016 m
cavities above ground	BST-00022		x	
cavities above ground	BST-00030		x	
cavities above ground	BST-00017			2535 m
	observation only	x	x	
groundnesting	MK441994, MK441994	x	x	
groundnesting	MK441992		x	
groundnesting	MK441996			2192 m
groundnesting	MK441995	x	x	
cavities above ground	BST-00009			2607 m
cavities above ground	BST-00013, BST-00065			2607 m
cavities above ground	BST-00044		x	
cavities above ground	BST-00043			3683 m
host nest	MG845953, MG845966	x	x	
	FOC-00055		x	
cavities above ground	FOC-00027, FOC-00063, FOC-00071		x	
cavities above ground	FOC-00016, FOC-00019, FOC-00048, FOC-00072		x	
cavities above ground	FOC-00003		x	
above and below ground	FOC-00040, FOC-00057		x	

Fockensteinstraße	*Bombus lucorum/terrestris*	*	polylectic
Fockensteinstraße	*Bombus pascuorum*	*	polylectic
Fockensteinstraße	*Colletes daviesanus*	*	oligolectic: Asteraceae
Fockensteinstraße	*Halictus rubicundus*	*	polylectic
Fockensteinstraße	*Halictus scabiosae*	*	polylectic
	Halictus subauratus	*	polylectic
Fockensteinstraße	*Halictus tumulorum*	*	polylectic
Fockensteinstraße	*Hoplitis adunca*	*	oligolectic: *Echium*
Fockensteinstraße	*Hylaeus brevicornis*	*	polylectic
Fockensteinstraße	*Hylaeus communis*	*	polylectic
Fockensteinstraße	*Hylaeus leptocephalus*	*	polylectic
Fockensteinstraße	*Hylaeus nigritus*	*	oligolectic: Asteraceae
Fockensteinstraße	*Lasioglossum calceatum*	*	polylectic
Fockensteinstraße	*Lasioglossum nitidulum*	*	polylectic
Fockensteinstraße	*Megachile ericetorum*	*	oligolectic: Fabaceae
Fockensteinstraße	*Megachile pilidens*	3	polylectic
Fockensteinstraße	*Megachile rotundata*	*	polylectic
Fockensteinstraße	*Megachile willhugbiella*	*	polylectic
Fockensteinstraße	*Osmia bicornis*	*	polylectic
Fockensteinstraße	*Osmia caerulescens*	*	polylectic
Fockensteinstraße	*Osmia spinulosa*	3	oligolectic: Asteraceae
Fockensteinstraße	*Sphecodes monilicornis*	*	parasitic
Kuntersweg	*Andrena chrysosceles*	*	polylectic
Kuntersweg	*Andrena labiata*	*	polylectic
Kuntersweg	*Bombus hortorum*	*	polylectic

groundnesting	observation only	x
above and below ground	FOC-00002, FOC-00059, FOC-00074	x
groundnesting	FOC-00028, FOC-00032	2009 m
groundnesting	MG792001, MG792002, MG792003	x
groundnesting	FOC-00044, FOC-00078	x
groundnesting	FOC-00051	x
groundnesting	barcode not abloaded due to bad sequence quality	x
cavities above ground	FOC-00026, FOC-00050	x
cavities above ground	FOC-00025	x
cavities above ground	observation only	x
cavities above ground	MG791999	1564 m
cavities above ground	FOC-00012, FOC-00020, FOC-00033	2291 m
groundnesting	MG791990	x
groundnesting	MG792011	x
cavities above ground	FOC-00031, FOC-00076	x
above and below ground	FOC-00017, FOC-00070	12983 m
cavities above ground	FOC-00030	x
cavities above ground	FOC-00007, FOC-00064, FOC-00075	x
cavities above ground	FOC-00054	x
cavities above ground	FOC-00029, FOC-00060	x
avities above groun	FOC-00023	7089 m
host nest	MG845963	x
groundnesting	KUN-00032	2172 m
groundnesting	KUN-00007	9863 m
above and below ground	KUN-00037	x

Kuntersweg	*Bombus lapidarius*	*	polylectic
Kuntersweg	*Bombus lucorum/terrestris*	*	polylectic
Kuntersweg	*Bombus pascuorum*	*	polylectic
Kuntersweg	*Chelostoma campanularum*	*	oligolectic: *Campanula*
Kuntersweg	*Chelostoma rapunculi*	*	oligolectic: *Campanula*
Kuntersweg	*Halictus subauratus*	*	polylectic
Kuntersweg	*Halictus tumulorum* group		
Kuntersweg	*Heriades truncorum*	*	oligolectic: Asteraceae
Kuntersweg	*Hylaeus nigritus*	*	oligolectic: Asteraceae
Kuntersweg	*Lasioglossum calceatum*	*	polylectic
Kuntersweg	*Lasioglossum leucozonium*	*	polylectic
Kuntersweg	*Lasioglossum morio*	*	polylectic
Kuntersweg	*Lasioglossum pauxillum*	*	polylectic
Kuntersweg	*Nomada lathburiana*	*	parasitic
Pasinger Stadtpark	*Andrena cineraria*	*	polylectic
Pasinger Stadtpark	*Andrena gravida*	*	polylectic
Pasinger Stadtpark	*Andrena nitida*	*	polylectic
Pasinger Stadtpark	*Bombus campestris*	*	parasitic
Pasinger Stadtpark	*Bombus hortorum*	*	polylectic
Pasinger Stadtpark	*Bombus lapidarius*	*	polylectic
Pasinger Stadtpark	*Bombus lucorum/terrestris*	*	polylectic
Pasinger Stadtpark	*Bombus pascuorum*	*	polylectic
Pasinger Stadtpark	*Bombus sylvarum*	V	polylectic
Pasinger Stadtpark	*Bombus vestalis*	*	parasitic
Pasinger Stadtpark	*Chelostoma florisomne*	*	oligolectic: *Ranunculus*

above and below ground	KUN-00011	1682 m
groundnesting	KUN-00040, KUN-00010	x
above and below ground	KUN-00013, KUN-00034, KUN-00051	x
cavities above ground	KUN-00046	2172 m
cavities above ground	KUN-00047	2511 m
groundnesting	KUN-00028	2457 m
	KUN-00031	x
cavities above ground	KUN-00016	2457 m
cavities above ground	KUN-00015, KUN-00019, KUN-00025, KUN-00039	4245 m
groundnesting	MG846681	x
groundnesting	MG791992	x
groundnesting	barcode not abloaded due to bad sequence quality	2457 m
groundnesting	MG791984, MK268701, MG846668, MG791985	2457 m
host nest	KUN-00009	3967 m
groundnesting	PAS-00008, PAS-00046	x
groundnesting	PAS-00015, PAS-00045	x
groundnesting	PAS-00007	x
host nest	PAS-00063	x
above and below ground	PAS-00011, PAS-00049	x
above and below ground	PAS-00005, PAS-00053	x
groundnesting	PAS-00003, PAS-00044	x
above and below ground	PAS-00001, PAS-00033, PAS-00036	x
above and below ground	PAS-00032	x
host nest	PAS-00012	x
cavities above ground	PAS-00050	x

Pasinger Stadtpark	*Halictus rubicundus* group		
Pasinger Stadtpark	*Halictus subauratus*	*	polylectic
Pasinger Stadtpark	*Halictus tumulorum*	*	polylectic
Pasinger Stadtpark	*Hylaeus nigritus*	*	oligolectic: Asteraceae
Pasinger Stadtpark	*Lasioglossum calceatum*	*	polylectic
Pasinger Stadtpark	*Lasioglossum leucopus*	*	polylectic
Pasinger Stadtpark	*Lasioglossum pauxillum*	*	polylectic
Pasinger Stadtpark	*Megachile versicolor*	*	polylectic
Pasinger Stadtpark	*Nomada fabriciana*	*	parasitic
Pasinger Stadtpark	*Nomada fulvicornis*	*	parasitic
Pasinger Stadtpark	*Nomada goodeniana*	*	parasitic
Pasinger Stadtpark	*Nomada marshamella*	*	parasitic
Pasinger Stadtpark	*Osmia bicornis*	*	polylectic
Pasinger Stadtpark	*Sphecodes ephippius*	*	parasitic
Rathenaustraße	*Andrena cineraria*	*	polylectic
Rathenaustraße	*Andrena gravida*	*	polylectic
Rathenaustraße	*Andrena haemorrhoa*	*	polylectic
Rathenaustraße	*Andrena nitida*	*	polylectic
Rathenaustraße	*Andrena tibialis*	*	polylectic
Rathenaustraße	*Bombus hypnorum*	*	polylectic
Rathenaustraße	*Bombus lucorum/terrestris*	*	polylectic
Rathenaustraße	*Bombus pascuorum*	*	polylectic
Rathenaustraße	*Bombus sylvarum*	V	polylectic
Rathenaustraße	*Halictus scabiosae*	*	polylectic
Rathenaustraße	*Halictus subauratus*	*	polylectic
Rathenaustraße	*Halictus tumulorum*	*	polylectic
Rathenaustraße	*Heriades truncorum*	*	oligolectic: Asteraceae
Rathenaustraße	*Lasioglossum calceatum*	*	polylectic

	PAS-00041				x	
groundnesting	PAS-00025				x	
groundnesting	MG846688				x	
cavities above ground	PAS-00027				x	
groundnesting	loaded due to bad sequence quality				x	
groundnesting	MG846680					2081 m
groundnesting	MG846670, MG846671, MG846675					2081 m
cavities above ground	PAS-00028					2081 m
host nest	PAS-00022, PAS-00023, PAS-00024, PAS-00042				x	
host nest	PAS-00021, PAS-00043				x	
host nest	PAS-00018, PAS-00019, PAS-00020, PAS-00051					4110 m
host nest	PAS-00052				x	
cavities above ground	PAS-00009				x	
host nest	MK268697					2426 m
groundnesting	RAT-00023					1944 m
groundnesting	RAT-00005					1944 m
groundnesting	RAT-00006			x	x	
groundnesting	RAT-00007					3931 m
groundnesting	RAT-00024			x	x	
cavities above ground	observation only	x	x	x	x	
groundnesting	observation only	x	x	x	x	
above and below ground	observation only	x	x	x	x	
above and below ground	observation only				x	
groundnesting	RAT-00028					2430 m
groundnesting	RAT-00016				x	
groundnesting	MK442004, MG846685, MG846687, MG846689				x	
cavities above ground	RAT-00013	x	x	x	x	
groundnesting	MG846684	x	x	x	x	

Rathenaustraße	*Lasioglossum laticeps*	*	polylectic
Rathenaustraße	*Lasioglossum leucopus*	*	polylectic
Rathenaustraße	*Lasioglossum morio*	*	polylectic
Rathenaustraße	*Lasioglossum pauxillum*	*	polylectic
Rathenaustraße	*Nomada flavoguttata*	*	parasitic
Rathenaustraße	*Nomada guttulata*	*	parasitic
Rathenaustraße	*Osmia bicornis*	*	
Weitlstraße	*Andrena cineraria*	*	polylectic
Weitlstraße	*Anthidium oblongatum*	V	polylectic
Weitlstraße	*Bombus hortorum*	*	polylectic
Weitlstraße	*Bombus lapidarius*	*	polylectic
Weitlstraße	*Bombus lucorum/terrestris*	*	polylectic
Weitlstraße	*Bombus pascuorum*	*	polylectic
Weitlstraße	*Bombus pratorum*	*	polylectic
Weitlstraße	*Bombus sylvarum*	V	polylectic
Weitlstraße	*Chelostoma florisomne*	*	oligolectic: *Ranunculus*
Weitlstraße	*Chelostoma rapunculi*	*	oligolectic: *Campanula*
Weitlstraße	*Halictus scabiosae*	*	polylectic
Weitlstraße	*Halictus tumulorum*	*	polylectic
Weitlstraße	*Heriades truncorum*	*	oligolectic: Asteraceae
Weitlstraße	*Hylaeus communis*	*	polylectic
Weitlstraße	*Hylaeus nigritus*	*	oligolectic: Asteraceae
Weitlstraße	*Lasioglossum pauxillum*	*	polylectic
Weitlstraße	*Megachile rotundata*	*	

groundnesting	barcode not abloaded due to bad sequence quality	x	x	x	x	
groundnesting	barcode not abloaded due to bad sequence quality					2443 m
groundnesting	MG846677, MG846678		x	x	x	
groundnesting	MG846673, MG846674			x	x	
host nest	RAT-00015			x	x	
host nest	RAT-00014					no record in Munich in the last 20 years
	RAT-00004			x	x	
groundnesting	observation only					2462 m
cavities above ground	WEI-00010, WEI-00024					1868 m
above and below ground	WEI-00021					1868 m
above and below ground	WEI-00022			x	x	
groundnesting	observation only					1868 m
above and below ground	observation only					1868 m
above and below ground	WEI-00023					2006 m
above and below ground	WEI-00011, WEI-00016					1932 m
cavities above ground	WEI-00020					2704 m
cavities above ground	WEI-00027					1868 m
groundnesting	WEI-00014			x	x	
groundnesting	WEI-00029					2006 m
cavities above ground	WEI-00013			x	x	
cavities above ground	WEI-00012			x	x	
cavities above ground	WEI-00025			x	x	
groundnesting	MK441999, MK442000, MK442001, MG791986, MG846672			x	x	
	WEI-00019					1868 m

Weitlstraße	*Nomada cf fucata*	*	parasitic
Weitlstraße	*Sphecodes monilicornis*	*	parasitic
Werner-Seelenbinder-Weg	*Andrena cineraria*	*	polylectic
Werner-Seelenbinder-Weg	*Bombus lapidarius*	*	polylectic
Werner-Seelenbinder-Weg	*Bombus lucorum/terrestris*	*	polylectic
Werner-Seelenbinder-Weg	*Halictus tumulorum* group		
Werner-Seelenbinder-Weg	*Halictus scabiosae*	*	polylectic
Werner-Seelenbinder-Weg	*Lasioglossum calceatum*	*	polylectic
Werner-Seelenbinder-Weg	*Lasioglossum laticeps*	*	polylectic
Werner-Seelenbinder-Weg	*Lasioglossum leucozonium*	*	polylectic
Werner-Seelenbinder-Weg	*Lasioglossum pauxillum*	*	polylectic
Werner-Seelenbinder-Weg	*Megachile versicolor*	*	polylectic
Werner-Seelenbinder-Weg	*Megachile willughbiella*	*	polylectic
Werner-Seelenbinder-Weg	*Osmia bicornis*	*	polylectic
Willy-Brandt-Allee	*Bombus humilis*	3	polylectic
Willy-Brandt-Allee	*Bombus lapidarius*	*	polylectic
Willy-Brandt-Allee	*Bombus lucorum/terrestris*	*	polylectic
Willy-Brandt-Allee	*Bombus pascuorum*	*	polylectic
Willy-Brandt-Allee	*Bombus sylvarum*	*	polylectic
Willy-Brandt-Allee	*Halictus confusus* group		
Willy-Brandt-Allee	*Halictus erygnathus* group		
Willy-Brandt-Allee	*Halictus scabiosae*	*	polylectic
Willy-Brandt-Allee	*Halictus subauratus*	*	polylectic
Willy-Brandt-Allee	*Heriades truncorum*	*	oligolectic: Asteraceae
Willy-Brandt-Allee	*Hoplitis adunca*	*	oligolectic: *Echium*
Willy-Brandt-Allee	*Hylaeus communis*	*	polylectic

host nest	WEI-00007			2350 m
host nest	MG845964, MG845965	x	x	
groundnesting	WSW-00014		x	
above and below ground	WSW-00027	x	x	
groundnesting	WSW-00005		x	
	WSW-00017		x	
groundnesting	WSW-00025			3450 m
groundnesting	MG846682, MG846683		x	
groundnesting	MG846696		x	
groundnesting	MK441998			1723 m
groundnesting	barcode not abloaded due to bad sequence quality		x	
cavities above ground	WSW-00013			1587 m
cavities above ground	WSW-00026			1587 m
cavities above ground	observation only			1970 m
cavities above ground	WBA-00047			2076 m
above and below ground	WBA-00023, WBA-00031			1952 m
groundnesting	observation only			2076 m
above and below ground	WBA-00003, WBA-00048			1952 m
above and below ground	WBA-00028		x	
	WBA-00025			
	WBA-00032			
groundnesting	WBA-00027, WBA-00046			6052 m
groundnesting	WBA-00010, WBA-00016			4172 m
cavities above ground	observation only			2076 m
cavities above ground	WBA-00033			4108 m
cavities above ground	WBA-00040			1952 m

Willy-Brandt-Allee	*Hylaeus nigritus*	*	oligolectic: Asteraceae
Willy-Brandt-Allee	*Lasioglossum leucozonium* group		
Willy-Brandt-Allee	*Lasioglossum morio* group		
Willy-Brandt-Allee	*Nomada flava*	*	parasitic
Willy-Brandt-Allee	*Osmia spinulosa*	3	oligolectic: Asteraceae
Willy-Brandt-Allee	*Sphecodes puncticeps*	*	parasitic

1) Red List Stati: * = not threatened, V = pre-warning list, 3 = threatened
2) Diversity Work Bench accession numbers start with three letters for the site;
the remaining numbers are GenBank accessions of DNA barcodes.
Physical vouchers were deposited in the Zoologische Staatssammlung München.

cavities above ground	WBA-00006, WBA-00007 WBA-00008 WBA-00009 WBA-00022		2076 m
	WBA-00011, WBA-00020		
host nest	WBA-00004		7705 m
cavities above ground	WBA-00042	x	
host nest	MG845958		7705 m

Table S3. Species recorded within the last twenty years
at 500, 1000, and 1500 m distance from the respecitve flower strip

500 m	**1000 m**	**1500 m**
Altostraße		
n = 24	n = 43	n = 400
	Andrena bicolor	Andrena bicolor
		Andrena carantonica
		Andrena cineraria
		Andrena fulvata
		Andrena fulva
		Andrena haemorrhoa
		Andrena helvola
	Andrena minutula	Andrena minutula
		Andrena minutuloides
		Andrena nitida
		Andrena ovatula
		Andrena praecox
		Andrena subopaca
		Andrean varians
		Andrean ventralis
		Andrena viridescens
Andrena wilkella	Andrena wilkella	Andrena wilkella
		Anthidium manicatum
Anthidium oblongatum	**Anthidium oblongatum**	**Anthidium oblongatum**
	Anthidium punctatum	Anthidium punctatum
		Bombus barbutellus
		Bombus bohemicus
		Bombus hortorum
Bombus humilis	Bombus humilis	Bombus humilis
Bombus hypnorum	Bombus hypnorum	Bombus hypnorum
Bombus lapidarius	**Bombus lapidarius**	**Bombus lapidarius**
Bombus lucorum	**Bombus lucorum**	**Bombus lucorum**
Bombus pascouroum	**Bombus pascouroum**	**Bombus pascouroum**
Bombus pratorum	Bombus pratorum	Bombus pratorum
		Bombus rupestris
		Bombus soroeensis
		Bombus sylvarum
Bombus terrestris	**Bombus terrestris**	**Bombus terrestris**
Bombus vestalis	**Bombus vestalis**	**Bombus vestalis**
		Ceratina cyanea
Chelostoma rapunculi	Chelostoma rapunculi	Chelostoma rapunculi
		Coelioxys conica
		Colletes daviesanus
		Colletes similis
		Epeolus variegatus
	Halictus confusus	Halictus confusus
		Halictus eurygnathus
		Halictus maculatus
Halictus rubicundus	**Halictus rubicundus**	**Halictus rubicundus**

		Halictus scabiosae
Halictus simplex	Halictus simplex	Halictus simplex
		Halictus subauratus
		Halictus tumulorum
		Heriades truncorum
Hoplitis adunca	Hoplitis adunca	Hoplitis adunca
		Hoplitis claviventris
		Hoplitis leucomelana
		Hylaeus brevicornis
Hylaeus communis	**Hylaeus communis**	**Hylaeus communis**
		Hylaeus confusus
		Hylaeus gibbus
Hylaeus gracilicornis	Hylaeus gracilicornis	Hylaeus gracilicornis
		Hylaeus gredleri
		Hylaeus hyalinatus
Hylaeus nigritus	Hylaeus nigritus	Hylaeus nigritus
	Hylaeus signatus	Hylaeus signatus
		Lasioglossum albipes
Lasioglossum calceatum	Lasioglossum calceatum	Lasioglossum calceatum
Lasioglossum fulvicorne	Lasioglossum fulvicorne	Lasioglossum fulvicorne
Lasioglossum laticeps	Lasioglossum laticeps	Lasioglossum laticeps
		Lasioglossum leucopus
		Lasioglossum leucozonium
		Lasioglossum lineare
		Lasioglossum malachurum
Lasioglossum morio	Lasioglossum morio	Lasioglossum morio
		Lasioglossum nitidiusculum
		Lasioglossum nitidulum
Lasioglossum pauxillum	**Lasioglossum pauxillum**	**Lasioglossum pauxillum**
		Lasioglossum rufitarse
		Lasioglossum villosulum
		Lasioglossum zonulum
Megachile ericetorum	Megachile ericetorum	Megachile ericetorum
		Megachile nigriventris
		Megachile rotundata
	Megachile versicolor	Megachile versicolor
Megachile willughbiella	**Megachile willughbiella**	**Megachile willughbiella**
		Melitta haemorrhoidalis
		Melitta lepornia
		Nomada flava
		Nomada flavoguttata
		Nomada fucata
		Nomada marshamella
		Nomada moeschleri
		Nomada panzeri
		Nomada succincta
	Osmia bicornis	Osmia bicornis
		Osmia claviventris
		Osmia rufohirta
	Osmia spinulosa	Osmia spinulosa

		Panurgus banksianus
		Pseudoanthidium nanum
		Sphecodes crassus
		Sphecodes ephippius
	Sphecodes ferruginatus	Sphecodes ferruginatus
		Sphecodes gibbus
		Sphecodes miniatus
		Sphecodes monilicornis
		Sphecodes puncticeps
		Sphecodes rufiventris
		Trachusa byssina
Biedersteinstraße		
	n = 50	n = 149
	Andrena bicolor	**Andrena bicolor**
	Andrena chrysosceles	Andrena chrysosceles
	Andrena cineraria	**Andrena cineraria**
		Andrena denticulata
		Andrena labialis
		Andrena fulva
	Andrena gravida	Andrena gravida
		Andrena haemorrhoa
	Andrena hattorfiana	Andrena hattorfiana
	Andrena helvola	Andrena helvola
	Andrena labialis	Andrena labialis
		Andrena minutula
		Andrena minutuloides
		Andrena mitis
		Andrena nitida
		Andrena ovatula
	Andrena proxima	Andrena proxima
	Andrena subopaca	Andrena subopaca
	Andrena tibialis	Andrena tibialis
	Andrena vaga	Andrena vaga
	Andrena ventralis	Andrena ventralis
		Andrena viridescens
		Andrena wilkella
	Anthidium manicatum	**Anthidium manicatum**
	Anthophora plumipes	Anthophora plumipes
		Bombus distinguendus
		Bombus pomorum
		Bombus barbutellus
		Bombus campestris
		Bombus humilis
		Bombus hypnorum
		Bombus lapidarius
		Bombus muscorum
	Bombus pascuorum	**Bombus pascuorum**
		Bombus pratorum
		Bombus ruderarius

		Bombus rupestris
		Bombus soroeensis
		Bombus subterraneus
		Bombus sylvarum
		Bombus terrestris
	Bombus vestalis	Bombus vestalis
		Ceratina cyanea
	Colletes cunicularius	Colletes cunicularius
	Halictus rubicundus	**Halictus rubicundus**
	Halictus tumulorum	**Halictus tumulorum**
		Hylaeus communis
		Hylaeus hyalinatus
	Hylaeus signatus	**Hylaeus signatus**
		Hylaeus styriacus
	Lasioglossum albipes	**Lasioglossum albipes**
	Lasioglossum calceatum	Lasioglossum calceatum
		Lasioglossum laticeps
	Lasioglossum leucozonium	Lasioglossum leucozonium
	Lasioglossum malachurum	Lasioglossum malachurum
		Lasioglossum nitidulum
	Lasioglossum pauxillum	**Lasioglossum pauxillum**
		Lasioglossum sexstrigatum
		Lasioglossum zonulum
	Nomada alboguttata	Nomada alboguttata
	Nomada fabriciana	Nomada fabriciana
	Nomada fulvicornis	Nomada fulvicornis
	Nomada goodeniana	Nomada goodeniana
	Nomada lathburiana	Nomada lathburiana
		Nomada marshamella
		Nomada panzeri
	Nomada ruficornis	Nomada ruficornis
		Nomada signata
		Osmia bicornis
	Sphecodes albilabris	Sphecodes albilabris
		Sphecodes crassus
	Sphecodes ephippius	Sphecodes ephippius
	Sphecodes monilicornis	**Sphecodes monilicornis**
		Xylocopa violacea
Fockensteinstraße		
n = 1	n = 1	n = 79 (observations from 1600 m distance)
		Andrena bicolor
		Andrena chrysosceles
		Andrena cineraria
		Andrena flavipes
		Andrena fulva
		Andrena fulvata
		Andrena gravida
		Andrena intermedia

		Andrena minutula
		Andrena ovatula
		Andrena praecox
		Andrena semilaevis
		Andrena subopaca
		Andrena tibialis
		Andrena viridescens
		Andrena wilkella
		Anthidium manicatum
		Anthidium oblongatum
		Anthidium punctatum
		Anthophora plumipes
		Anthophora quadrimaculata
		Bombus humilis
		Bombus hypnorum
		Bombus lapidarius
		Bombus lucorum
		Bombus pascuorum
Bombus terrestris	**Bombus terrestris**	**Bombus terrestris**
		Ceratina cyanea
		Chelostoma rapunculi
		Halictus rubicundus
		Halictus scabiosae
		Halictus subauratus
		Halictus tumulorum
		Heriades truncorum
		Hoplitis adunca
		Hoplitis leucomelana
		Hylaeus brevicornis
		Hylaeus communis
		Hylaeus confusus
		Hylaeus gracilicornis
		Hylaeus gredleri
		Hylaeus hyalinatus
		Hylaeus rinki
		Hylaeus signatus
		Hylaeus sinuatus
		Lasioglossum albipes
		Lasioglossum calceatum
		Lasioglossum fulvicorne
		Lasioglossum laticeps
		Lasioglossum leucopus
		Lasioglossum leucozonium
		Lasioglossum morio
		Lasioglossum nitidulum
		Lasioglossum pauxillum
		Lasioglossum villosulum
		Macropis europaea
		Macropis fulvipes
		Megachile ericetorum

		Megachile rotundata
		Megachile willughbiella
		Melecta albifrons
		Nomada fabriciana
		Nomada flava
		Nomada flavoguttata
		Nomada marshamella
		Nomada signata
		Osmia aurulenta
		Osmia bicolor
		Osmia bicornis
		Osmia caerulescens
		Osmia cornuta
		Sphecodes ephippius
		Sphecodes ferruginatus
		Sphecodes monilicornis
		Stelis breviuscula
		Stelis ornatula
Kuntersweg		
n = 1	n = 1	n = 72
		Andrena barbilabris
		Andrena cineraria
		Andrena denticulata
		Andrena flavipes
		Andrena fucata
		Andrena haemorrhoa
		Andrena helvola
		Andrena nitida
		Andrena praecox
		Andrena wilkella
		Bombus bohemicus
		Bombus hortorum
		Bombus humilis
		Bombus pascouroum
		Bombus ruderatus
		Bombus soroeensis
		Bombus subterraneus
		Bombus sylvarum
		Bombus terrestris
		Bombus vestalis
		Bombus veteranus
		Coelioxys aurolimbata
		Coelioxys rufescens
		Chelostoma florisomne
		Dufourea dentiventris
		Eucera longicornis
		Halictus simplex
Halictus tumumlorum	**Halictus tumumlorum**	**Halictus tumumlorum**
		Hoplitis villosa

	Hylaeus communis
	Hylaeus sinuatus
	Lasioglossum calceatum
	Lasioglossum latriventre
	Lasioglossum leucozonium
	Lasioglossum sexnotatum
	Macropis europaea
	Macropis fulvipes
	Megachile circumcincta
	Megachile versicolor
	Nomada braunsiana
	Nomada facilis
	Nomada ferruginata
	Nomada fucata
	Nomada goodeniana
	Nomada marshamella
	Osmia aurulenta
	Osmia bicolor
	Osmia leaiana
	Osmia parietina
	Osmia xanthomelana
	Stelis phaeoptera
	Trachusa byssina
Pasinger Stadtpark	n = 329
	Andrena bicolor
	Andrena bucephala
	Andrena carantonica
	Andrena chrysopyga
	Andrena cineraria
	Andrena coitana
	Andrena combinata
	Andrena decipiens
	Andrena denticulata
	Andrena dorsata
	Andrena flavipes
	Andrena floricola
	Andrena fulvata
	Andrena fulvida
	Andrena gravida
	Andrena gelriae
	Andrena haemorrhoa
	Andrena hattorfiana
	Andrena helvola
	Andrena humilis
	Andrena labiata
	Andrena labialis
	Andrena lathyri

Andrena minutula
Andrena nigroaenea
Andrena nitida
Andrena nitiduscula
Andrena ocreata
Andrena pandellei europaea
Andrena pilipes
Andrena praecox
Andrena proxima
Andrena rosae
Andrena ruficrus
Andrena schencki
Andrena symphyti
Andrena synadelpha
Andrena tibialis
Andren thoracica
Andrena vaga
Andrena ventralis
Andrena wilkella
Anthophora furcata
Anthophora plumipes
Bombus barbutellus
Bombus bohemicus
Bombus campestris
Bombus confusus
Bombus hortorum
Bombus humilis
Bombus hypnorum
Bombus jonellus
Bombus lapidarius
Bombus pascuorum
Bombus pomorum
Bombus quadricolor
Bombus ruderarius
Bombus ruderatus
Bombus rupestris
Bombus soroeensis
Bombus subterraneus
Bombus sylvarum
Bombus sylvestris
Bombus terrestris
Bombus vestalis
Bombus veteranus
Bombus wurfleini mastrucatus
Ceratina cyanea
Chelostoma campanularum
Chelostoma florisomne
Chelostoma rapunculi
Coelioxys conica
Colletes conicularis

Colletes daviesanus
Colletes similis
Epeolus variegatus
Eucera longicornis
Eucera nigrescens
Halictus maculatus
Halictus rubicundus
Halictus simplex
Halictus subauratus
Halictus tumulorum
Hoplitis leucomelana
Hoplitis mitis
Hylaeus brevicornis
Hylaeus communis
Hylaeus difformis
Hylaeus hyalinatus
Hylaeus nigritus
Hylaeus punctulatissimus
Hylaeus signatus
Hylaeus sinuatus
Lasioglossum calceatum
Lasioglossum costulatum
Lasioglossum fulvicorne
Lasioglossum laevigatum
Lasioglossum laticeps
Lasioglossum leucozonium
Lasioglossum quadrinotatulum
Lasioglossum sabulosum
Lasioglossum sexnotatum
Lasioglossum villosulum
Lasioglossum xanthopus
Lasioglossum zonulum
Macropis europaea
Megachile centuncularis
Megachile circumcincta
Megachile ericetorum
Megachile lagopoda
Megachile ligniseca
Megachile nigriventris
Megachile willughbiella
Melitta haemorrhoidalis
Melitta nigricans
Melitta tricincta
Nomada alboguttata
Nomada braunsiana
Nomada errans
Nomada fabriciana
Nomada ferruginata
Nomada flava
Nomada flavoguttata

		Nomada fucata
		Nomada fulvicornis
		Nomada furva
		Nomada hirtipes
		Nomada integra
		Nomada kohli
		Nomada lathburiana
		Nomada leucophthalma
		Nomada marshamella
		Nomada obscura
		Nomada obtusifrons
		Nomada opaca
		Nomada panzeri
		Nomada roberjeotiana
		Nomada ruficornis
		Nomada rufipes
		Nomada sexfasciata
		Nomada striata
		Nomada succincta
		Osmia aurulenta
		Osmia bicornis
		Osmia caerulescens
		Osmia cerinthidis
		Osmia claviventris
		Osmia leaiana
		Osmia lepeletieri
		Osmia rufohirta
		Osmia uncinata
		Panurgus banksianus
		Panuurgus calcaratus
		Sphecodes ferruginatus
		Stelis punctulatissima
		Trachusa byssina
Rathenaustraße		
n = 39	n = 79	n = 117
	Andrena bicolor	Andrena bicolor
		Andrena carantonica
	Andrena chrysosceles	Andrena chrysosceles
	Andrena falsifica	Andrena falsifica
Andrena flavipes	Andrena flavipes	Andrena flavipes
	Andrena fulva	Andrena fulva
	Andrena haemorrhoa	**Andrena haemorrhoa**
		Andrena hattorfiana
		Andrena humilis
	Andrean minutula	Andrean minutula
	Andrena minutuloides	Andrena minutuloides
	Andrena tibialis	**Andrena tibialis**
	Andrena viridescens	Andrena viridescens
		Andrena wilkella

Anthidium manicatum	Anthidium manicatum	Anthidium manicatum
Anthidium oblongatum	Anthidium oblongatum	Anthidium oblongatum
Bombus bohemicus	Bombus bohemicus	Bombus bohemicus
Bombus hortorum	Bombus hortorum	Bombus hortorum
		Bombus humilis
Bombus hypnorum	**Bombus hypnorum**	**Bombus hypnorum**
Bombus lapidarius	Bombus lapidarius	Bombus lapidarius
Bombus lucorum	**Bombus lucorum**	**Bombus lucorum**
Bombus pascouroum	**Bombus pascouroum**	**Bombus pascouroum**
		Bombus pratorum
		Bombus rupestris
		Bombus sylvarum
		Bombus terrestris
		Bombus vestalis
Ceratina cyanea	Ceratina cyanea	Ceratina cyanea
Chelostoma campanularum	Chelostoma campanularum	Chelostoma campanularum
	Chelostoma rapunculi	Chelostoma rapunculi
		Halictus eurygnathus
	Halictus rubicundus	Halictus rubicundus
		Halictus simplex
		Halictus subauratus
		Halictus tumulorum
Heriades truncorum	**Heriades truncorum**	**Heriades truncorum**
Hoplitis adunca	Hoplitis adunca	Hoplitis adunca
Hylaeus communis	Hylaeus communis	Hylaeus communis
		Hylaeus confusus
Hylaeus hyalinatus	Hylaeus hyalinatus	Hylaeus hyalinatus
Hylaeus nigritus	Hylaeus nigritus	Hylaeus nigritus
Hylaeus signatus	Hylaeus signatus	Hylaeus signatus
		Hylaeus sinuatus
	Lasioglossum albipes	Lasioglossum albipes
Lasioglossum calceatum	**Lasioglossum calceatum**	**Lasioglossum calceatum**
		Lasioglossum laevigatum
Lasioglossum laticeps	**Lasioglossum laticeps**	**Lasioglossum laticeps**
Lasioglossum leucozonium	Lasioglossum leucozonium	Lasioglossum leucozonium
Lasioglossum morio	**Lasioglossum morio**	**Lasioglossum morio**
	Lasioglossum pauxillum	**Lasioglossum pauxillum**
		Megachile ericetorum
Megachile rotundata	Megachile rotundata	Megachile rotundata
Megachile versicolor	Megachile versicolor	Megachile versicolor
Megachile willughbiella	Megachile willughbiella	Megachile willughbiella
	Nomada flavoguttata	**Nomada flavoguttata**
	Nomada fulvicornis	Nomada fulvicornis
	Osmia aurulenta	Osmia aurulenta
	Osmia bicolor	Osmia bicolor
	Osmia bicornis	**Osmia bicornis**
Osmia caerulescens	Osmia caerulescens	Osmia caerulescens

	Osmia claviventris	Osmia claviventris
	Osmia spinulosa	Osmia spinulosa
	Sphecodes crassus	Sphecodes crassus
		Sphecodes ferruginatus
	Sphecodes geoffrellus	Sphecodes geoffrellus
	Sphecodes gibbus	Sphecodes gibbus
	Sphecodes miniatus	Sphecodes miniatus
	Sphecodes monilicornis	Sphecodes monilicornis
Weitlstraße		
	n = 15	n = 19
		Andrena chrysosceles
	Anthidium strigatum	Anthidium strigatum
	Bombus humilis	Bombus humilis
	Bombus lapidarius	**Bombus lapidarius**
	Ceratina cyanea	Ceratina cyanea
	Halictus rubicundus	Halictus rubicundus
	Halictus scabiosae	**Halictus scabiosae**
	Heriades truncorum	**Heriades truncorum**
	Hylaeus communis	**Hylaeus communis**
	Hylaeus nigritus	**Hylaeus nigritus**
	Lasioglossum calceatum	Lasioglossum calceatum
	Lasioglossum laticeps	Lasioglossum laticeps
	Lasioglossum morio	Lasioglossum morio
	Lasioglossum pauxillum	**Lasioglossum pauxillum**
	Lasioglossum villosulum	Lasioglossum villosulum
	Sphecodes monilicornis	**Sphecodes monilicornis**
Werner-Seelenbinder-Weg		
	n = 8	n = 78
		Andrena cineraria
		Andrena minutula
		Andrena nitida
		Andrena ovatula
		Anthidium manicatum
		Anthidium oblongatum
		Anthidium strigatum
		Bombus barbutellus
		Bombus campestris
		Bombus distinguendus
		Bombus humilis
		Bombus hypnorum
	Bombus lapidarius	**Bombus lapidarius**
		Bombus lucorum
	Bombus pascouroum	Bombus pascouroum
	Bombus pomorum	Bombus pomorum
	Bombus ruderarius	Bombus ruderarius
	Bombus rupestris	Bombus rupestris
		Bombus soroeensis
		Bombus subterraneus
		Bombus sylvarum

		Bombus terrestris
		Bombus vestalis
		Ceratina cyanea
		Halictus confusus
		Halictus rubicundus
		Halictus tumulorum
		Heriades truncorum
		Hoplitis adunca
		Hylaeus communis
		Hylaeus confusus
		Hylaeus nigritus
	Lasioglossum albipes	Lasioglossum albipes
		Lasioglossum calceatum
		Lasioglossum fulvicorne
		Lasioglossum laticeps
		Lasioglossum morio
		Lasioglossum pauxillum
		Lasioglossum sexstrigatum
		Lasioglossum villosulum
		Macropis fulvipes
		Megachile rotundata
		Nomada lathburiana
		Osmia bicolor
		Osmia caerulescens
	Sphecodes ephippius	Sphecodes ephippius
		Sphecodes gibbus
		Sphecodes marginatus
		Sphecodes monilicornis
Willy-Brandt-Allee		n = 19 (observations from 1600 m distance)
		Andrena flavipes
		Andrena wilkella
		Anthidium punctatum
		Bombus sylvarum
		Ceratina cyanea
		Halictus simplex
		Halictus tumulorum
		Hylaeus signatus
		Lasioglossum calceatum
		Megachile circumcincta
		Nomada flavoguttata
		Nomada marshamella
		Osmia aurulenta
		Osmia bicolor
		Osmia spinulosa

Chapter 7

Bee species recorded between 1992 and 2017 from green roofs in Asia, Europe, and North America, with key characteristics and open research questions

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Review article

Bee species recorded between 1992 and 2017 from green roofs in Asia, Europe, and North America, with key characteristics and open research questions

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Abstract – Green roofs, which have become mandatory on new flat-topped buildings in many cities, increase habitat connectivity for wildlife and have contributed to a boom in urban beekeeping. The ecological benefits or risks of green roofs for wild bees (bee species other than the domesticated honey bee, *Apis mellifera*), however, have not been comprehensively analyzed. We therefore reviewed studies on insects caught on green roofs in Asia, Europe, or North America between 1992 and early 2017 and extracted information on wild bees. The resulting species list includes 236 Apidae identified in 35 studies, with thermophilic species probably overrepresented because roofs provide warm and dry habitats. The percentage of cavity-nesting bees on roofs is higher than that on nearby ground, while the percentage of pollen specialists is lower. Data are almost completely lacking on the reproductive success of bees on green roofs, the effect of roof age on bee diversity, and the genetic or demographic benefits of increased habitat connectivity. Our list of the bee species so far reported on green roofs will help in the selection and implementation of suitable soils, nesting aids, and plantings.

Bees / Cavity-nesting species / Ground-nesting species / Species diversity / Urban habitats

1. INTRODUCTION

The past 20 years have seen a dramatic increase in research on green roofs (reviewed in Bowler et al. 2010 and Blank et al. 2013), which are now mandatory on flat-topped buildings in Switzerland and a few other European countries and supported by incentives in the USA (Brenneisen 2006; Stutz 2010). Although there are different types of green roofs, one can generally distinguish between intensive and extensive roof greening. Intensive green roofs usually have a soil layer of at least 15 cm and sometimes up to 60 cm or more (Mann 1994), while extensive green roofs have only a thin layer of soil (5–15 cm), supporting mostly mosses, herbs, succulents, and grasses (Gedge and Kadas 2005). Roofs with shallow soil layers are a difficult growing environment for plants because of moisture stress, severe drought, and full exposure to sun and wind (Schneider and Riedmiller 1992; Dunnett and Kingsbury 2008). On the other hand, extensive roofs require minimal maintenance and can be self-sustaining.

Ecosystem services from green roofs include storm-water management (Getter and Rowe 2008; Berndtsson 2010), moderation of the urban heat island effect (Takebayashi and Moriyama 2007; Tabares-Velasco et al. 2012), lower building temperatures (Oberndorfer et al. 2007), and a role as urban wildlife habitat (for reviews, see Fernandez-Canero and Gonzalez-Redondo 2010, Williams et al. 2014, and Gonsalves 2016). An important aspect for the latter role is that green roofs are undisturbed by humans during most of the year, making them quiet

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habitats with low pesticide loads (Hui and Chan 2011). They also increase habitat connectivity for certain arthropods (Braaker et al. 2014).

Of the many arthropods living on green roofs, bees stand out because of their role as pollinators and because urban beekeepers tend to find beekeeping "restorative and empowering" (Moore and Cost 2013). While urban beekeeping has led to an increase of the density of honey bees in cities, the past 50 years have seen a decline in the abundance of wild bee species, attributed mostly to habitat loss and pesticides (Goulson et al. 2008), although hard data on change in bee abundances in urban spaces over time are scarce. Wild bees, most of which are solitary bees, are expected to benefit from the newly created habitat on green roofs because they may be able to forage both on the ground and on green roofs, and thermophilic species might also find nesting opportunities on green roofs. Surprisingly, however, the effects of green roofs on the diversity and abundance of wild bees in cities have received little attention despite repeated calls for bee-targeted green roof research (Zurbuchen and Müller 2012; Witt 2016). We here provide the first list of bee species recorded from green roofs, summarize key ecological traits of these bees, and point to important open questions about the role of green roofs as habitat for solitary bees.

2. MATERIALS AND METHODS

We searched relevant keywords, such as "green roof" (or "living roof," or "Gründach"), and "bee" (or hymenoptera or Wildbienen), using the search engines Web of Science (http://www.isiknowledge.com), ScienceDirect (http://www.sciencedirect.com), Google Scholar (https://scholar.google.de), and Google (https://www.google.de). We also included online-only journals, B.Sc., M.Sc., and diploma reports, and doctoral theses. Abstracts were checked to see whether a study covered wild bees on green roofs, and studies exclusively dealing with urban beekeeping were excluded because honeybees are a managed species.

Each found study was scanned for the following information: (i) Where and when was the study conducted? (ii) How many roofs were investigated and which sampling technique was used? (iii) Which roof type (extensive or intensive) was investigated and were there non-roof reference areas? (iv) Which taxa were found? Were the specimens identified to species level? Results were tabulated and a species list was created as a basis for future work on green-roof-occurring species.

3. RESULTS AND DISCUSSION

Based on the criteria laid out above, we found 35 studies dealing, at least partially, with wild bees on green roofs (Table S1, Supplementary Material). Compared to the 300 peer-reviewed studies about green roofs available by 2013 (Blank et al. 2013; a number supported by our search) and the large numbers of hits when searching for "green roof" on ScienceDirect ($n = 1982$, accessed 1 March 2017) or the Web of Science ($n = 916$, accessed 1 March 2017), a number of just 35 studies mentioning wild bees on green roofs is low. Almost 40% of these 300 publications on green roofs deal with engineering aspects, and another 37% with general aspects of the environment and ecology. Only 3% are assigned to the ISI category biodiversity conservation (Blank et al. 2013), a category that encompasses studies on plants, birds, beetles, collembolans, soil arthropods, spiders, and other invertebrates (Williams et al. 2014). Of the 35 studies, eight fully focus on wild bees (Brenneisen 2005; Colla et al. 2009; Tonietto et al. 2011; Ksiazek et al. 2012, 2014; Kratschmer 2015; MacIvor et al. 2015; Walker 2016); the remaining 27 included hymenopterans other than bees. The longest species lists contain 77 (Brenneisen 2006), 79 (Colla et al. 2009), 91 (Kratschmer 2015), or 126 species (Braaker et al. 2014), showing that green roofs are indeed an important habitat for wild bees.

Especially thermophilic species (not only bees but also other arthropods) adapted to living under dry conditions have been reported from green roofs, including a few rare species (Jones 2002; Kadas 2006; MacIvor and Lundholm 2011; Kratschmer 2015). Generally, intensive green roofs, have a higher bee diversity and abundance than extensive green roofs (Brenneisen 2006; Madre et al. 2013; Kratschmer 2015; Witt 2016), and unsurprisingly green roofs with a higher number of plant species tend to have a higher number of bee species (Köhler 2014).

So far, 236 species have been recorded on green roofs (Table S2, Supplementary Material), with several additional species present, but not identified to species level (at least $n = 13$). Several studies, unfortunately, mention species lists in the text, but fail to make them available (Mann 1996a, b; Köhler 2014; Braaker et al. 2014, 2017). Of the 236 species, 151 are from Europe and 72 from North America. Eleven species were found both in Europe and America. The only Asian study of bees on green roofs reported three species, including the honey bee (Nagase and Nomura 2014). For Africa and Australia, no studies about wild bees on green roofs were found.

Only three studies provide data on bee foraging behavior (Mann 1994; Kratschmer 2015; Witt 2016). All showed that oligolectic species are underrepresented on green roofs. While it is not known how many of the estimated 20,000 species of wild bees worldwide are oligolectic (Michener 2007), green roofs appear to be used by few oligolectic bees: Thus, 11% of the species found on green roofs in Vienna, Austria, and Hannover, Germany, were oligolectic (Kratschmer 2015; Witt 2016) and 4% of those on a roof in Böblingen, Germany (Mann 1994), while the number of oligolectic species in the Austrian, German, and Swiss bee faunas overall is ca. 30% (Zurbuchen and Müller, 2012: p. 26), which for Germany would be 193 (Schmidt et al. 2015). These findings fit with a noted decrease in foraging specialists among insect species in urban compared to rural areas (Hernandez et al. 2009).

Another "green roof bee fauna" characteristic is the high proportion of cavity-nesting compared to ground-nesting species. Of the ca. 580 wild bee species in Germany, Liechtenstein, Austria, and Switzerland (Schmidt et al. 2015), some 50% breed in the ground, 23% above ground, and 25% are parasites, but even in Europe, the nesting sites of at least 23 species are unknown (Zurbuchen and Müller, 2012: p. 57). On green roofs in Vienna, 31% of the wild bee species nested above ground (Kratschmer 2015) and in Chicago 30 to 35% (Tonietto et al. 2011; Ksiazek et al. 2014). By comparison, 40% of the green roof species in Vienna nested in the ground (Kratschmer 2015) and 60 to 70% of those in Chicago (Ksiazek et al. 2014; Tonietto et al. 2011). The latter high percentages may be partly a collecting artifact, since ground-nesting species are more likely to be caught in pan traps, which was the method used in these studies. Artificial nesting aids on green roofs may increase the species diversity of cavity-nesting bees, but if they are installed on the roofs of high raises, reproductive success, measured as finished brood cells, may be low (MacIvor 2016). Artificial nesting sites for ground-nesting bees, consisting of sand and earth layers with a thickness of 20 cm, can be sufficient for bees to nest (Brenneisen et al. 2014).

Regarding body size, one would expect relatively many large species on green roofs, since they have larger foraging distances and therefore may detect vertically distant foraging grounds more readily than small bee species (Greenleaf et al. 2007). Indeed, MacIvor et al. (2015) found more medium and large than small bees on green roofs in Toronto, Canada, but small bees dominated the species spectrum on roofs in Chicago and Vienna (Ksiazek et al. 2012; Kratschmer 2015). These different results may be partly explained by these authors' different collecting methods, namely netting vs. pan trapping. Small bees were especially frequent, when the soil depth exceeded 20 cm (Kratschmer 2015). Further studies are required to understand the correlation of green-roof nesting and bee body size, itself related to foraging distance, which is of prime importance in the successful reproduction of bees nesting on roofs.

Few of the plants that do well on green roofs are good nectar and pollen sources for wild bees, most important among them probably the species of *Sedum* (MacIvor et al. 2015), but the number of plant species on green roofs is extremely low compared to that on ground-level habitats (MacIvor and Lundholm 2011; Tonietto et al. 2011; Ksiazek et al. 2012, 2014; Braaker et al. 2014, 2017), and in spite of "habitat connectivity" (enhancing both gene flow and numbers of individuals) being among the most often quoted benefits of green roofs, only a single study so far has provided data supporting this notion (Braaker et al. 2014, 2017).

Table I summarizes expectations and findings about the species diversity and life history types of bees on green roofs. Based on the available data (Table I; Supplementary Material: Tables S1, S2),

Table I. Trends observed in bee size, diet, and nesting habitat when comparing bees from green roofs and nearby ground-level habitats

Green roof features	Predicted consequences for bee diversity	Results from the 35 studies reviewed here
Green roofs are hot and dry habitats.	Thermophilic species predominate on green roofs.	Increased proportion of thermophilic species (Jones 2002; Kadas 2006; MacIvor and Lundholm 2011; Kratschmer 2015)
Intensive roofs have higher plant diversity than extensive roofs.	Higher plant diversity can support higher bee diversity.	Higher abundances and species numbers on intensive, biodiverse green roofs (Köhler 2014; Brenneisen 2006; Madre et al. 2013; Kratschmer 2015; Witt 2016)
Reduced plant species numbers compared to ground-level habitats	Insufficient food supply for specialist bees	Oligolectic bee species are underrepresented on green roofs (Mann 1994; Kratschmer 2015; Witt 2016).
Extensive green roofs have a thin soil layer.	Ground-nesting species, especially larger species with deep nests, cannot breed on green roofs.	Increased proportion of cavity-nesting species compared to ground-nesting species (Tonietto et al. 2011; Ksiazek et al. 2014, Kratschmer 2015)
Green roofs are planted on buildings, thus more or less high above ground.	Vertical isolation from ground habitats is especially hard to overcome for small bee species.	Large and medium-sized species are some times overrepresented (MacIvor et al. 2015) but not always (Ksiazek et al. 2012; Kratschmer 2015).

more work is needed to better understand the potential of green roofs as an urban bee habitat. Thus, there are still no solid data on how readily wild (solitary and semi-social) bees change between roofs and ground-level habitats for foraging or nesting or whether they ever travel between different roofs (i.e., whether roofs connect habitats). Marking experiments are urgently required, such as have long been successfully applied in studies of other insects (Walker and Wineriter 1981; for reviews see Hagler and Jackson 2001). There are also only anecdotal observations of roof-breeding bees (e.g., Kratschmer 2015), rather than hard data on the breeding success or failure of bees that have accepted the nesting aids installed on green roofs. If green roofs are intended as an alternative habitat for bees, it is crucial to understand how well they can reproduce there. Otherwise, the risk that green roofs may become an "ecological trap," that is, habitats that cannot sustain reproducing populations (Donovan and Thompson 2001), is high, meaning that species accept green roofs for nesting, but then fail to rear their brood. This is the case in some ground-breeding birds, such as lapwings (*Vanellus vanellus*), that built nests on green roofs, but with low chick survival due to insufficient food and water on the roofs (Baumann 2006).

Another open question is the speed of colonization by wild bees of newly established green roofs and their development as bee habitat over time. Studies on this topic so far have focused on plants (Köhler 2006; Emilsson 2008; Nagase and Nomura 2014; Deng and Jim 2016; Lundholm 2016; but see Kadas 2006).

4. CONCLUSIONS

Despite public awareness of the importance of wild bees as pollinators of most flowering plants and the current enthusiasm for urban beekeeping (Moore and Kosut 2013), little is known about the role of green roofs as a habitat for wild bees, in terms of both foraging and for successful nesting. Small-scale local conditions determine the nest-site selection by bees in general as well as in urban areas (Everaars et al. 2011), and artificial nesting aids matching the preferences of specific bee species could promote bee reproduction on green roofs. Our list of the 236 species of wild bees that have so far been reported on green roofs (Table S2, Supplementary Material) will help in the selection and implementation of suitable soils, cavity-providing structures, or plants addressed to species managing to breed on green roofs. The promise of green roofs as urban bee habitat will only be fulfilled with more research on wild bees' requirements for successful reproduction.

CONTRIBUTIONS

MH compiled the data and wrote the first draft; MH and SSR co-wrote the final draft. Both authors read and approved the final manuscript.

Espèces d'abeilles inventoriées entre 1992 et 2017 sur les toits végétalisés en Asie, Europe et Amérique du Nord, avec leurs principales caractéristiques et des questions de recherche ouvertes

Abeilles / espèces nichant dans des cavités / espèces nichant au sol / diversité des espèces / habitats urbains

Bienenarten, die zwischen 1992 und 2017 auf Gründächern in Asien, Europa und Nordamerika nachgewiesen wurden, einschließlich von Schlüsselmerkmalen und bisher ungeklärten Forschungsfragen

Solitärbienen / höhlenbrütende Arten / bodenbrütende Arten / Artenvielfalt / urbane Habitate

REFERENCES

Baumann, N. (2006) Ground-nesting birds on green roofs in Switzerland: preliminary observations. Urban Habitats **4** , 37–50.

Berndtsson, J.C. (2010) Green roof performance towards management of runoff water quantity and quality: A review. Ecol. Eng. **36** , 351–360.

Blank, L., Vasl, A., Levy, S., Grant, G., Kadas, G., Dafni, A., Blaustein, L. (2013) Directions in green roof research: A bibliometric study. Build. Environ. **66** , 23–28.

Bowler, D.E., Buyung-Ali, L., Knight, T.M., Pullin, A.S. (2010) Urban greening to cool towns and cities: A systematic review of the empirical evidence. Landsc. Urban Planning **97** , 147–155.

Braaker, S., Ghazoul, J., Obrist, M.K., Moretti, M. (2014) Habitat connectivity shapes urban arthropod communities: the key role of green roofs. Ecology **95** , 1010–1021.

Braaker, S., Obrist, M.K., Ghazoul, J., Moretti, M. (2017) Habitat connectivity and local conditions shape taxonomic and functional diversity of arthropods on green roofs. J. Anim. Ecol. **86** : 521–531.

Brenneisen, S. (2005) The natural roof (NADA). Research project report of the use of extensive green roofs by wild bees. University of Wädenswil, Wädenswil, Switzerland.

Brenneisen, S. (2006) Space for urban wildlife: designing green roofs as habitats in Switzerland. Urban Habitats **4** , 27–36.

Brenneisen, S., Käppeli, S., Schneider, R. (2014) Förderung gefährdeter Wildbienen auf Flachdächern - Forschungsprojekt im Mandat für Pro Natura. https://www.zhaw.ch/no_cache/en/research/people-publications-projects/detail-view-project/projekt/1835/ (accessed April 10, 2017).

Coffman, R.R., Waite, T. (2011) Vegetated roofs as reconciled habitats: rapid assays beyond mere species counts. Urban Habitats 6 (electronic journal). http://www.urbanhabitats.org/v06n01/vegetatedroofs_full.html

Colla, S.R., Willis, E., Packer, L. (2009) Can green roofs provide habitat for urban bees (Hymenoptera: Apidae)? Cities Environ. **2** (4), 1–12.

Deng, H., Jim, C.Y. (2016) Spontaneous plant colonization and bird visits of tropical extensive green roof. Urban Ecosyst. **20** , 1–16.

Donovan, T. M., Thompson, F. R. (2001) Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecol. Appl. 11(3), 871–882.

Dunnett, N., Kingsbury N. (2008) Planting green roofs and living walls, 2nd edition. Timber Press, Portland, OR, USA.

Emilsson, T. (2008) Vegetation development on extensive vegetated green roofs: influence of substrate composition, establishment method and species mix. Ecol. Eng. **33** , 265–277.

Everaars, J., Strohbachm, M.W., Gruber, B., Dormann, C.F. (2011) Microsite conditions dominate habitat selection of the red mason bee (*Osmia bicornis* , Hymenoptera: Megachilidae) in an urban environment: A case study from Leipzig, Germany. Landsc. Urban Planning **103** , 15–23.

Fernandez-Canero, R., Gonzalez-Redondo, P. (2010) Green roofs as a habitat for birds: A review. J. Anim. Vet. Adv. **9** , 2041–2052.

Gedge, D., Kadas, G. (2005) Green roofs and biodiversity. Biologist **52** , 161–169.

Getter, K.L., Rowe, D.B. (2008) Media depth influences *Sedum* green roof establishment. Urban Ecosyst. **11** , 361–372.

Gonsalves, S.M. (2016) Green roofs and urban biodiversity: their role as invertebrate habitat and the effect of design on beetle community. Portland State University, Dissertations and Theses. Available from http://pdxscholar.library.pdx.edu/open_access_etds/2997/ (accessed February 14, 2017).

Goulson, D., Lye, G.C., Darvill, B. (2008) Decline and conservation of bumble bees. Annu. Rev. Entomol. **53** , 191–208.

Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C. (2007) Bee foraging ranges and their relationship to body size. Oecologia **153** , 589–596.

Hagler, J.R., Jackson, C.G. (2001) Methods for marking insects: current techniques and future prospects. Annu. Rev. Entomol. **46**, 511–543.

Hernandez, J.L., Frankie, G.W., Thorp, R.W. (2009) Ecology of urban bees: a review of current knowledge and directions for future study. Cities and the Environ. (CATE) **2**, 1–15.

Hietel, E. (2016) Biodiversität begrünter Dächer. Ergebnisse eines Forschungsprojektes der Forschungsinitiative RLP. Pages 13–16 14. Internationales FBB-Gründachsymposium 2016 - Tagungsband. Ditzingen, Germany.

Hui, S.C., Chan, K.L. (2011) Biodiversity assessment of green roofs for green building design. Proceedings of Joint Symposium on Integrated Building Design in the New Era of Sustainability. ASHRAE-HKC/CIBSE-HKB/HKIE-BSD. Available from https://hub.hku.hk/handle/10722/166901 (accessed February 16, 2017).

Jones, R.A. (2002) Tecticolous invertebrates: a preliminary investigation of the invertebrate fauna on green roofs in urban London. English Nature, London.

Kadas, G. (2006) Rare invertebrates colonizing green roofs in London. Urban Habitats **4**, 66–86.

Kaiser, C. (2014) Untersuchungen zu den Auswirkungen der extensiven Dachbegrünung auf lokale Biodiversität und Mikroklima. Bachelorarbeit. FH Bingen, Bingen, Germany.

Kälin, M. (2005) Wildbienen auf begrünten Dachflächen – Substrate und ihre Auswirkungen auf die Wildbienenfauna. Semesterarbeit. Züricher Hochschule für Angewandte Wissenschaften ZHAW, Wädenswil, Switzerland.

Käppeli, S. (2010) Wildbienen auf begrünten Dächern – Fördermöglichkeiten für gefährdete Arten? Semesterarbeit. Züricher Hochschule für Angewandte Wissenschaften ZHAW, Wädenswil, Switzerland.

Kessler, C. (2010) Wildbienen auf begrünten Dächern – Fördermöglichkeiten für gefährdete Arten? Semesterarbeit. Züricher Hochschule für Angewandte Wissenschaften ZHAW, Wädenswil, Switzerland.

Köhler, M. (2006) Long-term vegetation research on two extensive green roofs in Berlin. Urban Habitats **4**, 3–26.

Köhler, M. (2014) Untersuchungen zur Biodiversität begrünter Dächer. Pages 13–16 12. Internationales FBB-Gründachsymposium 2014, Tagungsband. Ditzingen, Germany.

Kratschmer, S.A. (2015) Summen auf den Dächern Wiens. Masterarbeit. Universität für Bodenkultur, Vienna, Austria.

Ksiazek, K., Fant, J., Skogen, K. (2012) An assessment of pollen limitation on Chicago green roofs. Landsc. Urban Plan. **107**, 401–408.

Ksiazek, K., Tonietto, R., Ascher, J.S. (2014) Ten bee species new to green roofs in the Chicago area. Mich. Entomol. Soc. **47**, 87–92.

Kuhlmann, M. (2015) Erfassung der Auswirkungen extensiver Dachbegrünung auf die lokale Abundanz und Vielfalt blütenbestäubender Insekten. Bachelorarbeit. FH Bingen, Germany.

Lundholm, J.T. (2016) Spontaneous dynamics and wild design in green roofs. Isr. J. Ecol. Evol. **62**, 23–31.

MacIvor, J.S. (2016) Building height matters: nesting activity of bees and wasps on vegetated roofs. Isr. J. Ecol. Evol. **62**, 88–96.

MacIvor, J.S., Lundholm, J. (2011) Insect species composition and diversity on intensive green roofs and adjacent level-ground habitats. Urban Ecosyst. **14**, 225–241.

MacIvor, J.S., Ruttan, A., Salehi, B. (2015) Exotics on exotics: Pollen analysis of urban bees visiting *Sedum* on a green roof. Urban Ecosyst. **18**, 419–430.

Madre, F., Vergnes, A., Machon, N., Clergeau, P. (2013) A comparison of 3 types of green roof as habitats for arthropods. Ecol. Eng. **57**, 109–117.

Mann, G. (1994) Ökologisch-faunistische Aspekte begrünter Dächer in Abhängigkeit vom Schichtaufbau. Diplomarbeit. Universität Tübingen, Germany.

Mann, G. (1996a) Faunistische Untersuchungen von drei Dachbegrünungen in Linz. Öko-L **18**, 3–14.

Mann, G. (1996b) Die Rolle begrünter Dächer in der Stadtökologie. Biol. Unserer Zeit. **26**, 292–299.

Mann, G. (2005) Vorkommen von Tieren auf begrünten Hochhäusern. Dach+ Grün **3**, 24–28.

Michener, C.D. (2007) Bees of the World, 2nd ed., John Hopkins University Press, Baltimore.

Moore, L.J., Kosut, M. (2013) Buzz: Urban beekeeping and the power of the bee. New York University Press, NY, USA.

Nagase, A., Nomura, M. (2014) An evaluation of one example of biotope roof in Japan: Plant development and invertebrate colonisation after 8 years. Urban For. & Urban Greening **13**, 714–724.

Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K.K.Y., Rowe, B. (2007) Green roofs as urban ecosystems: ecological structures, functions, and services. BioScience **57**, 823–833.

Riedmiller, J. (1991) Pflegeloses Pflanzendach - Ökologisches Untersuchungen auf einem neu bepflanzten Flachdach. Diplomarbeit. Universität Heidelberg, Germany.

Riedmiller, J., Schneider, P. (1993) Begrünte Dächer als Sekundärlebensräume für bestimmte Tier-und Pflanzenarten. Veröffentlichungen des Projekts Angewandte Ökologie der LFU Baden-Württemberg, Karlsruhe (Veröff. PAÖ) **7**, 155–162.

Schmidt, S., Schmid-Egger, C., Morinière, J., Haszprunar, G., Hebert, P.D.N. (2015) DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Mol. Ecol. Res. **15**, 985–1000.

Schneider, P., Riedmiller, J. (1992) Pflegeloses Pflanzendach: Neue Lebensräume in Städten. Nat.wiss. **79**, 560–561.

Stutz, B. (2010) Green roofs are starting to sprout in American cities. Yale Environment 360. Available from http://e360.yale.edu/features/green_roofs_are_starting_to_sprout_in_american_cities (accessed February 16, 2017).

Tabares-Velasco, P.C., Zhao, M., Peterson, N., Srebric, J., Berghage, R. (2012) Validation of predictive heat and mass transfer green roof model with extensive green roof field data. Ecol. Eng. **47**, 165–173.

Takebayashi, H., Moriyama, M. (2007) Surface heat budget on green roof and high reflection roof for mitigation of urban heat island. Build. Environ. **42**, 2971–2979.

Tonietto, R., Fant, J., Ascher, J., Ellis, K., Larkin, D. (2011) A comparison of bee communities of Chicago green roofs, parks and prairies. Landsc. Urban Plan. **103**, 102–108.

Walker, E.A. (2016) Green roofs as urban habitat for native plant seedlings and wild bees. Saint Mary's University. Available from http://library2.smu.ca/handle/01/26546 (accessed January 31, 2017).

Walker, T.J., Wineriter, S.A. (1981) Marking techniques for recognizing individual insects. Fla Entomol.t **64**, 18–29.

Westrich, P. (1990) Die Wildbienen Baden-Württembergs2., verb. Aufl. Ulmer, Stuttgart, Germany.

Williams, N.S.G., Lundholm, J., Scott MacIvor, J. (2014) FORUM: Do green roofs help urban biodiversity conservation? J. Appl. Ecol. **51**, 1643–1649.

Witt, R. (2016) Populationen von Wildbienen und Wespen auf Gründächern. Stadt+Grün 03/2016, 37–42.

Zehnder, J. (2011) Wildbienen auf begrünten Dächern – Fördermöglichkeiten für gefährdete Arten? Semesterarbeit. Züricher Hochschule für Angewandte Wissenschaften ZHAW, Wädenswil, Switzerland.

Zurbuchen, A., Müller, A. (2012) Wildbienenschutz - Von der Wissenschaft zur Praxis. Haupt Verlag, Bristol Stiftung Zürich, Switzerland.

Supplementary material from

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Table S1: Overview of green roof (= GR) studies involving wild bee species assessment

Location	**Time span**	**Roof type**	**Survey method**	**Species level ID (Y/N)**	**# species**	**Research Question(s)**	**Reference**
				European Studies			
Baden-Wuerttemberg, Germany	1990 - 1992	**“Pflegeloses Pflanzendach”** experimental extensive roof (only one layer, no drainage)	Pan traps	Y	19	Green roofs as secondary habitat	(Riedmiller 1991; Schneider & Riedmiller 1992; Riedmiller & Schneider 1993)
Berlin (7 roofs) and Neubrandenburg (5 roofs), Germany	April-September 2013	Green roofs of different ages (n=12)	Pan traps	Y (list not provided)	51	Influence of the number of plant species on the number of bee species	**(Köhler** 2014)
Bingen, Germany	July-September 2014 and June-August 2015	Extensive GR (n=5) and gravel roofs (n=4)	Observation	N	N/A	Comparison of insect abundancy, **density/m²** and diversity	(Hietel 2016 summarizing information from Kaiser 2014; Kuhlmann 2015)

Böblingen/ Sindelfingen, Germany	mainly May-August 1992	Extensive to intensive GR (n=4	Netting and hand capturing (two days each, 1-2h)	Y	49	Assessment of the arthropod spectrum on differently planted GR	(Mann 1994)
Böblingen, Germany and Linz, Austria		Extensive (n=4) and intensive (n=3) GR	Pan traps and Netting	Y (list not provided)	N/A	Faunistic assessment on different roof types	(Mann 1996a, 1996b)
Basel, Luzern, St Gallen, Zurich, Switzerland	2004 - 2005	Extensive GR (n=18)	Pan traps and observation	Y	77	Wild bees on extensive GRs; no comparison to ground-level habitats (reference samples lost due to disturbance)	(Brenneisen 2005)
St Gallen, Tessin, Vallis, Switzerland	2011 - 2013	GR (n=8), spontaneous GR (n=1), non-GR (n=3)	Observation, Netting (max 4x per year, 30 min each)	Y	44	Feasibility of nesting aids for ground-nesting species on GRs	(Brenneisen et al. 2014, summarizing information from **Kälin** 2005; Kessler 2010; **Käppeli** 2010; Zehnder 2011)

Hannover, Germany	June-July 2015	GR (n=10): extensive *Sedum*-roofs (n=3), some shrubs (n=2), intensive roofs	Netting, 1x June and 1x July	Y	28	Wild bees and wasps on GRs	(Witt 2016)
London, UK	Summer-Autumn 2004	GR (*Sedum*, n=3) and brown/biodiverse roofs (n=2)	Pan traps	Y	22	Invertebrate conservation and habitat mitigation; Comparison of green (*Sedum*) roofs, brown/biodiverse roofs and brownfields	(Kadas 2006)
London, UK	N/A	Extensive GR (n=8)	Suction sampler	Y	N/A 9 hymenopterans	Invertebrate survey	(Jones 2002)
Northern France	11 April - 7 June 2011	Moss/*Sedum*, herbaceous layer and shrubs (roofs (n=115)	Hand-sampling with pill bottles	Y	18	spider, true bug, beetle and hymenopteran abundance and species richness	(Madre et al. 2013)
Stuttgart, Wuerzburg, Germany	June-July 2005	Intensive (n=1) and extensive (n=2) GR	Pan traps	N	4	Height limitation of invertebrates on skyscrapers	(Mann 2005)

Vienna, Austria	March – September 2014	Intensive and extensive GR (n=9)	Netting	Y	91	Species composition and abundances on GR, influence of vegetation and surrounding area	(Kratschmer 2015)
Zurich, Switzerland	May - September 2010	Extensive GR (n=40)	Pan traps, non-directional traps	Y (list not provided)	126	Habitat connectivity by GR for taxa of different mobility	(Braaker et al. 2014, 2017)
			North American Studies				
Chicago, US	June – October 2008	GR dominated by native plants (n=2) or Sedum (n=4)	3x 15 min observation, netting, pan traps	Y	18	Comparison of GR with tallgrass prairie and city-park green spaces	(Tonietto et al. 2011)
Chicago, US	Three month	N/A (n=3)	Pan traps	N	N/A	Pollen limitation on GR compared to ground-level sites	(Ksiazek et al. 2012)
Chicago, US	2 years	Intensively maintained to extensive roofs (n=7)	Pan traps	Y	26	Species composition on GRs	(Ksiazek et al. 2014)
Halifax, Nova Scotia, US	May – October 2009	Established (>8) intensive roofs (> 30 cm growth medium)	Pan traps	N (only morpho-species)		Comparison of GR and ground-level habitats	(MacIvor & Lundholm 2011)

Halifax, Nova Scotia, US	June-August 2014	Native planted GR (n=2)	Netting	Y	24	Comparison of green roof, urban and coastal barrens habitats	(Walker 2016)
Michigan, US	June – July 2010	*Sedum* GR (n=2)	Netting	Y	1	Arthropod survey of Michigan	**(O'Brien,** Swanson, & Monsma, 2012)
Toronto, Canada	2004 – 2006	Actively seeded (n=1) and passively seeded (n=1) GR	Pan traps	Y	79	Diversity and abundance of bees 0n GR in comparison to ground-level sites	(Colla et al. 2009)
Toronto, Canada	5 days in June and July	Green Roof Innovation Testing Lab (University of Toronto)	Netting	Y	17	Pollen analysis of urban bees visiting Sedum on green roofs	(MacIvor et al. 2015)
Toronto, Canada	2011 - 2013	Vegetated and non-vegetated roofs (n=29)	Trap nests	Y	11	Nesting activity of bees on GR depending on building height	(MacIvor, 2016)
Upper Midwest Great lakes (MI, OH), US	July - August 2004	Extensive (n=1) and intensive (n=1) roof	Netting	N	59 morpho-species of insects	Rapid biodiversity assessment from presence-absence and relative abundance data	(Coffman & Waite 2011)

Other studies

Chiba City, Japan	May-November 2010	150 m² biotope roof, 8 years	Observation (7 x 3h), netting, pan traps	Y	3	Plant development and invertebrate colonization after 8 years	(Nagase & Nomura 2014)

References

Braaker, S., Ghazoul, J., Obrist, M.K., Moretti, M. (2014) Habitat connectivity shapes urban arthropod communities: the key role of green roofs. Ecology **95**, 1010–1021.

Braaker, S., Obrist, M.K., Ghazoul, J., Moretti, M. (2017) Habitat connectivity and local conditions shape taxonomic and functional diversity of arthropods on green roofs. Journal of Animal Ecology **86**: 521–531.

Brenneisen, S. (2005) The natural roof (NADA). Research project report of the use of extensive green roofs by wild bees. University of **Wädenswil, Wädenswil,** Switzerland.

Brenneisen, S., **Käppeli,** S., Schneider, R. (2014) **Förderung gefährdeter** Wildbienen auf **Flachdächern** - Forschungsprojekt im Mandat **für** Pro Natura. https://www.zhaw.ch/no_cache/en/research/people-publications-projects/detail-view-project/projekt/1835/ (accessed April 10, 2017).

Coffman, R.R., Waite, T. (2011) Vegetated roofs as reconciled habitats: rapid assays beyond mere species counts. Urban Habitats 6 (electronic journal). http://www.urbanhabitats.org/v06n01/vegetatedroofs_full.html

Colla, S.R., Willis, E., Packer, L. (2009) Can green roofs provide habitat for urban bees (Hymenoptera: Apidae)? Cities and the Environment **2**(4), 1–12.

Hietel, E. (2016) **Biodiversität begrünter Dächer.** Ergebnisse eines Forschungsprojektes der Forschungsinitiative RLP. Pages 13–16 14. Internationales FBB-**Gründachsymposium** 2016 - Tagungsband. Ditzingen, Germany.

Jones, R.A. (2002) Tecticolous invertebrates: a preliminary investigation of the invertebrate fauna on green roofs in urban London. English Nature, London.

Kadas, G. (2006) Rare invertebrates colonizing green roofs in London. Urban Habitats **4**, 66–86.

Kaiser, C. (2014) Untersuchungen zu den Auswirkungen der extensiven **Dachbegrünung** auf lokale **Biodiversität** und Mikroklima. Bachelorarbeit. FH Bingen, Bingen, Germany.

Kälin, M. (2005) Wildbienen auf begrünten Dachflächen – Substrate und ihre Auswirkungen auf die Wildbienenfauna. Semesterarbeit. Züricher Hochschule für Angewandte Wissenschaften ZHAW, Wädenswil, Switzerland.

Käppeli, S. (2010) Wildbienen auf begrünten Dächern – Fördermöglichkeiten für gefährdete Arten? Semesterarbeit. Züricher Hochschule für Angewandte Wissenschaften ZHAW, Wädenswil, Switzerland.

Kessler, C. (2010) Wildbienen auf begrünten Dächern – Fördermöglichkeiten für gefährdete Arten? Semesterarbeit. Züricher Hochschule für Angewandte Wissenschaften ZHAW, Wädenswil, Switzerland.

Ksiazek, K., Fant, J., Skogen, K. (2012) An assessment of pollen limitation on Chicago green roofs. Landscape and Urban Planning **107**, 401–408.

Ksiazek, K., Tonietto, R., Ascher, J.S. (2014) Ten bee species new to green roofs in the Chicago area. The Michigan Entomological Society **47**, 87–92.

Köhler, M. (2014) Untersuchungen zur Biodiversität begrünter Dächer. Pages 13–16 12. Internationales FBB-Gründachsymposium 2014, Tagungsband. Ditzingen, Germany.

Kratschmer, S.A. (2015) Summen auf den Dächern Wiens. Masterarbeit. Universität für Bodenkultur, Vienna, Austria.

Kuhlmann, M. (2015) Erfassung der Auswirkungen extensiver Dachbegrünung auf die lokale Abundanz und Vielfalt blütenbestäubender Insekten. Bachelorarbeit. FH Bingen, Germany.

MacIvor, J.S. (2016) Building height matters: nesting activity of bees and wasps on vegetated roofs. Israel Journal of Ecology & Evolution **62**, 88–96.

MacIvor, J.S., Lundholm, J. (2011) Insect species composition and diversity on intensive green roofs and adjacent level-ground habitats. Urban Ecosystems **14**, 225–241.

MacIvor, J.S., Ruttan, A., Salehi, B. (2015) Exotics on exotics: Pollen analysis of urban bees visiting *Sedum* on a green roof. Urban Ecosystems **18**, 419–430.

Madre, F., Vergnes, A., Machon, N., Clergeau, P. (2013) A comparison of 3 types of green roof as habitats for arthropods. Ecological Engineering **57**, 109–117.

Mann, G. (1994) Ökologisch-faunistische Aspekte begrünter Dächer in Abhängigkeit vom Schichtaufbau. Diplomarbeit. Universität Tübingen, Germany.

Mann, G. (1996a) Faunistische Untersuchungen von drei Dachbegrünungen in Linz. Öko-L **18**, 3–14.

Mann, G. (1996b) Die Rolle begrünter Dächer in der Stadtökologie. Biologie in Unserer Zeit **26**, 292–299.

Mann, G. (2005) Vorkommen von Tieren auf begrünten Hochhäusern. Dach+ Grün **3**, 24–28.

Nagase, A., Nomura, M. (2014) An evaluation of one example of biotope roof in Japan: Plant development and invertebrate colonisation after 8 years. Urban Forestry & Urban Greening **13**, 714–724.

O'Brien, M. F., Swanson, D. R., & Monsma, J. (2012). *Anthidium oblongatum* (Apoidea: Megachilidae) confirmed as a Michigan resident, with notes on other Michigan *Anthidium* species. *Gt. Lakes Entomol*, *45*, 102-105.

Hofmann, M., and S. S. Renner. Bee species recorded between 1992 and 2017 from green roofs in Asia, Europe, and North America, with key characteristics and open research questions. Apidologie. Online supporting material, Tables S1 and S2

Schneider, P., Riedmiller, J. (1992) Pflegeloses Pflanzendach: Neue Lebensräume in Städten. Die Naturwissenschaften **79**, 560–561.

Riedmiller, J. (1991) Pflegeloses Pflanzendach - Ökologisches Untersuchungen auf einem neu bepflanzten Flachdach. Diplomarbeit. Universität Heidelberg, Germany.

Riedmiller, J., Schneider, P. (1993) Begrünte Dächer als Sekundärlebensräume für bestimmte Tier-und Pflanzenarten. Veröffentlichungen des Projekts Angewandte Ökologie der LFU Baden-Württemberg, Karlsruhe (Veröff. PAÖ) 7, 155–162.

Tonietto, R., Fant, J., Ascher, J., Ellis, K., Larkin, D. (2011) A comparison of bee communities of Chicago green roofs, parks and prairies. Landscape and Urban Planning **103**, 102–108.

Walker, E.A. (2016) Green roofs as urban habitat for native plant seedlings and wild bees. Saint Mary's University. Available from http://library2.smu.ca/handle/01/26546 (accessed January 31, 2017).

Witt, R. (2016) Populationen von Wildbienen und Wespen auf Gründächern. Stadt+Grün 03/2016, 37–42.

Zehnder, J. (2011) Wildbienen auf begrünten Dächern – Fördermöglichkeiten für gefährdete Arten? Semesterarbeit. Züricher Hochschule für Angewandte Wissenschaften ZHAW, Wädenswil, Switzerland.

Hofmann, M., and S. S. Renner. Bee species recorded between 1992 and 2017 from green roofs in Asia, Europe, and North America, with key characteristics and open research questions. Apidologie. Online supporting material, Tables S1 and S2

Table S2: Alphabetical list of species reported on green roofs

Species	Location
European records	
Andrean fulva	Basel, CH
Andrena bicolor	Baden-**Württemberg,** DE; **Böblingen/Sindelfingen,** DE; Basel, St Gallen, CH; London, UK
Andrena ***blüthgeni***	Vienna, AT
Andrena chrysoceles	**Böblingen/Sindelfingen,** DE; Luzern, St. Gallen, CH
Andrena cineraria	Basel, CH
Andrena combinata	Tessin, CH
Andrena curvungula	**Böblingen/Sindelfingen,** DE
Andrena danuvia	Vienna, AT
Andrena denticulata	Hannover, DE
Andrena dorsata	Baden-**Württemberg,** DE; Hannover, DE; Vienna, AT
Andrena flavipes	Basel, Luzern, St. Gallen, Tessin ZH, CH; **Böblingen/Sindelfingen,** DE; Hannover, DE; London, UK; Northern France, FR; Vienna, AT

Andrena fucata	**Böblingen/Sindelfingen,** DE
Andrena fulva	**Böblingen/Sindelfingen,** DE; London, UK
Andrena gravida	**Böblingen/Sindelfingen,** DE; Vienna, AT
Andrena haemorrhoa	Basel, St Gallen, CH; **Böblingen/Sindelfingen,** DE
Andrena labialis	**Böblingen/Sindelfingen,** DE
Andrena labiata	**Böblingen/Sindelfingen,** DE
Andrena minutula	Baden-**Württemberg,** DE; **Böblingen/Sindelfingen,** DE; Basel, Tessin, CH; Hannover, DE; London, UK; Vienna, AT
Andrena minutuloides	Baden-**Württemberg,** DE; **Böblingen/Sindelfingen,** DE; Basel, CH
Andrena mnigroaena	London, UK
Andrena nigroaenea	Vienna, AT
Andrena nitida	St Gallen, ZH, CH
Andrena nitidiuscula	Baden-**Württemberg,** DE
Andrena ovatula	Vienna, AT; Tessin, CH
Andrena pandellei	**Böblingen/Sindelfingen,** DE
Andrena pilipes	Vienna, AT

Andrena scotica	London, UK; St Gallen, CH
Andrena spec.	Basel, Luzern, St. Gallen, ZH, CH
Andrena strohmella	**Böblingen/Sindelfingen,** DE
Andrena subopaca	Basel, St Gallen, CH; **Böblingen/Sindelfingen,** DE
Andrena tibialis	Vienna, AT
Andrena trimmerana	London, UK
Andrena varians	**Böblingen/Sindelfingen,** DE; Vienna, AT
Andrena viridescens	ZH, CH
Anthidium spec.	**Würzburg,** DE
Anthidium punctatum	St Gallen, CH
Anthidium strigatum	St Gallen, CH; Vienna, AT
Anthophora crinipes	Vienna, AT
Anthophora furcata	Basel, CH
Anthophora plumipes	Vienna, AT
Anthophora quadrimaculata	**Böblingen/Sindelfingen,** DE; Hannover, DE; Vienna, AT
Anthophora spec.	Basel, CH

Bombus alpestris	St. Gallen, CH
Bombus bohemicus	Vienna, AT
Bombus campestris	St. Gallen, CH
Bombus hortorum	**Böblingen/Sindelfingen,** DE; St. Gallen, Tessin, CH; Vienna, AT
Bombus humilis	**Böblingen/Sindelfingen,** DE; Luzern, St. Gallen, Tessin, CH; Vienna, AT
Bombus hypnorum	Basel, Luzern, St. Gallen, ZH, CH; Northern France, FR; Hannover, DE; Vienna, AT
Bombus lapidarius	Baden-**Württemberg,** DE; **Böblingen/Sindelfingen,** DE; Basel, Luzern, St. Gallen, ZH, CH; Hannover, DE; London, UK; Northern France, FR; Stuttgart, DE; Vienna, AT
Bombus lucorum	Hannover, DE; London, UK; Vienna, AT
Bombus pascuorum	Baden-**Württemberg,** DE; **Böblingen/Sindelfingen,** DE; Luzern, St Gallen, Tessin, ZH, CH; Hannover, DE; Northern France, FR; Vienna, AT
Bombus pratorum	**Böblingen/Sindelfingen,** DE; St Gallen, CH; Vienna, AT
Bombus ruderatus	Northern France, FR
Bombus rupestris	Vienna, AT
Bombus soroeensis	Basel, St Gallen, CH

Bombus spec.	St Gallen, CH
Bombus spec.	**Würzburg,** DE
Bombus sylvarum	Northern France, FR
Bombus sylvestris	Basel, St Gallen, CH; London, UK
Bombus terrestris	**Böblingen/Sindelfingen,** DE; Hannover, DE; London, UK; Northern France, FR; St. Galle, Wallis, CH; Vienna, AT
Ceratina cyanea	Tessin, CH
Chelostoma campanularum	St. Gallen, CH
Chelostoma florisomne	Vienna, AT
Chelostoma rapunculi	**Böblingen/Sindelfingen,** DE; St. Gallen, CH; Vienna, AT
Coelioxys aurolimbata	Baden-**Württemberg,** DE
Coelioxys echinata	Vienna, AT
Coelioxys elongata	Hannover, DE; Vienna, AT
Coelioxys haemorrhoa	Vienna, AT
Coelioxys mandibularis	Vienna, AT
Colletes daviesanus	Hannover, DE; Vienna, AT; ZH, CH

Colletes spec.	St. Gallen, CH
Dasypoda hirtipes	Tessin, CH
Eucera nigrescens	Basel, Luzern, Tessin, CH; Vienna, AT
Halictus aff. eurygnathus	Basel, CH
Halictus kessleri	Vienna, AT
Halictus maculatus	Vienna, AT
Halictus rubicundus	St. Gallen, Tessin, CH
Halictus scabiosae	Luzern, CH; Northern France, FR
Halictus seladonius	Vienna, AT
Halictus simplex	**Böblingen/Sindelfingen,** DE; Tessin, CH; Vienna, AT
Halictus spec.	St Gallen, CH
Halictus subauratus	Basel, Tessin, CH; Northern France, FR; Vienna, AT
Halictus tumulorum	Baden-**Württemberg,** DE; **Böblingen/Sindelfingen,** DE; Basel, Luzern, St. Gallen, CH; Hannover, DE; Vienna, AT
Heriades crenulatus	Vienna, AT
Heriades rubicola	Vienna, AT

Heriades truncorum	Hannover, DE; St. Gallen, CH; Vienna, AT
Hylaeus brevicornis	**Böblingen/Sindelfingen,** DE; St. Gallen, CH
Hylaeus cardioscapus	Vienna, AT
Hylaeus communis	Basel, Tessin, CH; Hannover, DE; Vienna, AT
Hylaeus confusus	St. Gallen, CH
Hylaeus dilatatus	Hannover, DE
Hylaeus gredleri	Vienna, AT
Hylaeus hyalinatus	Hannover, DE; Tessin, CH; Vienna, AT
Hylaeus imparilis	Vienna, AT
Hylaeus leptocephalus	**Böblingen/Sindelfingen,** DE
Hylaeus nigritus	**Böblingen/Sindelfingen,** DE; Basel, Luzern, St. Gallen, CH
Hylaeus pictipes	Vienna, AT
Hylaeus punctatus	Wallis, CH
Hylaeus sinuatus	Vienna, AT
Hylaeus spec.	**Würzburg,** DE
Hylaeus styriacus	Basel, CH; Vienna, AT

Hylaeus taeniolatus	Basel, CH
Lasioglossum albipes	Basel, Luzern, St. Gallen, ZH, CH
Lasioglossum calceatum	Baden-**Württemberg,** DE; Basel, Luzern, St. Gallen, ZH, CH; Hannover, DE; London, UK; Vienna, AT
Lasioglossum fulvicorne	Basel, Luzern, St. Gallen, Tessin, ZH, CH; Hannover, DE
Lasioglossum laticeps	Basel, Luzern, St. Gallen, ZH, CH; Hannover, DE; Vienna, AT
Lasioglossum lativentre	Basel, CH; London, UK
Lasioglossum leucopus	Basel, CH; **Böblingen/Sindelfingen,** DE; Hannover, DE; London, UK
Lasioglossum lucidulum	Tessin, CH
Lasioglossum malachurum	Northern France, FR; Vienna, AT; St. Gallen, ZH, CH
Lasioglossum marginatum	Vienna, AT
Lasioglossum minutissimum	Basel, CH; London, UK
Lasioglossum minutulum	Vienna, AT
Lasioglossum morio	Baden-**Württemberg,** DE; **Böblingen/Sindelfingen,** DE; Basel, Luzern, St. Gallen, Wallis, ZH, CH; Hannover, DE; London, UK; Vienna, AT
Lasioglossum nigripes	Vienna, AT

Lasioglossum nitidulum	**Böblingen/Sindelfingen,** DE; Hannover, DE; Vienna, AT
Lasioglossum parvulum	St Gallen, Wallis, CH
Lasioglossum pauxilium	Basel, Luzern, St. Gallen, Tessin, CH; **Böblingen/Sindelfingen,** DE; Hannover, DE; Vienna, AT
Lasioglossum politum	Baden-**Württemberg,** DE; Basel, Tessin, Wallis, CH; Northern France, FR; Vienna, AT
Lasioglossum sabulosum	Vienna, AT
Lasioglossum smeathmanellum	Basel, Luzern, CH; London, UK
Lasioglossum zonulum	St. Gallen, Tessin, CH
Megachile apicalis	Vienna, AT
Megachile circumcincta	**Böblingen/Sindelfingen,** DE
Megachile ericetorum	Baden-**Württemberg,** DE; **Böblingen/Sindelfingen,** DE; Northern France, FR; Vienna, AT
Megachile lagopoda	Vienna, AT
Megachile leachella	Vienna, AT
Megachile pilidens	Northern France, FR; Vienna, AT
Megachile spec.	**Würzburg,** DE

Megachile versicolor	Vienna, AT
Megachile willughbiella	Baden-**Württemberg,** DE; Basel, St. Gallen, Tessin, CH; Hannover, DE; Northern France, FR; Vienna, AT
Melecta albifrons	Vienna, AT
Melitta haemorrhoidalis	Vienna, AT
Melitta leporina	Vienna, AT
Nomada fabriciana	**Böblingen/Sindelfingen,** DE; London, UK
Nomada flava	**Böblingen/Sindelfingen,** DE
Nomada fucata	**Böblingen/Sindelfingen,** DE
Nomada goodeniana	Vienna, AT
Nomada spec.	St Gallen, ZH, CH
Nomada sheppardana	Hannover, DE
Nomada striata	St Gallen, CH
Nomada succincta	**Böblingen/Sindelfingen,** DE
Osmia adunca	Basel, Wallis, CH; Vienna, AT
Osmia aurulenta	**Böblingen/Sindelfingen,** DE

Osmia bicolor	St. Gallen, CH
Osmia bicornis	Hannover, DE
Osmia caerulescens	Tessin, CH
Osmia cornuta	Basel, CH; Vienna, AT
Osmia leucomelana	St Gallen, CH; Vienna, AT
Osmia mitis	St. Gallen, CH
Osmia rufa	Basel, Luzern, St. Gallen, ZH, CH; **Böblingen/Sindelfingen,** DE; Vienna, AT
Panurgus calcaratus	Basel, CH
Sphecodes albilabris	Vienna, AT
Sphecodes ephippius	**Böblingen/Sindelfingen,** DE; St. Gallen, CH
Sphecodes ferruginatus	St. Gallen, CH
Sphecodes monilicornis	Tessin, CH; Vienna, AT
Sphecodes niger	**Böblingen/Sindelfingen,** DE
Sphecodes ruficrus	Vienna, AT
Sphecodes schenckii	Tessin, CH

Stelis punctulatissima	Vienna, AT
Xylocopa violacea	Basel, CH
Records from both Europe and North America	
Anthidium manicatum	Baden-Württemberg, DE; Basel, Luzern, St. Gallen, CH; Chicago, IL; Toronto, ON; Vienna, AT
Anthidium oblongatum	Baden-Württemberg, DE; Chicago, IL; Northern France, FR; Vienna, AT; Wayne Co, Kent Co., Washtenaw Co., MI
*Apis mellifera**	Baden-Württemberg, DE; Böblingen/Sindelfingen, DE; Basel, Luzern, St. Gallen, Tessin, Wallis, ZH, CH; Chicago, IL; Halifax, NS; London, UK; Böblingen/Sindelfingen, DE; Northern France, FR; Stuttgart, DE; Toronto, ON; Vienna, AT
Halictus rubicundus	Böblingen/Sindelfingen, DE; Chicago, IL; Halifax, NS; Luzern, St. Gallen, CH; Toronto, ON; Vienna, AT
Hylaeus leptocephalus	Chicago, IL; Toronto, ON; Vienna, AT
Hylaeus punctatus	Chicago, IL; Toronto, ON; Vienna, AT
Lasioglossum leucozonium	Basel, St. Gallen, Tessin, CH; Böblingen/Sindelfingen, DE; London, UK; Toronto, ON; Vienna, AT
Lasioglossum villosulum	Basel, Luzern, S. Gallen, CH; Böblingen/Sindelfingen, DE; London, UK; Northern France, FR; Toronto, ON; Vienna, AT

Megachile centuncularis	Basel, Tessin, CH; Chicago, IL; London, UK; Toronto, ON; Vienna, AT
Megachile rotundata	Baden-**Württemberg,** DE; Basel, CH; Chicago, IL; Hannover, DE; Northern France, FR; Toronto, ON; Vienna, AT
Osmia caerulescens	Toronto, ON; Tessin, CH; Vienna, AT
North American records	
Agapenstemon virescens	Chicago, IL; Toronto, ON
Andrena ceanothi	Halifax, NS
Andrena commoda	Toronto, ON
Andrena crataegi	Halifax, NS
Andrena milwaukeensis	Halifax, NS
Andrena nasonii	Toronto, ON
Andrena nivalis	Halifax, NS
Andrena regularis	Halifax, NS
Andrena vicina	Toronto, ON
Andrena wilkella	Halifax, NS; Toronto, ON

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Andrena w-scripta	Halifax, NS
Anthidiellum notatum	Toronto, ON
Augochlorella aurata	Chicago, IL; Toronto, ON
Bombus bimaculatus	Halifax, NS; Toronto, ON
Bombus griseocollis	Toronto, ON
Bombus impatiens	Halifax, NS; Chicago, IL
Bombus perplexus	Toronto, ON
Bombus rufocinctus	Halifax, NS; Toronto, ON
Bombus terricola	Halifax, NS
Bombus vagans	Toronto, ON
Calliopsis andreniformis	Chicago, IL
Caratina calcarata	Toronto, ON
Ceratina dupla dupla	Toronto, ON
Coelioxys sayi	Toronto, ON
Halictus confusus	Chicago, IL; Toronto, ON
Halictus ligatus	Chicago, IL; Halifax, NS; Toronto,

	ON
Heriades carinata	Toronto, ON
Hoplitis affinis	Toronto, ON
Hoplitis cressoni	Toronto, ON
Hoplitis producta	Toronto, ON
Hylaeus affinis	Chicago, IL
Hylaeus mesillae	Chicago, IL; Halifax, NS
Hylaeus modestus	Toronto, ON
Lasioglossum anomalum	Chicago, IL
Lasioglossum coriaceum	Toronto, ON
Lasioglossum cressonii	Halifax, NS; Toronto, ON
Lasioglossum divergens	Toronto, ON
Lasioglossum ellisiae	Chicago, IL; Toronto, ON
Lasioglossum ephialtum	Toronto, ON
Lasioglossum fattigi	Toronto, ON
Lasioglossum foxii	Toronto, ON

Lasioglossum illinoense	Chicago, IL
Lasioglossum imitatus	Toronto, ON
Lasioglossum laevissimum	Toronto, ON
Lasioglossum lineatulum	Toronto, ON
Lasioglossum mitchelli	Chicago, IL
Lasioglossum paradmirandum	Toronto, ON
Lasioglossum pectorale	Chicago, IL
Lasioglossum perpunctatum	Toronto, ON
Lasioglossum perspicuum	Toronto, ON
Lasioglossum pilosum	Chicago, IL; Toronto, ON
Lasioglossum rohweri	Toronto, ON
Lasioglossum smilacinae	Chicago, IL
Lasioglossum spec.	Chicago, IL
Lasioglossum spec.	Chicago, IL
Lasioglossum tegulare	Toronto, ON
Lasioglossum zephyrum	Chicago, IL; Toronto, ON

Lasioglossum zophops	Chicago, IL
Lasiolgossum oblongum	Toronto, ON
Megachile brevis brevis	Toronto, ON
Megachile campanulae	Toronto, ON
Megachile dentiventris	Toronto, ON
Megachile frigida	Halifax, NS
Megachile illata	Toronto, ON
Megachile latimanus	Toronto, ON
Megachile melanophaea	Halifax, NS
Megachile pugnata	Toronto, ON
Megachile texana	Toronto, ON
Melissodes bimaculata	Chicago, IL
Melissodes desponsa	Chicago, IL; Toronto, ON
Osmia lignaria	Toronto, ON
Osmia pumila	Toronto, ON
Pepoapis pruinosa	Toronto, ON

Sphecodes spec.	Toronto, ON
Sphecodes spec.	Chicago, IL
Xylocopa virginica	Toronto, ON
Asian records	
Apis cerana jaopnica	Chiba City, Japan
Xylocopa appendiculata circumvolans	Chiba City, Japan

Chapter 8

A photo-based assessment of wild bees in a filled-up gravel pit in Riem, Munich – with a species list of bees found in Central European gravel pits

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A photo-based assessment of wild bees in a filled-up gravel pit in Riem, Munich– with a species list of bees found in Central European gravel pits

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Abstract

Gravel pits, both in active use and restored, provide important replacement habitats and nesting requisites for wild bees formerly specialized in nesting in dynamic fluvial landscapes. Species inventories in six Central European gravel pits report 239 species of wild bees, and this study found 48 species of wild bees and the domesticated *Apis mellifera* in the refilled section of the Obermayr gravel pit in Riem, Munich. The tested inventory method of *in-situ* photo-documentation, instead of voucher specimen collection, is feasible for most bee families, but is not applicable for Halictidae and some small nomad bees (genus *Nomada*) or mini-miners (*Andrena* subgenus *Micrandrena*), as well as species complexes in the genus *Bombus*.

Introduction

Dynamic riverside landscapes are an important habitat for various wild bee species (Völkl et al. 2002), but became increasingly rare in Central Europe. An assessment of more than 76.000 km of watercourses in Germany, conducted by the water management authorities of the federal states, showed that only 1.6 % of the rivers are in their natural state, another 6.2 % are only slightly modified and 11.9 % moderately changed, the rest falls in the classes considerably, strongly, very strongly or completely changed (Arle et al. 2017). Thus, many of the bee species naturally specialized on riverside habitats are nowadays found in sand and gravel pits instead (Escher 1974, Westrich 2018), as these provide manifold different niches, like deep and shallow ponds, accumulations of clay, sand, gravel, rocks, shrubland and steep faces (Krebs and Wildermuth 1976) – especially for many soil-nesting bees species, the presence of open, poorly vegetated, freshly exposed soils is an essential habitat demand (Westrich 1989, Falk 2015). The continuous de-novo succession of the habitat through ongoing gravel extraction simulates landscape dynamics typically induced in erosion banks and river landscapes by flooding events and fluvial erosion cycles (Meisterhans and Heusser 1970, Krebs and Wildermuth 1976). Inventories conducted in actively used and restored gravel pits in Central Europe identified 239 species of wild bees for this habitat (see *Results* section Tables 1 and 2 for references).

The gravel pit of the Obermayr Company in the East of Munich offers both renatured areas and areas which are still mined for sand and gravel. This study focused on a living bee inventory in the non-active parts of the gravel pit, applying a standardized *in-situ* photo-documentation, and vouchers were only collected for those taxonomically critical genera where determination in the field was not possible. Besides producing a species inventory for the Obermayr gravel pit in Riem, this study aimed to test the feasibility of using a non-invasive species determination based on bee specimen photography in the field instead of voucher collection. With current projects like the "Bundesprogramm Biologische Vielfalt – Schwerpunkt Sichern von Ökosystemdienstleistungen" of the Federal Office for Nature Conservation (BfN) and the Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU), non-invasive monitoring methods become increasingly important and the possibility of reliable, reproducible documentation fulfilling scientific standards without specimen collection needs to be tested.

Material and methods

Species list for Central European gravel pits

We are aware of five published studies which have monitored wild bees in gravel pits (Table 1). Additionally, we requested an unpublished report for another Munich gravel pit located in the East of Munich (Trudering). The species lists within these studies were compiled and a list of 239 species recorded in gravel pits was generated (Table 2). The honey bee *Apis mellifera* was excluded from the analyses, as this is a domesticated and ubiquist species. Each found study was scanned for the following information: (i) Where and when was the study conducted? (ii) Which sampling technique was used? (iii) Which taxa were found? If the information was not directly clear from the published material, the authors were contacted via email.

Study site “Kiesgrube Obermayr”

“Kiesgrube Obermayr” is situated in the East of Munich, in Riem at N48°8.833140´ E11°42.608280´ 520 m a.s.l.. While the southern part is still an active gravel pit, the northern part is refilled and maintained as an open-soil and nutrient-poor grassland site. The area is not open to the public and is maintained by the Landesbund für Vogelschutz (LBV) and the municipal department (Kommunalreferat). It borders to the Munich Trade Fair Center in the Southwest, a transshipment station in the West and arable fields to all other directions. Until 2004, the northern area had still been in active use as gravel pit, and then was refilled with several soil types. There are two experimental fields with washed dry mud (middle and eastern part), a fine sediment resulting from washing gravel, and washed sand, a sandy material also resulting from the washing process with fine cohesive components (H. Sedlmeier, pers. com.). The steep face in the northern part of the biotope also consists of this washed sand. Unwashed gravel had been piled up to several walls and hills at the site. There is also a south-east-facing wall of demolished concrete that is not covered by vegetation. In the middle of the biotope there is railroad basalt disposed from the railroad tracks of former Neuaubing station. The bigger stones probably originated from the alpine upland. Loamy gravel derived from the topsoil removed for gravel extraction forms the hills in the south and the smaller walls in the northeastern and northern part of the biotope, these artificial hills are sparsely covered by woody vegetation, mainly consisting of willows (*Salix* spp., Salicaceae). The rest of the area is covered by a thin, compressed loam-gravel-layer on building rubble. Flat areas, hills, and ponds create a highly-structured area (Figure 1). The area’s flora (> 545 documented species found during species monitorings from 2003 – 2016; a list excluding threatened taxa is available via the LBV administration) and its butterfly, grasshopper, and beetle fauna (see biotope reports available via the LBV administration) are extremely rich. Herbaceous plants and grasses were reintroduced by autochthonous transfer of mowed material from nearby dry grassland habitats of Munich, and *Hippophae rhamnoides, Sorbus aucuparia* and various *Rosa sp.,* all of Munich provenance, had been actively planted by the LBV. Hundreds of trees and shrubs of eight *Salix* species have established by themselves (H. Sedlmeier, pers. com.).

Species inventory

Between the 14th of March and the 8th of August 2017, the Obermayr gravel pit was visited by the first author in regular intervals (every 2-3 weeks), the initial spring species survey was conducted by both authors. Monitoring walks were conducted between 10 am and 4 pm on sunny, warm days with little or no wind. The mapping did not follow a strict route, but bees were searched for on flowers and nesting requisites. If possible, species were identified directly in the field and were documented via macro-photography in a standardized setup: for detailed pictures, the bees were caught with an insect net and cooled down for 10 minutes in an Eppendorf cupped plastic vial stored on ice in a cooled box. When the bees fell into rigor of cold, they were transferred onto scale paper (using a small box lined with millimeter paper on its bottom) and photographed from all sides (SLR camera: Pentax K-x; Lens: Sigma DG 17-70 mm, 1:2.8, macro), carefully turning them by hand or using a pair of watchmaker’s tweezers (see Figure 2 as an example of such a photo voucher). Within one to two minutes, they warmed up again and were released at the location they were also caught. For species that are taxonomically difficult to distinguish by morphology alone, like most members of the genera *Sphecodes*, *Lasioglossum* or *Halictus*, voucher specimens, preferably males (for morphological re-identification by genitalia preparations), were collected and identified morphologically and via DNA barcoding (methods and primers as described in Hofmann et al. 2018). Photo vouchers are accessible via the Diversity Workbench (DWB) server, DNA barcodes were uploaded to NCBI GenBank (see

Table 3 for GenBank Accession Numbers and DWB Accessions). The voucher specimens are deposited in the Zoologische Staatssammlung Munich (ZSM).

Additionally, we included species records from 2016 provided by M. Bräu in the species list. The domesticated honey bee *Apis mellifera* was abundantly observed at the Kiesgrube Obermayr, but not included in the species list.

Results

We found six studies with wild bee species lists for Central European gravel pits (Table 1). In these studies, 239 species were documented (Table 2). Of these, 108 species were reported by only one study, while 131 were reported in at least two different studies (two studies: 59 spp., three studies: 48 spp., four studies: 17 spp., five studies: 6 spp., all six studies: 1 spp.). Of the 239 species with records published from gravel pits, 184 are also native in the Munich area (M. Bräu, pers. com.). A total of 48 species were found in the survey area (see Table 3). 29 were documented via standardized *in-situ* photography, eight via DNA-barcoding, and 3 species were observed. Eight of theses have also been recorded by M. Bräu in 2016, and an additional six species had been documented in 2016, but were not seen in 2017. Amongst the observed species, four were oligolectic, 33 polylectic and eleven were cuckoo bees. Of the non-parasitic bees eleven nested above ground, five above and below ground and 32 below ground. A *Megachile* female could not be identified to species level, as the pollen brush was full and the colors relevant for determination were not visible. A *Megachile* male voucher (KGO-00081) was unclear, as coxa 1 and tergite 6 were not visible. Most likely it was a *Megachile rotundata* male, but it cannot be excluded that it was another species, thus we did not include it in our list. The photo voucher of *Megachile cf. versicolor* could also be *Megachile centuncularis,* as a definite separation of these two species is only possible via examination of the genitalia, but the redish tarsal segments hint towards *M. versicolor* (KGO-00021). The same applies for the *Halictus confusus/tumulorum* complex, the photo voucher was not unambiguous, but here we can confirm the presence of *H. tumulorum* via DNA barcoding (voucher MG792009). For one *Hylaeus* voucher, we strongly suspect it to be *H. nigritus*, but we lack a photo of sufficient quality of the face in frontal view to say for sure (KGO-00039). For *Andrena*, we had photo vouchers of one male and three females, where relevant features were not visible and they thus could not be identified. In total, 12% of the photo vouchers (excluding *Halictus*, *Lasioglossum* and *Sphecodes* pictures) were not identifiable to species level.

Discussion

With at least 48 species, the gravel pit Obermayr is an important wild bee habitat in the East of Munich, especially for ground-nesting species. In Germany, Austria and Switzerland, 50% of the bees are nesting in self-burrowed tunnels in the ground and 19% in hollow spaces which can be aboveground or underground (Zurbuchen and Müller 2012, p.57; Westrich 2018), but for the gravel pit the proportion ranges at 79%. This should be considered when it comes to the refill of idle gravel pits. By maintaining some open soil sites, they can enrich the landscape by providing nesting sites for wild bees. Moreover, if hollows and puddles hold the water, renatured gravel pits are important spawn habitats for amphibians (Escher 1974), and steep walls can serve swallows as nest sites (Wagner 1969), and such sites also have a high conservation value for butterflies (Lenda et al. 2011). With some planning effort, the conservation value of abandoned gravel pits can be strongly increased.

Photo-documentation *in-situ* instead of voucher collection proved feasible for most wild bee genera, but nevertheless taxonomic skills are necessary to be able to recognize bee sex and genera in the field, to be aware which different features need to be photographed or focused on in males and females and in different genera (see Table 4 for examples). The method is problematic for species from the genera *Sphecodes*, *Lasioglossum* and *Halictus*, but also in certain groups of *Andrena*, *Nomada* or *Bombus*, as some species in these groups differ only in minute texture features difficult to document by photography. Generally, small individuals (< 7 mm) can be problematic for another reason, as the rigor of cold only lasts for about a minute, thus time often is not sufficient to get all details documented. Moreover, another limitation to the photo-based identification of bee females is that individuals with pollen load usually cannot be identified, as the pollen generally obscures the colour of the scopae – hence we chilled down only foraging females without pollen load, and did not consider those carrying pollen.

Macro photographs need to be of sufficient quality, brightness and especially depth of field and resolution to be able to identify microstructures and sculpture on the thorax and tergites, thus a good macro lens is required, and if the weather is cloudy, an additional light source improves picture quality.

The big advantages of *in-situ* bee photo-documentation are the preservation of live individuals' color information (which is often lost in specimens) and the possibility to share voucher information (e.g. with taxonomic specialists) via a cloud, thus it is not necessary to send fragile specimens per mail, if the determination needs to be confirmed by a second person. However, in comparison with collecting voucher specimens, this method certainly has certain limitations and also some disadvantages: firstly, the photographer needs to be quick in taking pictures of all relevant features, because the rigor of cold does not last long. Secondly, if pictures are not good enough to see the characters you need, there is no chance to go back to the original individual, after it was released. Moreover, the time effort in the field is increased compared to specimen collection, thus only smaller or fewer sites can be monitored at a time.

Although photo-documentation cannot replace voucher collection completely, it can be an approach towards non-invasive species documentation (especially in larger bees and easier to recognize groups), which becomes increasingly important in times of drastic decreases in many insect taxa worldwide (Sánchez-Bayo and Wyckhuys 2019). That bee identification from photographs is possible to a certain degree (considering above-mentioned limitations to the method), at least in the larger genera (especially Megachilidae), has been repeatedly shown in numerous web-based insect identification forums and discussion groups (including social media), where good macro-photographs have enabled specialists to securely identify bee taxa to genus and even species level, sometimes contributing new regional records with this method (e.g., BWARS.com 2018; Wildbienen-Forum 2019; Hummelforum 2019; BugGuide.net 2019).

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References

Arle, J., Blondzik, K., Claussen, U., Duffek, A., Grimm, S., Hilliges, F., Kirschbaum, B., Kirst, I., Koch, D., Koschorrek, J., Lepom, P., Leujak, W., Mohaupt, V., Naumann, S., Pirntke, U., Rechenberg, J., Schilling, P., Ullrich, A., Wellmitz, J., Werner, S., Wolter, R. 2017. Gewässer in Deutschland: Zustand und Bewertung. Dessau-Roßlau (Umweltbundesamt).

BugGuide.net 2019. ID Request. https://bugguide.net/node/view/6/bgimage [last accessed 13 Feb. 2019]

BWARS.com 2018. Bees, Wasps and Ant Recording Society. http://www.bwars.com/forum [last accessed 13 Feb. 2019]

Cölln, K., Jakubzik, A. and Kinkler, H. 2012. Die Eignung von Wespen und Bienen als Bioindikatoren – Vergleichende Analayse der Faunen von zwei Sonderstandorten in Leverkusen (Hymenoptera Aculeata). Mitteilungen der Arbeitsgemeinschaft westfälischer Entomologen 28: 1-28.

Dubitzky, A. 2015. Erfassung der aktuellen Wildbienenfauna mit Entwicklung eines Pflegekonzeptes für das Gelände der ehemaligen Kiesgrube Roth in München Trudering. Gutachten im Auftrag des BUND Naturschutz in Bayern e.V. Kreisgruppe München.

Escher, K. 1974. Die Bedeutung der Kiesgruben als biologische Refugien. Vierteljahrsschriften der Naturforschenden Gesellschaft Zürich 119: 345-348.

Feitz, F., Gloden, R., Melchior, E. and Schneider, N. 2006. Wespen und Wildbienen des Naturschutzgebiets „Baggerweieren” im „Haff Réimech”, Luxemburg (Insecta, Hymenoptera, Aculeata). Bulletin de la Société des naturalistes luxembourgeois 106: 75-99.

Hofmann, M. M., Fleischmann, A. and Renner, S. S. 2018. Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. Oecologia 187: 701-706.

Hummelforum 2019. https://pollenhoeschen.de/Hummelforum/Forum/artbestimmung/ [last accessed 13 Feb. 2019]

Krebs, A. and Wildermuth, H. 1976. Kiesgruben als schützenswerte Lebensräume seltener Pflanzen und Tiere. Mitteilungen der Naturwissenschaftlichen Gesellschaft Winterthur 35: 19-73.

Lenda, M., Skórka, P., Moroń, D., Rosin, Z. M. and Tryjanowski, P. 2012. The importance of the gravel excavation industry for the conservation of grassland butterflies. Biological Conservation 148: 180-190.

Meisterhans, K. and Heusser, H. R. 1970. Amphibien und ihre Lebensräume: Gefährdung, Forschung, Schutz. Natur und Mensch 12: Heft 4.

Pachinger, B. and Prochazka, B. 2009. Die Wildbienen (Hymenoptera: Apoidea) in Rutzendorf (Niederösterreich) – ein Refugium mitten im Marchfeld. Beiträge zur Entomofaunistik 10: 31-47.

Sánchez-Bayo, F., and Wyckhuys, K. A. 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232: 8-27.

Schiel, F. J. and Rademacher, M. 2008. Artenvielfalt und Sukzession in einer Kiesgrube südlich Karlsruhe. Ergebnisse des Biotopmonitoring zum Naturschutzgebiet „Kiesgrube am Hardtwald Durmersheim”. Naturschutz und Landschaftplanung 40: 87-94.

Völkl, W., Heßbert, A.v., Mader, D., Metzner, J., Gerstberger, P., Hoffman, K. H., Rebhan, H. and Krec, R. 2002. Natural succession in a dynamic riverine landscape and the protection of open areas. In: Pasture Landscapes and Nature Conservation. Heidelberg and Berlin (Springer).

Wagner, G. 1969. Die Uferschwalbenkolonien im Kanton Zürich in 1958-1968. Schweizer Naturschutz 3: 64-66.

Westrich, P. 1989. Die Wildbienen Baden-Württembergs. Band 1: Allgemeiner Teil: Lebensräume, Verhalten, Ökologie und Schutz. Stuttgart (Ulmer).

Westrich, P. 2018. Die Wildbienen Deutschlands. Stuttgart (Ulmer).

Wildbienen-Forum 2019. https://239771.forumromanum.com/member/forum/forum.php?action=std_tindexandUSER=user_239771andthreadid=2 [last accessed 13 Feb. 2019]

Zurbuchen, A. and Müller, A. 2012. Wildbienenschutz-von der Wissenschaft zur Praxis. Zürich (Bristol Stiftung).

Table 1: Inventories of active and renatured gravel pits in Central Europe, with study period and sampling method.

Site	Study period	Sampling method	Publication
inactive gravel pit complex in Leverkusen	2000-2005	net sampling	[1] Cölln et al. 2012
former gravel pit Roth in Trudering, Munich	4 monitoring walks in 2015; additional investigation day in 2008	net sampling	[2] Dubitzky, A. (unpublished)
Ramsar area "Baggerweieren" at "Haff Réimech", Luxembourg	1997 to 2004; 209 monitoring walks	net sampling	[3] Feitz et al. 2006
gravel pits between Rhine and Lake Zurich	N/A	N/A	[4] Krebs and Wildermuth 1976
closed gravel pit Rutzendorf, Lower Austria	2003-2005 and 2007-2008; four-weekly rhythm	net sampling	[5] Pachinger and Prochazka 2009; with additional data from B. Pachinger for 2009 and later (pers. communication)
gravel pit "am Hardtwald Durmersheim" south of Karlsruhe	1993 to 2005	net sampling	[6] Schiel and Rademacher 2008; with additional data from A. Schanowski for 2007 (pers. communication)

Table 2: List of wild bees reported for Central European gravel pits. The numbers in squared brackets indicate the studies where the species was reported (numbers refer to Table 1). Species marked in bold were also found in this study.

Species	Family	Study
Andrena agilissima (Scopoli, 1770)	Andrenidae	[3]
Andrena apicata Smith, 1847	Andrenidae	[2]
Andrena barbilabris (Kirby, 1802)	Andrenidae	[1,6]
***Andrena bicolor* Fabricius, 1775**	Andrenidae	[1,2,6]
Andrena carantonica Pérez, 1902	Andrenidae	[1,6]
Andrena chrysopus Pérez, 1903	Andrenidae	[6]
***Andrena chrysosceles* (Kirby, 1802)**	Andrenidae	[3,5]
Andrena cineraria (Linnaeus, 1758)	Andrenidae	[2,3,6]
Andrena denticulata (Kirby, 1802)	Andrenidae	[6]
***Andrena dorsata* (Kirby, 1802)**	Andrenidae	[1,5,6]

Andrena flavipes Panzer, 1798	Andrenidae	[1,5,6]
Andrena fulva (Müller, 1766)	Andrenidae	[1,3]
Andrena fulvata Stoeckhert, 1930	Andrenidae	[2]
Andrena gelriae van der Vecht, 1927	Andrenidae	[6]
Andrena gravida Imhoff, 1832	Andrenidae	[2]
Andrena haemorrhoa (Fabricius, 1781)	Andrenidae	[1,3,5,6]
Andrena hattorfiana (Fabricius, 1775)	Andrenidae	[3]
Andrena helvola (Linnaeus, 1758)	Andrenidae	[2]
Andrena impunctata Pérez, 1895	Andrenidae	[5]
Andrena intermedia Thomson, 1870	Andrenidae	[2]
Andrena labiata Fabricius, 1781	Andrenidae	[1,6]
Andrena lathyri Alfken, 1899	Andrenidae	[6]
Andrena minutula (Kirby, 1802)	Andrenidae	[1,3,6]
Andrena minutuloides Perkins, 1914	Andrenidae	[1,5]
Andrena mitis Schmiedeknecht, 1883	Andrenidae	[6]
Andrena nigroaenea (Kirby, 1802)	Andrenidae	[5]
Andrena nitida (Müller, 1776)	Andrenidae	[3]
Andrena nobilis Morawitz, 1873	Andrenidae	[5]
Andrena oralis Morawitz, 1876	Andrenidae	[5]
Andrena ovatula (Kirby, 1802)	Andrenidae	[1,5,6]
Andrena pilipes Fabricius, 1781	Andrenidae	[1,5,6]
Andrena praecox (Scopoli, 1763)	Andrenidae	[1,2,6]
Andrena propinqua Schenck, 1853	Andrenidae	[5]
Andrena proxima (Kirby, 1802)	Andrenidae	[1]
Andrena pusilla Pérez, 1903	Andrenidae	[6]
Andrena ruficrus Nylander, 1848	Andrenidae	[2]
Andrena schencki Morawitz, 1866	Andrenidae	[3]
Andrena scita Eversmann, 1852	Andrenidae	[5]
Andrena similis Smith, 1849	Andrenidae	[6]
Andrena simontornyella Noskiewicz, 1939	Andrenidae	[5]
Andrena strohmella Stoeckhert, 1928	Andrenidae	[2]
Andrena subopaca Nylander, 1848	Andrenidae	[3,6]
Andrena symphyti Schmiedeknecht, 1883	Andrenidae	[5]
Andrena vaga Panzer, 1799	Andrenidae	[1,2,3,4,6]
Andrena ventralis Imhoff, 1832	Andrenidae	[2]
Andrena viridescens Viereck, 1916	Andrenidae	[6]
Andrena wilkella (Kirby, 1802)	Andrenidae	[1,6]
Anthidiellum strigatum (Panzer, 1805)	Megachilidae	[3,4,6]
Anthidium manicatum (Linnaeus, 1758)	Megachilidae	[3]
Anthidium nanum Mocsary, 1881	Megachilidae	[3,5]
Anthidium oblongatum (Illiger, 1806)	Megachilidae	[3]
Anthidium punctatum Latreille, 1809	Megachilidae	[3,5]
Anthophora bimaculata (Panzer, 1798)	Apidae	[6]
Anthophora plumipes (Pallas, 1772)	Apidae	[1,2,3,4]
Anthophora quadrimaculata (Panzer, 1798)	Apidae	[1]
Anthophora retusa (Linnaeus, 1758)	Apidae	[1,3,6]

***Bombus hortorum* (Linnaeus, 1761)**	Apidae	[1,2,5]
Bombus humilis Illiger, 1806	Apidae	[5,6]
***Bombus hypnorum* (Linnaeus, 1758)**	Apidae	[1,3]
***Bombus lapidarius* (Linnaeus, 1758)**	Apidae	[1,2,5,6]
***Bombus lucorum* (Linnaeus, 1761)**	Apidae	[1,2,5]
***Bombus pascuorum* (Scopoli, 1763)**	Apidae	[1,2,3,5,6]
***Bombus pratorum* (Linnaeus, 1761)**	Apidae	[1,2]
***Bombus rupestris* (Fabricius, 1793)**	Apidae	[1,2,6]
Bombus soroeensis (Fabricius, 1776)	Apidae	[2]
***Bombus sylvarum* (Linnaeus, 1761)**	Apidae	[3,5,6]
***Bombus terrestris* (Linnaeus, 1758)**	Apidae	[1,3,5]
***Bombus vestalis* (Geoffroy, 1785)**	Apidae	[1,2,5]
Camptopoeum frontale (Fabricius, 1804)	Andrenidae	[5]
Ceratina chalybea Chevrier, 1872	Apidae	[5]
Ceratina cucurbitina (Rossi, 1792)	Apidae	[1,3,5,6]
Ceratina cyanea (Kirby, 1802)	Apidae	[1,2,3,4,5,6]
Chelostoma campanularum (Kirby, 1802)	Megachilidae	[1,6]
Chelostoma distinctum (Stöckhert, 1929)	Megachilidae	[3,6]
Chelostoma florisomne (Linnaeus, 1758)	Megachilidae	[3]
Chelostoma rapunculi (Lepeletier, 1841)	Megachilidae	[1,3,6]
Coelioxys afra Lepeletier, 1841	Megachilidae	[3,6]
Coelioxys aurolimbata Förster, 1853	Megachilidae	[3]
***Coelioxys elongata* Lepeletier, 1841**	Megachilidae	this study
Coelioxys mandibularis Nylander, 1848	Megachilidae	[1]
Coelioxys quadridentata (Linnaeus, 1758)	Megachilidae	[1,3]
***Colletes cunicularius* (Linnaeus, 1761)**	Colletidae	[1,2,3,6]
***Colletes daviesanus* Smith, 1846**	Colletidae	[1,4,5]
Colletes fodiens (Geoffroy, 1785)	Colletidae	[1,6]
Colletes hederae Schmidt and Westrich, 1993	Colletidae	[3]
Colletes similis Schenck, 1853	Colletidae	[1,6]
Dasypoda hirtipes (Fabricius, 1793)	Melittidae	[3,4,5,6]
Dioxys tridentata (Nylander, 1848)	Megachilidae	[3]
Epeoloides coecutiens (Fabricius, 1775)	Apidae	[3]
Epeolus variegatus (Linnaeus, 1758)	Apidae	[1,3,6]
Eucera longicornis (Linnaeus, 1758)	Apidae	[3,5]
Eucera nigrescens Pérez, 1879	Apidae	[3,5,6]
Eucera pollinosa Smith, 1854	Apidae	[5]
Halictus confusus Smith, 18*53*	Halictidae	[6]
***Halictus eurygnathus* Blüthgen, 1931**	Halictidae	[3]
Halictus gavarnicus Pérez, 1903	Halictidae	[5]
Halictus kessleri Bramson, 1879	Halictidae	[5]
Halictus langobardicus Blüthgen, 1944	Halictidae	[3,6]
Halictus leucaheneus Ebmer, 1972	Halictidae	[6]
Halictus maculatus Smith, 1848	Halictidae	[3,5,6]
Halictus pollinosus Sichel, 1860	Halictidae	[5]
Halictus quadricinctus (Fabricius, 1777)	Halictidae	[5,6]

***Halictus rubicundus* (Christ, 1791)**	Halictidae	[1,3,6]
***Halictus scabiosae* (Rossi, 1790)**	Halictidae	[1,3,6]
Halictus seladonius (Fabricius, 1794)	Halictidae	[5]
Halictus sexcinctus Fabricius, 1775	Halictidae	[4,5,6]
Halictus simplex Bluethgen, 1923	Halictidae	[5,6]
Halictus smaragdulus Vachal, 1895	Halictidae	[6]
***Halictus subauratus* (Rossi, 1792)**	Halictidae	[3,5,6]
***Halictus tumulorum* (Linnaeus, 1758)**	Halictidae	[1,2,3,5,6]
Heriades crenulatus Nylander, 1856	Megachilidae	[6]
Heriades truncorum (Linnaeus, 1758)	Megachilidae	[1,3,5,6]
Hoplitis acuticornis (Dufour and Perris, 1840)	Megachilidae	[3]
Hoplitis adunca (Panzer, 1798)	Megachilidae	[5]
Hoplitis claviventris (Thomson, 1872)	Megachilidae	[3]
Hoplitis leucomelana (Kirby, 1802)	Megachilidae	[1,2,3,4,5]
Hoplitis tridentata (Dufour and Perris, 1840)	Megachilidae	[3,6]
Hylaeus angustatus (Schenck, 1859)	Colletidae	[3,6]
***Hylaeus annularis* (Kirby, 1802)**	Colletidae	[1,3,6]
Hylaeus brevicornis Nylander, 1852	Colletidae	[1,5,6]
Hylaeus cardioscapus Cockerell, 1924	Colletidae	[5]
Hylaeus clypearis (Schenck, 1853)	Colletidae	[3]
***Hylaeus communis* Nylander, 1852**	Colletidae	[1,6]
Hylaeus confusus Nylander, 1852	Colletidae	[1,2,6]
Hylaeus cornutus Curtis, 1831	Colletidae	[1,3,5]
Hylaeus difformis (Eversmann, 1852)	Colletidae	[3]
Hylaeus dilatatus (Kirby, 1802)	Colletidae	[5]
Hylaeus gibbus Saunders, 1850	Colletidae	[5,6]
Hylaeus gredleri Foerster, 1871	Colletidae	[1,3,5,6]
Hylaeus hyalinatus (Smith, 1842)	Colletidae	[1,3,5]
Hylaeus nigritus (Fabricius, 1798)	Colletidae	[3]
Hylaeus punctatus (Brullé, 1832)	Colletidae	[3]
Hylaeus punctulatissimus Smith, 1842	Colletidae	[1]
Hylaeus signatus (Panzer, 1798)	Colletidae	[1,3]
Hylaeus variegatus (Fabricius, 1798)	Colletidae	[3,6]
Lasioglossum aeratum (Kirby, 1802)	Halictidae	[5,6]
Lasioglossum albipes (Fabricius, 1781)	Halictidae	[6]
Lasioglossum brevicorne (Schenck, 1869)	Halictidae	[6]
Lasioglossum calceatum (Scopoli, 1763)	Halictidae	[1,2,3,5,6]
Lasioglossum clypeare (Schenck, 1853)	Halictidae	[5]
Lasioglossum costulatum (Kriechbaumer, 1873)	Halictidae	[3,6]
Lasioglossum discum (Smith, 1853)	Halictidae	[5]
Lasioglossum fulvicorne (Kirby, 1802)	Halictidae	[3,6]
Lasioglossum glabriusculum (Moraw., 1872)	Halictidae	[3]
Lasioglossum intermedium (Schenck, 1869)	Halictidae	[1.3]
Lasioglossum interruptum (Panzer, 1798)	Halictidae	[5]
***Lasioglossum laticeps* (Schenck, 1869)**	Halictidae	[1,3,6]
Lasioglossum lativentre (Schenck, 1853)	Halictidae	[3,5,6]

Lasioglossum leucopus (Kirby, 1802)	Halictidae	[1,6]
***Lasioglossum leucozonium* (Schrank, 1781)**	Halictidae	[1,2,3,6]
Lasioglossum limbellum (Morawitz, 1876)	Halictidae	[3,6]
Lasioglossum lucidulum (Schenck, 1861)	Halictidae	[6]
Lasioglossum malachurum (Kirby, 1802)	Halictidae	[3,4,5,6]
Lasioglossum minutissimum (Kirby, 1802)	Halictidae	[1,6]
Lasioglossum monstrificum (Morawitz, 1891)	Halictidae	[1]
***Lasioglossum morio* (Fabricius, 1793)**	Halictidae	[1,2,3,5,6]
Lasioglossum nigripes (Lepeletier, 1841)	Halictidae	[5]
Lasioglossum nitidiusculum (Kirby, 1802)	Halictidae	[3]
Lasioglossum pauperatum (Brullé, 1832)	Halictidae	[6]
***Lasioglossum pauxillum* (Schenck, 1853)**	Halictidae	[1,3,6]
Lasioglossum politum (Schenck, 1853)	Halictidae	[5,6]
Lasioglossum punctatissimum (Schenck, 1853)	Halictidae	[1,6]
Lasioglossum puncticolle (Morawitz, 1872)	Halictidae	[3]
Lasioglossum quadrinotatulum (Schenck, 1861)	Halictidae	[3,6]
Lasioglossum quadrinotatum (Kirby, 1802)	Halictidae	[5,6]
Lasioglossum semilucens (Alfken, 1914)	Halictidae	[3]
*Lasioglossum sexnotatum (*Kirby, 1802)	Halictidae	[5,6]
Lasioglossum sexstrigatum (Schenck, 18*69)*	Halictidae	[1,6]
Lasioglossum trichopygum (Bluethgen, 1923)	Halictidae	[5]
Lasioglossum villosulum (Kirby, 1802)	Halictidae	[1,3,6]
Lasioglossum xanthopus (Kirby, 1802)	Halictidae	[5,6]
Lasioglossum zonulum (Smith, 1848)	Halictidae	[5,6]
Macropis europaea Warncke, 1973	Melittidae	[3]
*Megachile alpicola*Alfken, 1924	Megachilidae	[6]
Megachile centuncularis (Linnaeus, 1758)	Megachilidae	[1,6]
Megachile circumcincta (Kirby, 1802)	Megachilidae	[1,2,3]
Megachile ericetorum Lepeletier, 1841	Megachilidae	[1,2,3]
Megachile lagopoda (Linnaeus, 1761)	Megachilidae	[5]
Megachile ligniseca (Kirby, 1802)	Megachilidae	[3]
Megachile nigriventris Schenk, 1869	Megachilidae	[2]
Megachile parietina (Geoffroy, 1785)	Megachilidae	[4]
Megachile pilidens Alfken, 1924	Megachilidae	[1,3,6]
Megachile rotundata (Fabricius, 1787)	Megachilidae	[6]
***Megachile versicolor* Smith, 1844**	Megachilidae	[1,2,5]
***Megachile willughbiella* (Kirby, 1802)**	Megachilidae	[1,3,4,5]
Melecta albifrons (Forster, 1771)	Apidae	[4]
Melitta leporina (Panzer, 1799)	Melittidae	[1,3,5,6]
Melitta nigricans Alfken, 1905	Melittidae	[3]
Nomada alboguttata Herrig-Schaeffer, 1839	Apidae	[1,3,5,6]
Nomada bifasciata Olivier, 1811	Apidae	[3]
Nomada fabriciana (Linnaeus, 1767)	Apidae	[1,2,3,6]
Nomada ferruginata (Linnaeus, 1767)	Apidae	[2,3]
Nomada flava Panzer, 1798	Apidae	[1,3,6]
***Nomada flavoguttata* (Kirby, 1802)**	Apidae	[1,3,6]

Nomada flavopicta (Kirby, 1802)	Apidae	[3]
Nomada fucata Panzer, 1798	Apidae	[1,3,6]
Nomada fulvicornis Fabricius, 1793	Apidae	[1,6]
Nomada fuscicornis Nylander, 1848	Apidae	[6]
***Nomada goodeniana* (Kirby, 1802)**	Apidae	[6]
***Nomada lathburiana* (Kirby, 1802)**	Apidae	[2,3,6]
Nomada leucophthalma (Kirby, 1802)	Apidae	[3]
Nomada marshamella (Kirby, 1802)	Apidae	[1,3]
Nomada obscura Zetterstedt, 1838	Apidae	[6]
Nomada panzeri Lepeletier, 1841	Apidae	[2,6]
Nomada rufipes Fabricius, 1793	Apidae	[6]
Nomada sexfasciata Panzer, 1799	Apidae	[3]
Nomada sheppardana (Kirby, 1802)	Apidae	[6]
Nomada signata Jurine, 1807	Apidae	[3]
Nomada succincta Panzer, 1798	Apidae	[1,3]
Nomada zonata Panzer, 1798	Apidae	[1]
***Osmia aurulenta* (Panzer, 1799)**	Megachilidae	[3,4]
***Osmia bicolor* (Schrank, 1781)**	Megachilidae	[1,3,4]
Osmia bicornis (Linnaeus, 1758)	Megachilidae	[1,3]
Osmia brevicornis (Fabricius, 1798)	Megachilidae	[3]
Osmia caerulescens (Linnaeus, 1758)	Megachilidae	[6]
Osmia gallarum Spinola, 1808	Megachilidae	[3,6]
Osmia rufohirta Latreille, 1811	Megachilidae	[3]
***Osmia spinulosa* (Kirby, 1802)**	Megachilidae	[3,5]
Panurgus calcaratus (Scopoli, 1763)	Andrenidae	[1,5,6]
Rhophitoides canus (Eversmann, 1852)	Halictidae	[5]
Sphecodes albilabris (Fabricius, 1793)	Halictidae	[1,3,6]
***Sphecodes crassus* Thomson, 1870**	Halictidae	[1,2,6]
Sphecodes cristatus Hagens, 1882	Halictidae	[6]
***Sphecodes ephippius* (Linnaeus, 1767)**	Halictidae	[1,5,6]
Sphecodes ferruginatus Hagens, 1882	Halictidae	[1]
Sphecodes geoffrellus (Kırby, 1802)	Halictidae	[1,6]
***Sphecodes gibbus* (Linnaeus, 1758)**	Halictidae	[1,5,6]
Sphecodes longulus Hagens, 1882	Halictidae	[1,6]
Sphecodes marginatus Hagens, 1882	Halictidae	[2]
Sphecodes miniatus Hagens, 1882	Halictidae	[1,2,5,6]
***Sphecodes monilicornis* (Kirby, 1802)**	Halictidae	[1,2,5,6]
Sphecodes niger Hagens, 1874	Halictidae	[1]
Sphecodes pellucidus Smith, 1845	Halictidae	[1,6]
***Sphecodes puncticeps* Thomson, 1870**	Halictidae	[1,6]
Sphecodes reticulatus Thomson, 1870	Halictidae	[1,6]
Sphecodes rufiventris (Panzer, 1798)	Halictidae	[6]
Stelis odontopyga Noskiewicz, 1925	Megachilidae	[3]
Stelis ornatula (Klug, 1807)	Megachilidae	[1]
Tetraloniella dentata (Germar, 1839)	Apidae	[5]
Trachusa byssina (Panzer, 1804)	Megachilidae	[3]

Table 3: Species List for gravel pit Obermayr. The record type refers to the mode of documentation (o = observation, p = photo-documentation, b = barcoding of voucher specimen, ext = external data from M. Bräu), the record ID gives the GenBank or Biodiversiy Workbench accession numbers for barcoded or photographic vouchers, lecty describes the foraging preference and nest site preference whether a bee builds its nest below or above the surface or is parasitic. Species where determination was not sure on the photograph are printed in grey.

Species	**record type**	**record ID**	**lecty**	**nest site preference**
Andrena bicolor Fabricius, 1775	o	observation on 28.03.2017	polylectic	ground
Andrena chrysosceles (Kirby, 1802)	p	KGO-00099	polylectic	ground
Andrena dorsata (Kirby, 1802)	ext	M.Bräu, 21.04.2016	polylectic	ground
Andrena flavipes Panzer, 1798	ext, p	M.Bräu, 21.04.2016 KGO-00028	polylectic	ground
Andrena gravida Imhoff, 1832	p	KGO-00097	polylectic	ground
Andrena haemorrhoa (Fabricius, 1781)	p	KGO-00084	polylectic	ground
Andrena vaga Panzer, 1799	ext, p	M.Bräu, n.d. KGO-00096 KGO-00106	oligolectic	ground
Andrena viridescens Viereck, 1916	ext	M.Bräu, 21.04.2016	oligolectic	ground
Anthidium manicatum (Linnaeus, 1758)	p	KGO-00035	polylectic	above
Anthidium oblongatum (Illiger, 1806)	p	KGO-00014	polylectic	above
Anthidium punctatum Latreille, 1809	p	KGO-00073	polylectic	above
Bombus hortorum (Linnaeus, 1761)	p	KGO-00082	polylectic	above and ground
Bombus hypnorum (Linnaeus, 1758)	p	KGO-00074	polylectic	above
Bombus lapidarius (Linnaeus, 1758)	p	KGO-00069 KGO-00100	polylectic	above and ground
Bombus lucorum (Linnaeus, 1761)	p	KGO-00065	polylectic	ground
Bombus pascuorum (Scopoli, 1763)	p	KGO-00067	polylectic	above and ground
Bombus pratorum (Linnaeus, 1761)	o	observed 28.03.2017	polylectic	above
Bombus rupestris(Fabricius, 1793)	p	KGO-00070	parasitic	parasitic
Bombus sylvarum (Linnaeus, 1761)	p	KGO-00002 KGO-00068	polylectic	above and ground
Bombus terrestris (Linnaeus, 1758)	p	KGO-00079	polylectic	ground
Bombus vestalis (Geoffroy, 1785)	ext, p	M.Bräu, 21.04.2016 KGO-00101	parasitic	parasitic

Coelioxys elongata Lepeletier, 1841	p	KGO-00080	parasitic	parasitic
Colletes cunicularius (Linnaeus, 1761)	ext, p	M.Bräu, n.d. KGO-00107	polylectic	ground
Colletes daviesanus Smith, 1846	o	observed 14.08.2017	oligolectic	ground
Halictus eurygnathus Blüthgen, 1931	p	KGO-00022 KGO-00034	polylectic	ground
Halictus rubicundus (Christ, 1791)	p	KGO-00103	polylectic	ground
Halictus scabiosae (Rossi, 1790)	p	KGO-00006	polylectic	ground
Halictus subauratus (Rossi, 1792)	b	MG792004	polylectic	ground
Halictus tumulorum (Linnaeus, 1758)	b	MG792009	polylectic	ground
Hylaeus cf. *nigritus* (Kirby, 1802)	p	KGO-00039	polylectic	above
Hylaeus communis Nylander, 1852	p	KGO-00027 KGO-00050 KGO-00052	polylectic	above
Lasioglossum laticeps (Schenck, 1869)	b	MG791965 MG791966 MG791967	polylectic	ground
Lasioglossum leucozonium (Schrank, 1781)	b	MG791993 MG791991	polylectic	ground
Lasioglossum morio (Fabricius, 1793)	b	MG791969 MG791970 MG791971 MG791972	polylectic	ground
Lasioglossum pauxillum (Schenck, 1853)	b, ext	M.Bräu, 21.04.2016, and 20.5.2016 MG791980 MG791981 MG791983	polylectic	ground
Megachile cf. *versicolor* Smith, 1844	p	KGO-00021	polylectic	above
Megachile willughbiella (Kirby, 1802)	p	KGO-00036 KGO-00037	polylectic	above and ground
Nomada flavoguttata (Kirby, 1802)	ext	M.Bräu, 21.04.2016	parasitic	parasitic
Nomada goodeniana(Kirby, 1802)	ext	M.Bräu, 21.04.2016	parasitic	parasitic
Nomada lathburiana (Kirby, 1802)	ext	M.Bräu, 21.04.2016	parasitic	parasitic
Osmia aurulenta (Panzer, 1799)	ext, p	M.Bräu, 20.05.2016 KGO-00071 KGO-00104	polylectic	above
Osmia bicolor (Schrank, 1781)	p	KGO-00105	polylectic	above
Osmia spinulosa (Kirby, 1802)	p	KGO-00072	oligolectic	above
Sphecodes crassus Thomson, 1870	b	MG845959	parasitic	parasitic
Sphecodes ephippius (Linnaeus, 1767)	ext	M.Bräu, 21.04.2016	parasitic	parasitic

Sphecodes gibbus (Linnaeus, 1758)	ext	M.Bräu, 21.04.2016	parasitic	parasitic
Sphecodes monilicornis (Kirby, 1802)	ext	M.Bräu, 21.04.2016	parasitic	parasitic
Sphecodes puncticeps Thomson, 1870	b	MG 845968	parasitic	parasitic

Table 4: Species features for photo-documentation. This list is not attempting to be comprehensive and must be adapted depending on time and region of the monitoring and should be in accordance with the respective identification keys.

General features:	
Overview photograph from top, side and bottom	size, colors, body shape
Frontal view of the face	shape, colors, hairs, mandibles, clypeus, labrum
Details of thorax from above	sculpturation of scutum and potential rugosity of propodeum
Detail of abdomen from above	tergite bands and sculpturation
For females:	
Pollen brush or scopae with flocci	color(s), extension
For males:	
Sternites	spines, shape of last sternite
Additional genus-specific features:	
Andrena males:	frontal and side view of the head, detail of antennae (front view) and mandibules
Anthophora males:	mid-tarsi and mid-basitarsi, hind tibiae and basitarsi
Bombus females:	sternite 6, head in front and side view, hind tibiae and basitarsi
Bombus males:	detail of antennae, hind tibiae and basitarsi
Chelostoma males:	sternites 2 and 4
Coelioxys females:	tergite 6 and sternites 5 and 6, mandibules
Coelioxys males:	tergite 5 edges and sternite 4, mandibules
Colletes females:	hind margin of tergite 1, back of thorax, dorsal fringe of hind tibiae, galeae, clypeus
Colletes males:	**sternite 6**, galeae
Hylaeus:	**frontal face** and antennal **view**, pronotal collar, presence or absence of lateral hair fringes on the first tergites additionally for males: mandibles and labrum
Megachile females:	tergite 6 in sideview, tibiae, basitarsi
Megachile males:	front tarsi, front coxae, tip of antennae
Nomada:	frontal and side view of head, labrum and tip of mandibles, detail of antennae, detail of hind femora and tibiae (esp. inner sides)
Osmia:	spurs of hind tibiae, shape of sternite 6, antennae, clypaeus

Figure Captions

Figure 1: The study site “Kiesgrube Obermayr” (modified from https://www.google.de/maps/@48.1462044,11.7084456,606m/data=!3m1!1e3, last accessed 19 Feb. 2019)

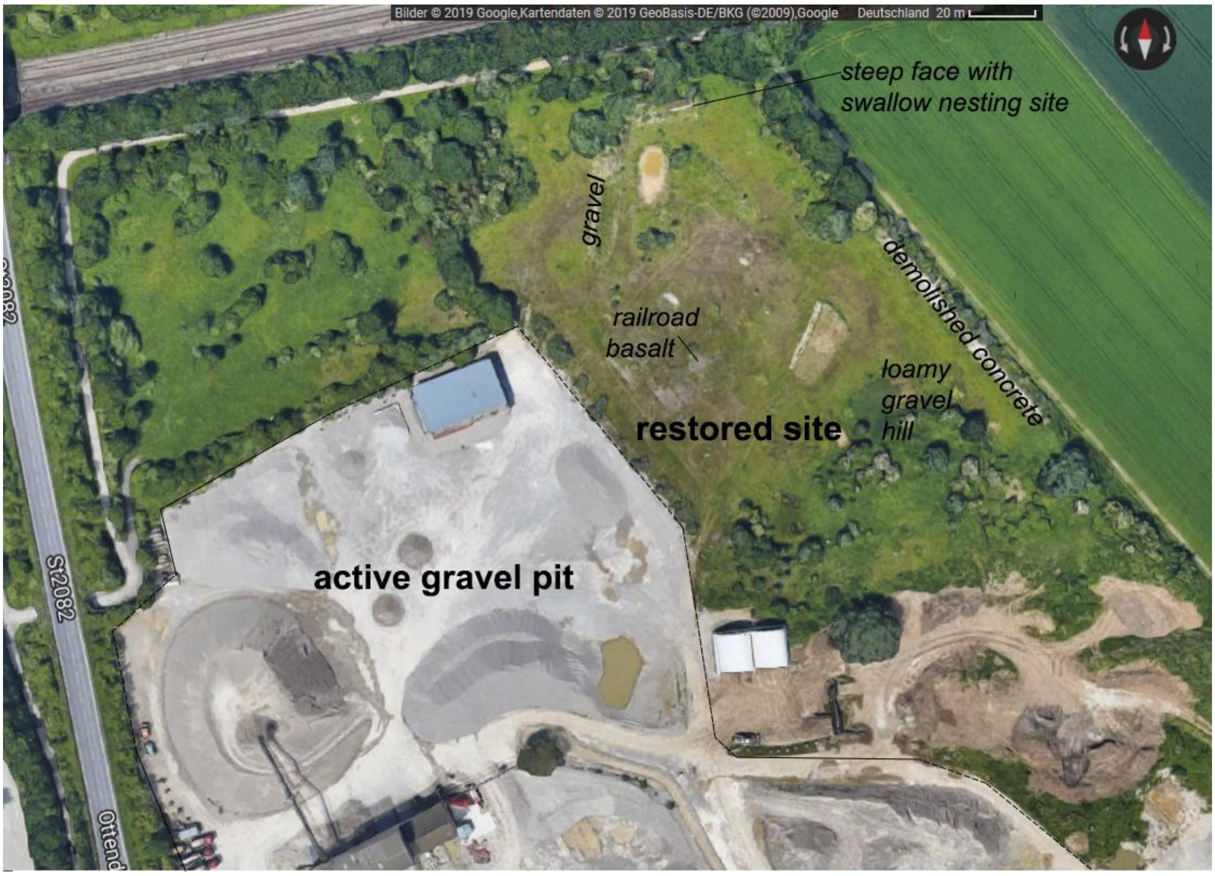
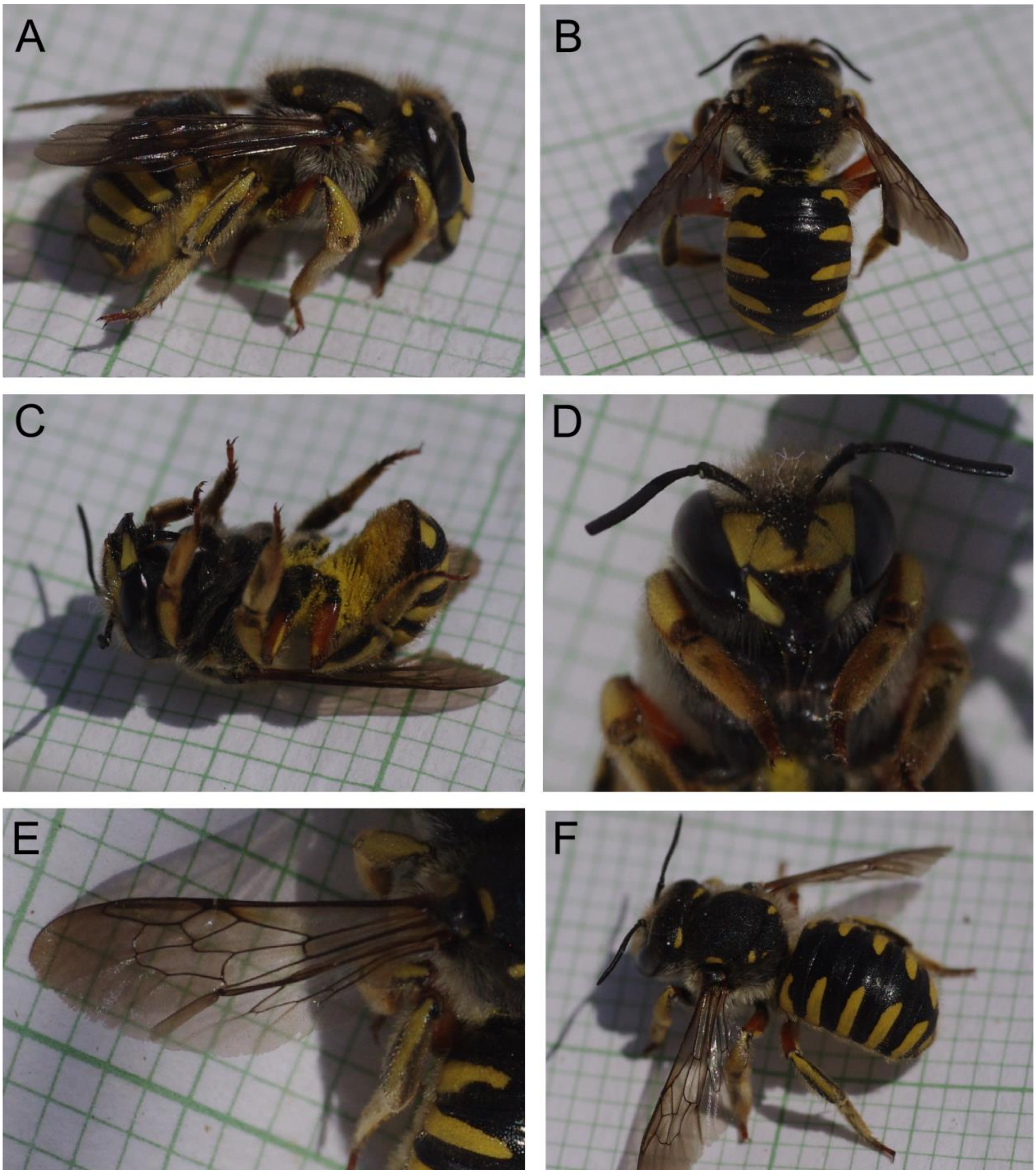


Figure 2: Picture plate of an *Anthidium manicatum* female: A) Lateral view; B) Dorsal view; C) Ventral view; D) Detail face and front legs; E) Detail wings; F) Thorax and abdomen pattern. Images A-E: individual immobilized by chilling. F: recovering from paralyzation. Square grid = 1 mm. All photographs by M. Hofmann.



Chapter 9

Courtship behaviour in the genus *Nomada*–antennal grabbing and possible transfer of male secretions

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Courtship behaviour in the genus *Nomada* – antennal grabbing and possible transfer of male secretions

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Abstract

Due to low population densities, copulation in the cuckoo bee genus *Nomada* has not previously been observed, although a seminal paper by Tengö and Bergström (1977) on the chemomimesis between these parasitic bees and their *Andrena* or *Melitta* hosts postulated that secretions from male glands might be sprayed onto females during copulation. Our observations on the initiation and insertion phase of copulation in three species of *Nomada* now indicate antennal grabbing as a mechanism by which chemicals are transferred between the sexes. Histological studies of the antennae of *N. fucata* and *N. lathburiana* reveal antennal modifications associated with cell aggregations that represent glandular cells, and SEM studies revealed numerous excretory canals.

Keywords

Antennal structure, copulation, chemomimesis, male secretions, cuckoo bees

Introduction

Bees (Apoidea, Apiformes) use visual, auditory and chemical signals to locate potential mates, and males may search for females at flowers, nest sites, or perch spots by non-aggressively patrolling along a strict route or by defending a territory in which females are likely to be encountered (Alcock et al. 1978, Eickwort and Ginsberg 1980). Observations on the actual copulation, which usually occurs on the wing, are scarce (Alcock et al. 1978, Michener 2007). Especially kleptoparasitic bees, which have low population densities, are rarely observed during mating, which comprises initiation, insertion, and separation. Here we report on the mating behavior of three species of *Nomada*, a genus of kleptoparasitic bees in the tribe Nomadini of the family Apidae (Hedtke et al. 2013) that comprises around 700 species occurring throughout the Holarctic, the Neotropics, sub-Saharan Africa, and the oriental region (Michener 2007; Ascher and Pickering 2017).

Nomada parasitizes predominantly species of *Andrena* (Tengö and Bergström 1977, Michener 2007), and the females use olfactory cues for detecting suitable host nests, but visual cues for finding nest entrance holes (Cane 1983, Schindler 2005). *Nomada* courtship includes “swarming” of males at shrubs of willow (*Salix* spec.) and gooseberry (*Ribes uva-crispa*; Friese 1923: 384) or males patrolling in groups with males of the host species (Tengö and Bergström 1977). Alcock (1978) saw males rubbing their abdomen and the lower surface of their head against blades of grass from which he inferred that they mark rendezvous places with sexual pheromones, an inference supported by an observation of a *N. fabriciana* male rubbing itself against a leaf (Smit 2005). Female dummies prepared with extracts of conspecific females elicit the initiation of copulation (Fleck 1995). The mandibular gland secretions of *N. bifida*, *N. flavoguttata*, *N. flavopicta*, *N. goodeniana*, *N. leucophthalma*, *N. lineola*, *N. marshamella*, and *N. panzeri* contain chemical compounds identical to those of the Dufour´s glands of their host species (Tengö and Bergström 1977), and Tengö and Bergström hypothesized that these secretions are sprayed on the females during mating to help them enter the host species´ nests. Figure 3 in Bergström (2008) shows a *Nomada lathburiana* female waiting to enter the nest of an *Andrena cineraria* female.

The present study of the courtship and mating behaviour of *Nomada* is based on field and lab observations of *N. fucata* and *N. lathburiana* in central Germany (Schindler 2005) and field studies on *N. flavoguttata* in southern Germany. *Nomada flavoguttata* is distributed across Eurasia, *N. fucata* from Portugal to Central Asia and from Sweden to Northern Africa, and *N. lathburiana* in Eurasia and Northern Africa (Scheuchl and Willner 2016). Observation of a previously unreported behavior during the initiation of copulation, which we term “antennal grabbing”, indicated that males transfer a chemical substance to the antennae of the females. This led us to investigate the morphology and histology of the antennae.

Methods

Behavioral observations

Courtship behavior in *Nomada fucata* F. and *N. lathburiana* (K.) was studied both in the field and in the lab. The courtship phase was observed at nesting sites of the host species *Andrena flavipes* Panz. and *A. vaga* Panz. and at foraging plants in an abandoned gravel pit near Bonn (50.773293°N, 7.147145°E, about 50 m a.s.l.) in 1998 and 1999. The initiation and insertion phase of copulation in *N. flavoguttata* (K.) was observed on 24 May 2017 in the conservation area "Allacher Heide" in Munich (48.206729°N, 11.474383°E, 517 m a.s.l.). It was the first sunny and warm day after a longer period of cold and moist weather, leading to a major hatching event of several *Nomada* species. Within 5 m^2, more than 50 *Nomada* bees could be observed foraging and mating on *Taraxacum officinale s.l.* (Fig. 1). Three bees were also identified via DNA barcoding (see Appendix 1 for a description of lab procedures).

Studies in the lab were carried out with virgin males and females of *N. fucata* and *N. lathburiana*. Bees were collected with emergence traps at the nests and released in flight cages (4 × 2 × 2 m) or transferred in petri-dishes (ø 15 cm) for observation. *Nomada* individuals were kept in refrigerators at 6 °C before being placed into the arena. Petri-dishes were illuminated with artificial light. Courtship behavior was documented with macro photographs and video records that were then analyzed frame by frame. Courtship was divided into the following phases, a) Courtship or pre-copula phase: males discovering mates, males approaching females, males mounting the abdomen of the females and attempting to copulate. b) Copula phase: male inserting his genital into the female's genital aperture. We did not observe the separation phase of copulation.

Morphological studies

Flagella morphology of males of *Nomada fucata* and *N. lathburiana* was studied under a photo stereomicroscope, with photos taken at 10 to 40 x. Morphological terminology for the antennae follows Michener (1944), those for the cuticular structures Esslen and Kaissling (1976). Elevated modifications on the flagella of *Nomada* males are called tyloids, following Schönitzer et al. (2000). Morphological structures of the outer and the inner surface of the flagella of *N. fucata* and *N. lathburiana* males were examined under scanning electron microscopy (SEM). Study objects were dried, mounted on aluminum stubs and gold coated or in the case of the flagella of *N. flavoguttata* platinum coated. Some antennae were cleaned by macerating in 5% KOH for 12 hours at 40 °C and dehydrated in graded ethanol series. To study the inner surface of the flagella, they were embedded in hot-melt glue, opened transversally with industrial blades, macerated and dehydrated as described above.

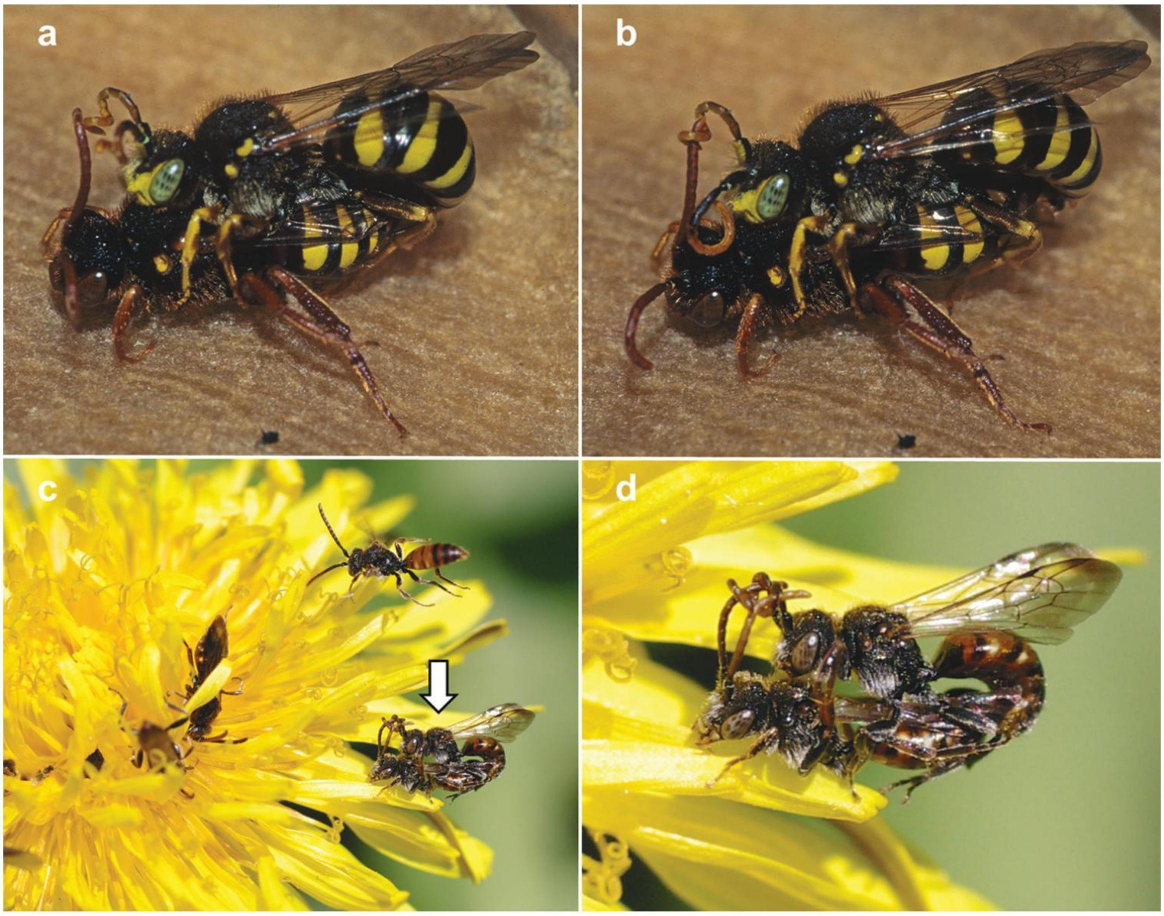

Figure 1. Mating of *Nomada lathburiana* (**a, b**) in the lab and of *N. flavoguttata* on *Taraxacum officinale s.l.*. (**c, d**). **a** ♂ mounts the ♀ and fixes its wings with its mid and hind legs and tries to entangle the female´s antennae spirally with its flagella. ♂ lifts the abdomen of the ♀ with its hind legs and tries to insert its genitalia in the female´s genital opening **b** ♂ repeatedly spirally entangles the female´s antennae with its left and right flagellum and pulls it off medially to apically. ♂ tries to insert its genitalia repeatedly **c** ♂♂ patrolling at a blossom of *T. officinale* **d** Insertion phase of copulation. Antennation of ♂ as described in (**b**).

Histological studies

Antennae of males of *N. fucata* and *N. lathburiana* were fixed in a Duboscq-Brasil solution (Romeis 1989) and then transferred in 70% ethanol. They were dissected (transversally and longitudinally), dehydrated in graded ethanol series and embedded in EMbed 812 (Electron Microscopy Sciences, Hatfield, PA). Semi-thin sections of flagella 4–7 (*N. fucata*) and flagella 9–11 (*N. lathburiana*) were made with glass knives on a rotation microtome. Sections were stained with toluidinblue and analysed under a photo-microscope.

Results

Courtship behavior of *Nomada flavoguttata*, *N. fucata*, and *N. lathburiana*

Field observations revealed that males of *N. fucata* patrol together with males of *Andrena flavipes*, the host species, at foraging plants and above the entrances of the

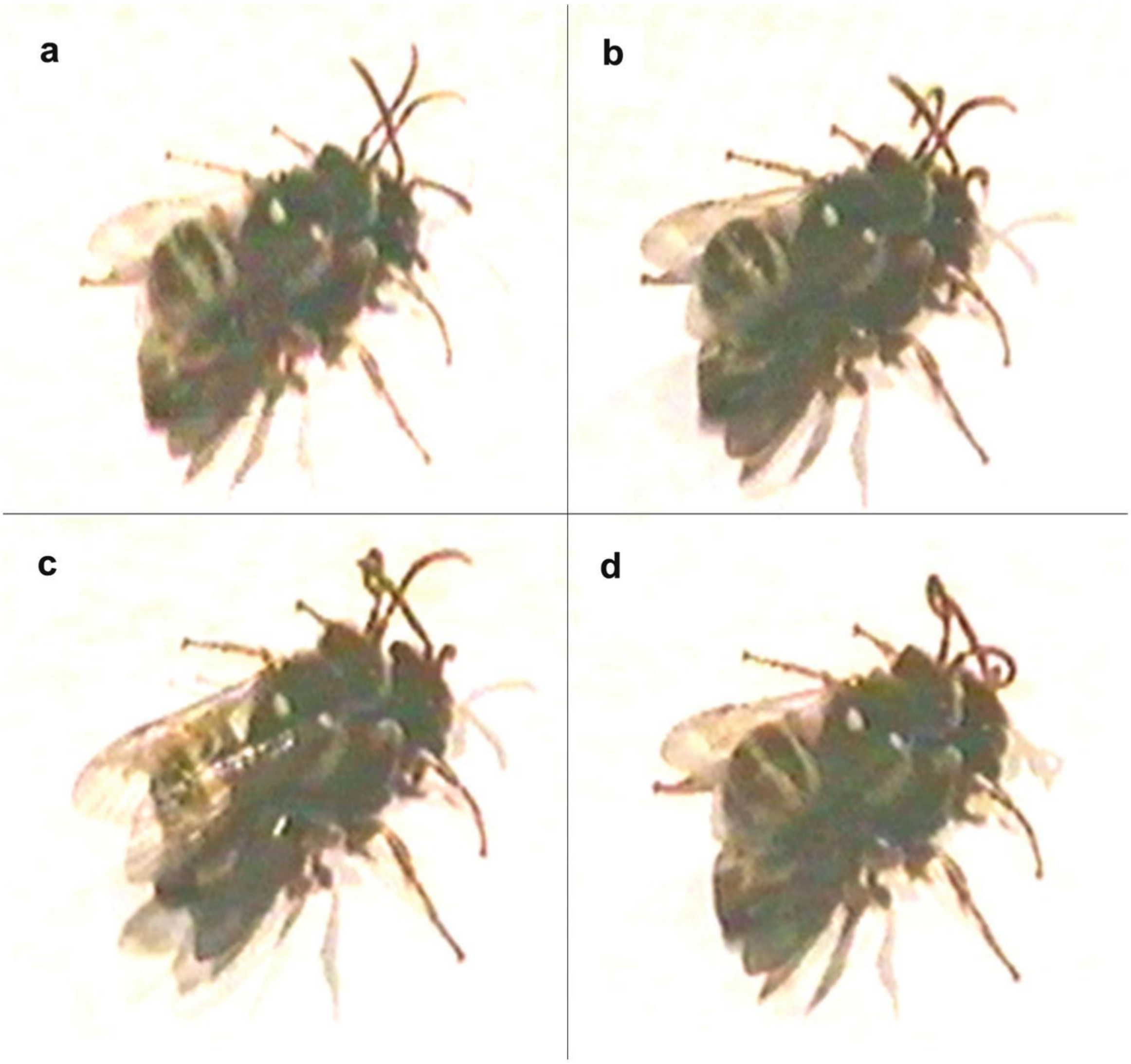

Figure 2. Mating of *Nomada fucata* (singular images of a video sequence). **a** ♂ mounts the ♀ and fixes its wings with its mid and hind legs. ♂ lifts the abdomen of the ♀ with its hind legs and tries to insert its genitalia in the female´s genital opening **b** ♂ entangles the female´s left antenna with its left flagellum **c** ♂ pulls its left flagellum from medial to apical along the female antenna **d** ♂ repeatedly entangles the female´s antennae with its left and right flagellum and pulls it off medially to apically. ♂ tries to insert its genitalia.

fossorial host nests. During these flights, we observed neither inter- nor intraspecific aggression. *Nomada* males attempted to copulate with females that they discovered on flowers or on the ground, but females rejected the males in all observed attempts (n = 11). Males of *N. lathburiana* did not patrol potential rendezvous sites.

For both *N. fucata* and *N. lathburiana*, copulation was studied in the laboratory, with females chilled down for immobilization (since mobile females repelled the males in the lab experiment). For *N. fucata*, two copulations were observed, and for *N. lathburiana* four. Males mounted the abdomen of the females, fixed their forelegs on the side of the females' thorax, clinched the wings of the females with their middle legs and lifted their mates' abdomen with their hind legs to insert the genitalia. In this position the males' head was above the pronotum of the female. During the initiation of copulation males repeatedly wound their flagella (in case of *N. lathburiana* in a spiral) around

Table 1. Tyloid-like structures on the flagella of central-European *Nomada* males. The preselection of most species followed descriptions from Celary 1995 and Scheuchl 2000. Systematics after Alexander and Schwarz (1994); Abbreviations: gr. = Group, flg. = flagellomere.

Species	Species-group	Tyloid-like structures	
		position	morphology
N. bifasciata Olivier	*bifasciata*-gr.	figs 3–8	inconspicuous tubercles
N. fucata Panzer	*bifasciata*-gr.	figs 3–8	inconspicuous tubercles
N. melanopyga Schmied.	*bifasciata*-gr.	figs 4–9	inconspicuous tubercles
N. succincta Panzer[1]	*bifasciata*-gr.	figs 3–8	inconspicuous tubercles
N. flavoguttata (Kirby)	*flavoguttata*-gr.	figs. 3–7	inconspicuous tubercles
N. bluethgeni Stöckhert	*furva*-gr.	figs 2–4	spiky spots
N. distinguenda Morawitz	*furva*-gr.	figs 3–5	inconspicuous tubercles
N. furvoides Stöckhert	*furva*-gr.	figs 3–5	spiky to rounded elevation
N. kohli Schmied.	*furva*-gr.	figs 3–5	rounded spots
N. posthuma Blüthgen[2]	c.f. *furva*-gr.	figs 3–6	spots
N. argentata Herr.-Schäf.	*integra*-gr.	figs 4–8	tubercles
N. beaumonti Schwarz	*integra*-gr.	figs 4–10	spiky spots
N. facilis Schwarz	*integra*-gr.	figs 3–9	spiky spots
N. integra Brullé	*integra*-gr.	figs 3–10	transverse ridges
N. pleurosticta Herr.-Schäf.	*integra*-gr.	figs 4–9	transverse ridges
N. stigma Fabricius	*integra*-gr.	figs 4–9	transverse ridges
N. braunsiana Schmied.	*ruficornis*-gr.	figs 2–9	spots
N. castellana Dusmet	*ruficornis*-gr.	figs 4–12	spots
N. lathburiana (Kirby)	*ruficornis*-gr.	figs 1–11	thorn-like spots
N. striata Fabricius	*ruficornis*-gr.	figs 3–7	inconspicuous tubercles

[1] the taxa *Nomada succincta* and *Nomada goodenia* were not separated,

[2] species for this study not available.

the female's antennae and then stroked the female's antennae (Fig. 1 and 2). For *N. flavoguttata*, the first stages of copulation were observed in the field (Fig. 1). We observed about 50 males and females foraging and resting on flowers of dandelion (*Taraxacum*). Males attempted to mount females from the back and grabbed the females' antennae with their flagella, similar to the behavior observed in the lab for *N. lathburiana*.

Morphology of the flagella

In all three species, the flagella of the males' antennae bear tyloid like-structures (Table 1, Fig. 3). In *N. fucata*, these tyloids are inconspicuous tubercles at the lateral side of flagella 3 to 8. The tubercles show numerous pores with diameters of 0.6 to 1 µm out of which paste-like substances were secreted. In *N. flavoguttata*, the tyloids are most prominent laterally on flagella 3 to 7 but can also be seen on flagella 8 to 10. There also are numerous pores (ca. 0.5 µm) and 3 to 5 µm-long setae. In *N. lathburiana*, thorn-like cuticular modifications can be seen at the ventral side of flagella 2 to 11, the surface of which appears to be coated with secretions; there were no pores.

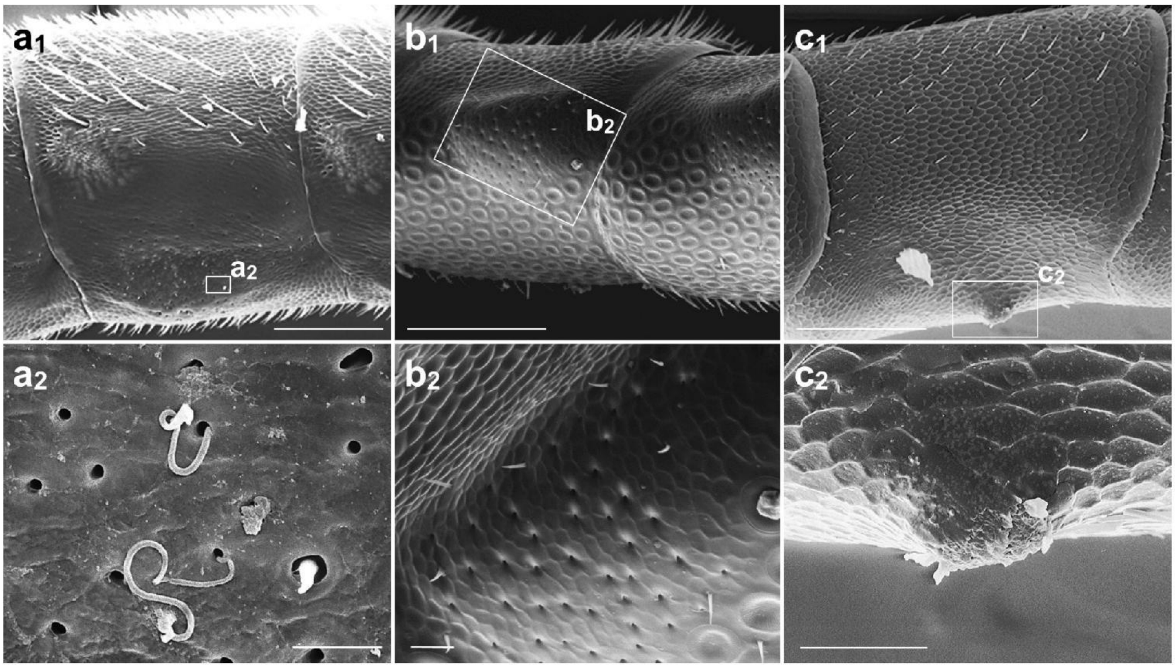

Figure 3. Modifications on the antennae of *Nomada fucata* ♂ (**a**) (left antenna, dorsal), *N. flavoguttata* ♂ (**b**) (right antenna, ventral) and *N. lathburiana* ♂ (**c**) (left antenna, lateral). SEM micrographs. **a**$_1$ weak elevation on flagellum 6 laterally. Scale unit: 0.1 mm **b**$_1$ weak elevations on flagellum 4 ventrally. Scale unit: 0.1 mm **c**$_1$ nodule on flagellum 9. Scale unit: 0.1 mm **a**$_2$ pores and secretions on the elevation. Scale unit: 0.01 mm **b**$_2$ pores and setae on the elevations. Scale unit: 0.01 mm **c**$_2$ nodule covered with secretions. Scale unit: 0.02 mm.

Antennal glands

Histological studies of *N. fucata* and *N. lathburiana* corroborated that these antennal modifications are associated with glands (Fig. 4). Longitudinal and cross semi-thin sections of several flagella revealed two cell aggregations that represent glandular cells of type 1 and type 3 (Noirot and Quennedy 1991). SEM studies of the inner surface of the modifications revealed numerous excretory canals (see Fig. 5)

Discussion

This is the first report of the mating behavior in *Nomada*. The males use their antennae to grab the females' antennae for a chemical signal transfer, while they use their feet to pin down the female. In Hymenoptera and other insects, transfer of sexual pheromones from the males to the females is widespread (e.g. Hymenoptera, Terebrantes: Dahms 1984, Bin and Vinson 1986, Isidoro et al. 1999; Hymenoptera, Aculeata: Isidoro et al. 1996, 2002, Romani et al. 2003; Coleoptera: de Marzo and Vit 1983, Bartlet et al. 1994; Trichoptera: Roemhild 1980), with the organs of transfer usually assumed to be the antennae on the basis of histological studies that revealed male antennal glands. Antennal movements during mating have been observed in Halictidae, Megachildae,

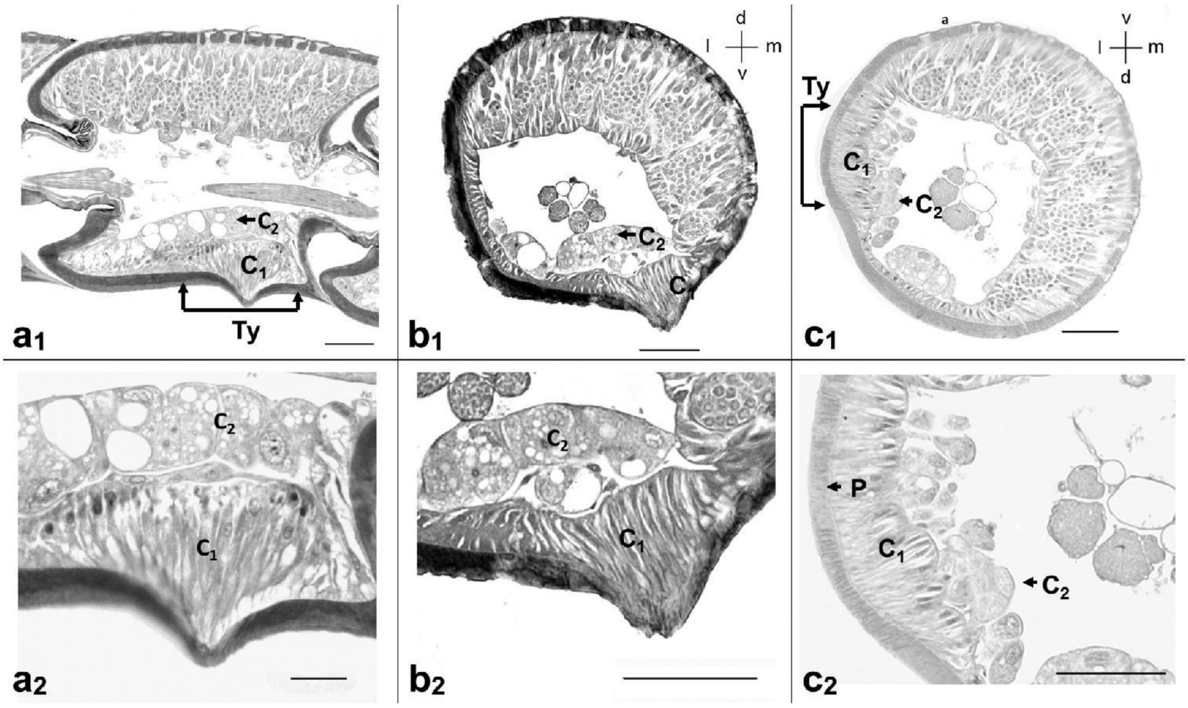

Figure 4. Semi-thin sections of antennomere 9 of *Nomada lathburiana* ♂ [a=longitudinal, b=cross. Ty=Thyloid, C_1=compact epidermal cells, C_2= gland cells, type III (Noirot & Quennedey 1991). Scale unit: 0.05 mm (**a**$_1$, **b**$_1$, **b**$_2$), 0.02 mm (**a**$_2$). Topography: l=lateral, m=medial, v=ventral, d=dorsal] and of antennomere 7 of *Nomada fucata* ♂ [c=cross. Ty=Tyloid, C_1= compact epidermal cells, C2=gland cells, type III, P=porous cuticle (Noirot & Quennedey 1991). Scale unit: 0.05 mm (**c**$_1$, **c**$_2$) Topography: l=lateral, m=medial, v=ventral, d=dorsal].

Colletidae, and Anthophoridae (Barrows 1975, Batra 1978, Wcislo et al. 1992, Wcislo 1995, Wcislo and Buchmann 1995, Felicioli et al. 1998). A winding of the male's antennae around the females' antennae, which we here term "antennal grabbing," has been observed in the widespread west Palearctic species *Melecta albifrons* (Jacobi 2005), and similar antennal rubbing behaviors have been documented for Dryinidae (Waloff 1974), Tiphiidae (Rivers et al. 1979), Sphecidae (Blösch 1999, 2000), and Vespidae (Romani et al. 2005).

Male antennation has been interpreted in terms of sensory exploration of visual and tactile stimuli as well as the transfer of pheromones (Isidoro et al. 1996, Bin et al. 1989, Schönitzer et al. 2000, Ayasse et al. 2001, Romani et al. 2003). Our observations suggest that *Nomada* males transfer liquid pheromones secreted from antennal glands to the females. Paste-like excretions as we saw on flagella pores of *N. fucata* may serve as contact pheromones that are spread directly onto the female antennae (Wittmann and Blochtein 1995, Isidoro et al. 1996). In *Osmia cornuta*, males in copula position rhythmically move their antennae, but without touching the females' antennae (Felicioli et al. 1998), suggesting that volatile, not liquid, pheromones are applied onto the females' antennae. In *Megachile* and *Xylocopa*, by contrast, males bring their modified fore or middle leg basitarsus in contact with the female flagella (Wittmann & Blochtein 1995, Wittmann et al. 2004), suggesting the

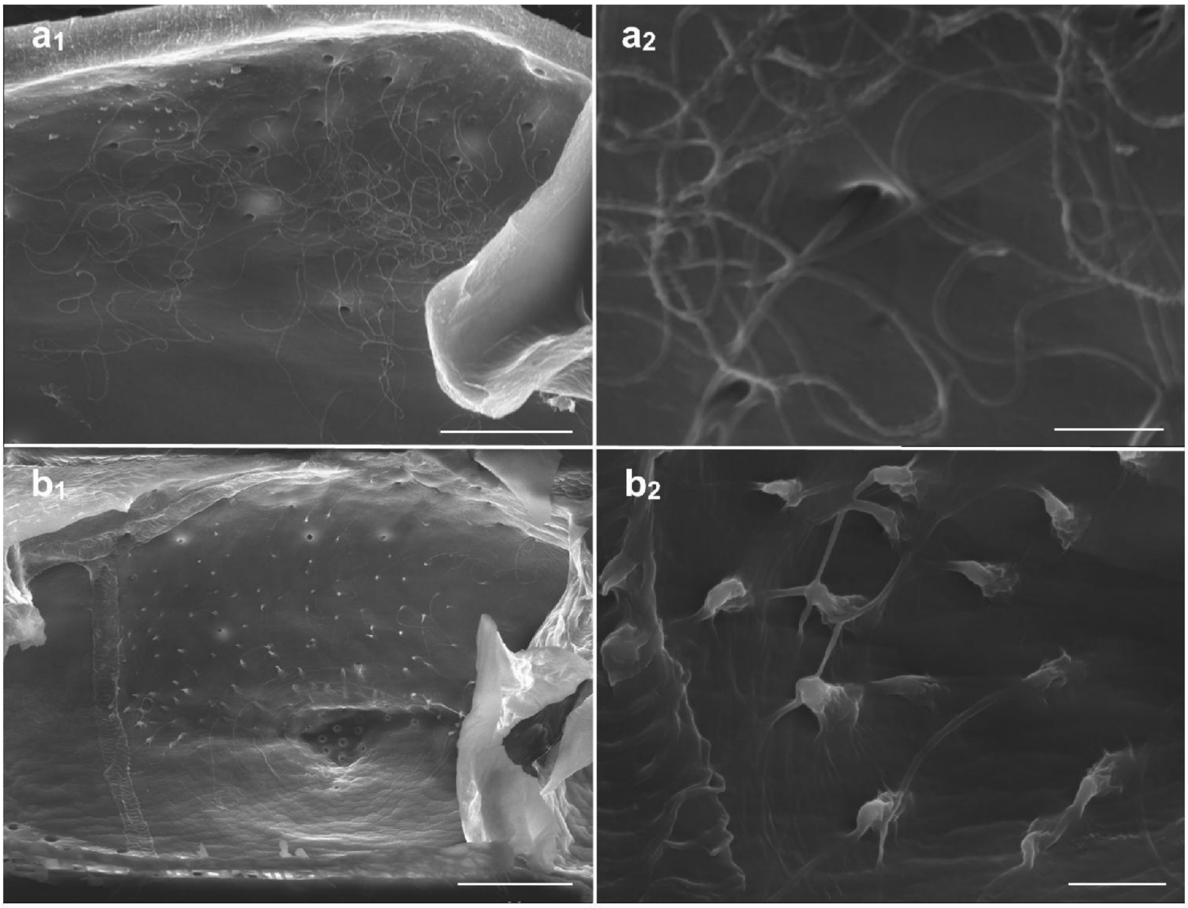

Figure 5. Excretory canals at the inner surface of the tyloid-like structures on the antennomere 6 of *Nomada fucata* ♂ (**a**$_1$, **a**$_2$) and antennomere 5 of *Nomada lathburiana* ♂ (**b**$_1$, **b**$_2$). SEM micrographs. Scale unit: 0.03mm (**a**$_1$), 0,004mm (**a**$_2$), 0.06 mm (**b**$_1$), 0.01 mm (**b**$_2$).

transfer of pheromones from tarsal glands. In males of *Anthophora plumipes*, finally, sexual pheromones produced in abdominal glands are transferred with the hind legs to specialized setae of the elongate middle legs that then brush them onto the females' antennae (Wittmann et al. 2004).

The biological function of the substance transferred by *Nomada* males to females during antennal grabbing may lie in making inseminated females unattractive to other males as suggested for *Centris adani* (Frankie et al. 1980) or in males perfuming females to facilitate odor mimetism of the host bees as suggested for five of eight chemically investigated *Nomada*/host pairs (Tengö and Bergström 1977). Identical compounds (isoprenoid and straight chain esters of short acids) in the nest-parasitic *Nomada* females and their *Andrena* or *Melitta* hosts presumably make it easier for the parasites to gain entrance into the nests of host-bee females without being attacked. Tengö and Bergström (1977) reported that the *Nomada* compounds they investigated are produced in the males' mandibular glands (in the head), but it appears that entire heads may have been used for chemical extraction. These authors also had no opportunity to observe any mating behavior. Interestingly, *Nomada flavoguttata*, the only species included in both studies, was not found to produce identical compounds as its host.

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Constructive comments from the editor, Michael Ohl, an anonymous reviewer, and Gunnar Bergström are much appreciated.

References

Alcock J (1978) Notes on male mate-locating behaviour in some bees and wasps of Arizona (Hymenoptera: Anthophoridae, Pompilidae, Sphecidae, Vespidae). Pan-Pacific Entomologist 54: 215–225.

Alcock J, Barrows EM, Gordh G, Hubbard LJ, Kirkendall L, Pyle DW, Ponder TL, Zalom FG (1978) The ecology and evolution of male reproductive behaviour in the bees and wasps. Zoological Journal of the Linnean Society 64: 293–326. https://doi.org/10.1111/j.1096-3642.1978.tb01075.x

Alexander BA, Schwarz M (1994) A catalogue of the species of *Nomada* (Hymenoptera: Apoidea) of the world. University of Kansas Science Bulletin 55: 239–270.

Ayasse M, Paxton RJ, Tengö J (2001) Mating behavior and chemical communication in the order Hymenoptera. Ann. Rev. Ent. 46: 31–78. https://doi.org/10.1146/annurev.ento.46.1.31

Ascher JS, Pickering J (2017) Bee species guide (Hymenoptera: Apoidea: Anthophila). Discover Life. http://www.discoverlife.org/mp/20q?guide=Apoidea_species&flags=HAS

Barrows EM (1975) Mating behavior in halictine bees (Hymenoptera: Halictidae): III. Copulatory behavior and olfactory communication. Insectes Sociaux 22: 307–331. https://doi.org/10.1007/BF02223079

Bartlet E, Isidoro N, Williams IH (1994) Antennal glands in *Psylliodes chrysocephala*, and their possible role in reproductive behaviour. Physiological Entomology 19: 241–250. https://doi.org/10.1111/j.1365-3032.1994.tb01048.x

Batra SWT (1978) Aggression, territoriality, mating and nest aggregation of some solitary bees (Hymenoptera: Halictidae, Megachilidae, Colletidae, Anthophoridae). Journal of the Kansas Entomological Society 51: 547–559.

Bergström LG (2008) Chemical communication by behaviour-guiding olfactory signals. Chemical Communications 34: 3941–4080. https://doi.org/10.1039/b712681f

Bin F, Colazza S, Nunzio I, Solinas M (1989) Antennal chemosensilla and glands, and their possible meaning in the reproductive behaviour of *Trissolcus basalis* (Woll.) (Hym.: Scelionidae). Entomologica 24: 33–97. https://doi.org/10.15162/0425-1016/623

Blochtein B (1995) Die Bedeutung spezialisierter Beinstrukturen und Duftdrüsen der Männchen in der Paarungsbiologie von Blattschneiderbienen (Hymenoptera; Megachilidae). Doctoral dissertation, University of Tübingen, Germany.

Blösch M (1999) Präkopulationsverhalten bei *Passaloecus*-Arten: *P. corniger* Shuckard, *P. eremita* Kohl, *P. insignis* Vander Linden, *P. singularis* Dahlbom (Hymenoptera: Sphecidae). Bembix - Zeitschrift für Hymenopterologie 12: 17–20.

Blösch M (2000) Die Grabwespen Deutschlands. Tierwelt Deutschlands 71: 1–480.

Cane JH (1983) Olfactory evaluation of *Andrena* host nest suitability by kleptoparasitic *Nomada* bees (Hymenoptera, Apoidea). Animal Behaviour 31: 138–144. https://doi.org/10.1016/S0003-3472(83)80181-X

Celary W (1995) Nomadini [Hymenoptera, Apoidea, Anthophoridae] in Poland. Monografie Fauny Polskiej 20: 1–281.

Dahms EC (1984) An interpretation of the structure and function of the antennal organs of *Melittobia australica* (Hymenoptera: Eulophidae) with the discovery of a large dermal gland in the male scape. Memoirs of the Queensland Museum 21: 361–377.

De Marzo L, Vit S (1983) Antennal male glands of *Batrisus* and *Batrisodes*: Morphology, histology and taxonomic implications. Entomologica 18: 77–110.

Eickwort G, Ginsberg HS (1980). Foraging and mating behaviour in Apoidea, Annual Review of Entomology 25: 421–446. https://doi.org/10.1146/annurev.en.25.010180.002225

Esslen J, Kaissling KE (1976) Zahl und Verteilung antennaler Sensillen bei der Honigbiene (*Apis mellifera* L.). Zoomorphologie 83: 227–251. https://doi.org/10.1007/BF00993511

Felicioli A, Isidoro N, Romani R, Bin F, Pinzauti M (1998) Ethological and morphological analysis of mating behaviour in *Osmia cornuta* Latr. (Hymenoptera, Megachilidae). Insect Social Life 2: 137–144.

Fleck O (1995) Identifizierung und Synthese flüchtiger Inhaltsstoffe von parasitären Bienen der Gattung *Nomada*. Doctoral dissertation, University of Hamburg, Germany.

Frankie GW, Vinson SB, Coville RE (1980) Territorial behavior of *Centris adani* and its reproductive function in the Costa Rican dry forest (Hymenoptera: Anthophoridae). Journal of the Kansas Entomological Society 53: 837–857.

Friese H (1923) Die europäischen Bienen (Apidae), Das Leben und Wirken unserer Blumenwespen, Walter De Gruyter & Co, Berlin, 456 pp.

Hedtke SM, Patiny S, Danforth BN (2013). The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. BMC Evolutionary Biology 13: 138, 13 pages. https://doi.org/10.1186/1471-2148-13-138

Isidoro N, Bin F, Colazza S, Vinson SB (1996) Morphology of antennal gustatory sensilla and glands in some parasitoid Hymenoptera with hypothesis on their role in sex and host recognition. Journal of Hymenoptera Research 5: 206–239.

Isidoro N, Bin F, Romani R (1999) Diversity and function of male antennal glands in Cynipoidea (Hymenoptera). Zoologica Scripta 28: 165–174. https://doi.org/10.1046/j.1463-6409.1999.00013.x

Isidoro N, Romani R, Bin F (2002) Ultrastructure of antennal glands in some Hymenoptera Aculeata: Structures for chemo-sexual communication? Abstract. ESA Annual Meeting and Exhibition, D0314.

Jacobi B (2005): Beinarbeit und Fühlerspiel: Das Paarungsverhalten von *Melecta albifrons*. Bembix Zeitschrift für Hymenopterologie 20: 6–10.

Michener CD (1944) Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bulletin of the American Museum of Natural History 82: 157–326.

Michener CD (2007) The Bees of the World. 2nd. Ed. Johns Hopkins, Baltimore, 913 pp.

Noirot C, Quennedey A (1991) Glands, gland cells, glandular units: some comments on terminology and classification. Annales de la Société entomologique de France 27: 123–128.

Rivers RL, Mayo ZB, Helms TJ (1979) Biology, behavior and description of *Tiphia berbereti* (Hymenoptera: Tiphiidae) a parasite of *Phyllophaga anxia* (Coleoptera: Scarabaeidae). Journal of the Kansas Entomological Society 52: 362–372.

Roemhild G (1980) Pheromone glands of microcaddisflies (Trichoptera: Hydroptilidae). Journal of Morphology 163: 9–12. https://doi.org/10.1002/jmor.1051630103

Romani R, Isidoro N, Riolo P, Bin F (2003) Antennal glands in male bees: structures for sexual communication by pheromones? Apidologie 34: 603–610. https://doi.org/10.1051/apido:2003053

Romani R, Isidoro N, Riolo P, Bin F, Fortunato A, Turillazzi S, Beani L (2005) A new role for antennation in paper wasps (Hymenoptera, Vespidae): antennal courtship and sex dimorphic glands in antennomeres. Insectes Sociaux 52: 96–102. https://doi.org/10.1007/s00040-004-0780-y

Romeis B (1989) Mikroskopische Techniken, 17th ed. Urban und Schwarzenberg, Wien. 697 pp.

Scheuchl, E. (2000) Illustrierte Bestimmungstabelle der Wildbienen Deutschlands und Österreichs. Band I: Anthophoridae. 2nd ed., Velden, 1–158.

Scheuchl E, Willner W (2016) Taschenlexikon der Wildbienen Mitteleuropas: alle Arten im Porträt. Quelle et Meyer Verlag, 1–917.

Schindler M (2005) Biologie kleptoparasitischer Bienen und ihrer Wirte (Hymenoptera, Apiformes). Doctoral dissertation. University of Bonn, Germany. Eigenverlag, Bonn, 120 pp.

Schönitzer K, Hower E, Melzer R, Diller E (2000) Sensillentypen an den Antennen der Gattung *Dirophanes* (Ichneumonidae, Ichneumoninae, Alomyini). Beiträge zur Hymenopteren-Tagung Stuttgart 2000: 57–59.

Smit J (2005) Bijzondere waarneming aan *Nomada*'s. Bzzz Nieuwsbrief sectie Hymenoptera van de Nederlandse Entomologische Vereniging 21: 31–32.

Tengö J, Bergström G (1977) Cleptoparasitism and odor mimetism in bees: Do *Nomada* males imitate the odor of *Andrena* females? Science 196: 1117–1119. https://doi.org/10.1126/science.196.4294.1117

Waloff N (1974) Biology and behaviour of some species of Dryinidae (Hymenoptera). Physiological Entomology 49: 97–109. https://doi.org/10.1111/j.1365-3032.1974.tb00073.x

Wcislo WT (1995) Sensilla numbers and antennal morphology of parasitic and non-parasitic bees (Hymenoptera: Apoidea). International Journal of Insect Morphology and Embryology 24: 63–81. https://doi.org/10.1016/0020-7322(94)E0006-B

Wcislo WT, Buchmann SL (1995) Mating behaviour in the bees, *Dieunomia heteropoda* and *Nomia tetrazonata*, with a review of courtship in Nomiinae (Hymenoptera: Halictidae). Journal of Natural History 29: 1015–1027. https://doi.org/10.1080/00222939500770391

Wcislo WT, Minckley RL, Spangler HC (1992) Pre-copulatory courtship behavior in a solitary bee, *Nomia triangulifera* Vachal (Hymenoptera: Halictidae). Apidologie 23: 431–442. https://doi.org/10.1051/apido:19920505

Wittmann D, Blochtein B (1995) Why males of leafcutter bees hold the females' antennae with their front legs during mating. Apidologie 26: 181–196. https://doi.org/10.1051/apido:19950302

Wittmann D, Schindler M, Blochtein B, Bahrouz D (2004) Mating in bees. How males hug their mates. Proceedings of the 8th IBRA International Conference of Tropical Bees, and VI Encontro sobre Abelhas: 374–380.

Appendix 1

DNA extraction, amplification and sequencing

DNA was isolated with the QIAGEN DNeasy-Blood & Tissue Kit (Qiagen GmbH, Hilden, Germany), using one leg per bee and following the QIAGEN Quick-Start Protocol (January 2011) with two modifications: The legs were incubated in Lysis Buffer (ATL) and Proteinase K for at least 48 h at room temperature and 5 to 10 hours at 56 °C. To increase DNA concentration, we used 100 µL elution buffer (PE; 5 mM Tris/HCL pH 8.5). A fragment of the mitochondrial cytochrome c oxidase (COI) gene with a 658 bp target region near the 5´terminus of COI was amplified using primers described in Schmidt et al. (2015), namely COIfor (ATT CAA CCA ATC ATA AAG ATA TTG G) and COIrev (TAA ACT TCT GGA TGT CCA AAA AAT CA). Polymerase chain reactions (PCR) were performed using standard conditions. Amplified products were sequenced on an ABI 3100 Avant capillary sequencer (Applied Biosystems), and forward and reverse sequences were manually edited and assembled,using Sequencher 5.1 (Gene Codes Corporation, Ann Arbor, Michigan, USA) and BLAST searching in GenBank. All species sequenced for this study have been previously barcoded for the GBOL-project, and reference sequences were therefore available in NCBI GenBank under DOIs: dx.doi.org/10.5883/DS-GBAPI anddoi.org/10.5883/DS-GBAPS. Three new sequences were generated for this study and are available under as GenBank accessions MG845937, MG845938, and MG845939.

Schmidt S, Schmid-Egger C, Morinière J, Haszprunar G, and Hebert PDN (2015) DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Molecular Ecology Resources 15: 985–1000.

Chapter 10

General Discussion

BEE DIVERSITY IN MUNICH

At least 565 species of wild bees have been recorded from Germany since about 1800 (Westrich 2018) of which 506 (90%) occur in Bavaria (Mandery et al. 2003a). Of these 506 species, 40 are considered locally extinct and 79 threatened by extinction (Mandery et al. 2003b). For the city of Munich, 324 species have been recorded since 1795, of which 58 have not been re-collected since 1919 and thus may be extinct with the city perimeter. Another 22 have not been seen in the last 50 years (chapter 4). As far as I was able to ascertain, 244 species have been recorded for the city area of Munich since 1969, of which I found 142 species (58%) at one or more of my study areas. In the cause of this research, I submitted 183 Cytochrome c Oxidase subunit 1 sequences to GenBank (https://www.ncbi.nlm.nih.gov/genbank), each linked to a voucher in the Zoological Collections in Munich (https://www.zsm.mwn.de), and uploaded 390 photo vouchers at the Diversity Workbench server of the Bavarian Natural History Collections (https://diversityworkbench.net/Portal/Diversity_Workbench). I also collected and needled 266 specimens, all deposited in the Zoological Collections. Lastly, 84 plant specimens were collected and deposited in the Munich Botanical Collections (http://www.botanischestaatssammlung.de) as part of my research.

Diversity hotspots were the Munich Botanical Garden (21 ha) with 105 species, and the Allacher Lohwald site (150 ha) with 81 species. By comparison, the renatured gravel pit Obermayr (18 ha) in the east of Munich had only 48 species, 54% of them ground-nesting (chapter 8), pointing to its suitability for wild bees in terms of nesting sites. The increased percentage of sealed surfaces in cities reduces the nesting space for ground-nesting wild bees, which is thought to pose severe problems for the 369 (i.e. 50% of 745) bee species in Germany, Austria and Switzerland that nest in self-burrowed tunnels in the ground. In addition, 143 species nest in hollow spaces either aboveground or belowground (Zurbuchen and Müller 2012, p. 57; Westrich 2018) and may also experience a lack of nesting sites, but few data on this topic are available.

Several mostly thermophilic species have been recorded for Munich only since the 2000s. For instance, *Osmia cornuta*, a Mediterranean species that nests in sun-exposed loess and clay walls (Scheuchl and Willner 2016) was first recorded for Munich in 2010, but has now established a large breeding population in the Munich Botanical Garden at sun-exposed wooden nesting aids (>100 individuals). *Halictus scabiosae*, a distinctly thermophilic species (Westrich 2018) was first seen in Munich 2016, also in the Botanical Garden, and has since then been recorded multiple times in the entire city area. Its spread started in the 21st century and has also been described for other regions, including Hesse, Thuringia, and Saxony (Frommer and Flügel 2005; Burger and Frommer 2010). Due to its increasing commonness and distinct look, which allows its ready identification in the field, *Halictus scabiosae* was the “Wildbiene des Jahres 2018”, i.e., the wild bee of the year 2018 (https://www.nabu.de/news/2017/12/23600.html, last accessed 22 Sep. 2018).

Another thermophilic new species for Munich that I was able to make during this study is the rare *Anthophora bimaculata*, which I saw in the Botanical Garden in its sleeping position on a blade of grass in the heath area. This species had never been registered for the Munich area before. Its habitat requirements --dry, warm locations with sand or clay for digging the nests-- may be limiting its expansion (Westrich 2018). The spread of yet another new species for Munich since 2004, *Hoplitis adunca*, can be explained by the geographic expansion of its pollen source, species in the genus *Echium*. The viper´s bugloss, *E. vulgare*, is currently expanding its range on Germany as winters become shorter and temperatures warmer, and with it, the number of records for *H. adunca* has also been increasing. Last year, 2018, I could observe a further new species for the Munich Botanical Garden, *Colletes hederae*. This late-flying bee appears in mid-August and was only been described in 1993

(Schmidt and Westrich 1993). It has expanded northwards within the last ten years (Hopfenmüller 2014). All these new records of thermophilic species reflect a change in the community composition towards warm-loving species caused by warmer temperatures over the last years. This effect is particularly visible in urban habitats, as these are generally warmer than adjoining rural areas, which is referred to as the urban heat island effect (Myrup 1969). As winters are shorter (in Munich chill days with temperatures below 5°C have decreased by 7.3 days per decade, Zohner and Renner 2014, Figure S2), bee species from warmer areas have higher probabilities to sustain the winter.

In contrast to these new finds (of species that appear to expanding their ranges), I could not find several other species that had been present at my study sites 20 years ago, despite targeted search efforts. An example is *Andrena rufizona* Imhoff, 1834, which had one of its largest known populations in Germany in the Allacher Lohe before the marshalling yard was built, but was reduced from about 20 breeding females to one female and several males by 1999 (Schuberth 2000). The last sighting of this species was in 2002 (J. Schuberth, Munich, personal communication, 2019).

Despite such losses, greenspace-rich urban areas, such as Munich, can support high numbers of wild bee species as long as conservation measures are undertaken to increase the bees´ nesting and foraging opportunities to maintain self-sustaining populations. In my view, this will only be achieved, however, if conservation goals in urban landscapes change from solely public education-oriented to active floral and faunal preservation measures, a topic taken up in the next section.

URBAN BEE DIVERSITY AND NOVEL BEE HABITATS

For a long time, nature protection in urban spaces has focused on environmental education, the raising of the public's awareness of the plight of nature, and on fundraising, as cities have high densities of humans, many of them affluent and well educated (McCleery 2014). City kids are thought to become increasingly disconnected from nature due to a lack of opportunities for experiencing the natural world. This can be overcome by offering outdoor activities and learning opportunities. For example, a six-week-long project about bird-feeding and monitoring on the school grounds of eight primary schools in Brighton and Hove (UK) increased the children´s awareness of local biodiversity as well as their bird identification skills (White et al. 2018). Interest in urban wildlife, however, is also increasing in the field of ecology (cf. introduction of this dissertation), and research collaborations have formed, such as the Urban Wildlife Information Network (UWIN), which aims to systematically collect long-term data sets in several cities on multiple species (Magle et al. 2019).

An emerging field in urban biodiversity research is the study of green roofs (reviewed in Bowler et al. 2010, and Blank et al. 2013), which are now mandatory on flat-topped buildings in Switzerland and a few other European countries, and which are supported by citizen incentives in the USA (Brenneisen 2006, Stutz 2010). Most green roofs fall in the category of extensive green roofs, which only have a thin layer of soil (5-15 cm) and have little or no maintenance costs because of robust roof top vegetation, while only a few are intensive green roofs that have a soil layer of at least 15 cm and require regular garden care (Mann 1994). Besides positive effects of green roofs due to storm-water management (Getter and Rowe 2008, Berndtsson 2010), moderation of the urban heat island effect (Takebayashi and Moriyama 2007, Tabares-Velasco et al. 2012), and lower building temperatures (Oberndorfer et al. 2007), they also constitute mostly undisturbed wildlife habitats with low pesticide loads (for reviews, see Fernandez-Canero and Gonzalez-Redondo 2010, Williams et al. 2014, and Gonsalves 2016). There are reports of 236 species of wild bees on green roofs worldwide (chapter 7). The longest species list exists for Zurich, Switzerland, where 126 species were registered on green roofs (Braaker et al. 2014), showing the importance of this habitat for wild bees. The bees found on green roofs are mostly thermophilic and adapted to dry conditions, as the microclimate on green roofs is often times hot and dry (literature summarized in Hofmann and Renner 2018; chapter 7). These conditions lead to a low plant diversity, which then again influences the wild bee species composition. Oligolectic species are underrepresented on green roofs, as suitable foraging plants are often missing, while the highest bee diversity and abundance are found on intensive green roofs with high plant species numbers. Due to thin substrate layers on green roofs, the wild bee communities have a high proportion of cavity-nesting species and low numbers of ground-nesting bees (Tonietto et al. 2011, Ksiazek et al. 2014, Kratschmer 2015). Although there are reports of wild bees nesting on green roofs, my review of the literature (chapter 7) showed that there is a lack of data about their realized reproductive success, which is crucial for judging the value of such a new habitat for bee conservation. Another aspect that needs further research is the question of the contribution of green roofs to habitat connectivity. So far, only one study has provided data supporting that green roofs can contribute to linking habitats by being stepping stones between urban greenspaces separated by built-up sites (Braaker et al. 2014, 2017). Whilst I was originally hoping to investigate bees on green roofs in Munich-Pasing, this proofed to be logistically too challenging, and I therefore ended up not pursuing this project idea.

Another possibility of connecting habitats within urban areas, which are often isolated by buildings and impervious surfaces in the urban landscape, is roadside vegetation. However, if this is mown frequently, its attractiveness for pollinators is low. A conservation measure for improving such sites is the establishment of flower strips. Flower strips are man-made patches of flowering plants that provide foraging resources for flower-visiting insects, especially bees, butterflies, and flies (e.g. Haenke et al. 2009), as well as retreat possibilities, shelter and overwintering space for many taxa (Haaland et al. 2011). Monitoring and experiments in the rural landscape have shown that such strips enhance the local plant and insect diversity (e.g. Kirmer and Tischew 2014, Schmid-Egger and Witt 2014, Scheper et al. 2015, Dicks et al. 2017 review 80 studies of flower strips), but conservation agencies have only just started to establish flower strips also in urban areas. While pest control and enhanced yield of insect-pollinated crops are the major goals of flower strips in the agricultural context (e.g. Tschumi et al. 2016), the conservation of pollinators and an increase in plant and insect diversity are the major goals of such strips in cities, with increased insect diversity then benefitting other animals, including birds.

My study of the catchment area of One-to-two-year-old flower strips in the city of Munich revealed that most species found *on* the flower strips are also found within a radius of about 1500 m *around* the flower strip (chapter 6). As one would have expected, most of the bee species I recorded at the flower strips were common species that in Germany are not threatened (Westrich et al. 2011). A large proportion are polylectic, and the few oligolectic species were mostly specialized on Asteraceae pollen. The foraging preferences in the all-Munich species pool of 165 polylectic, 72 oligolectic and 87 parasitic species compared to the 43 polylectic, 10 oligolectic and 15 parasitic species found on the flower strips did not differ significantly, however, showing that a species-rich flower strip can support a large number of species even if they are specialized on the pollen of particular plants. Especially strips with plants flowering over a long period of time have a high conservation value (Scheper et al. 2015), and this can be achieved by a suitable species mix and mowing regime. The numbers of bee species on the flower strips are probably increasing with time, but my sample size was too low for statistical testing; nevertheless, the flower strip at Fockensteinstraße established in 2015 showed the highest bee diversity compared to the eight flower strips sown in 2017. An increase in bee diversity over time would be in line with the results of Freyer and colleagues (2010) who suggested that flower strips should be composed of annual and perennial plants and be left growing for at least three years.

Since flower strips only provide food resources, but not nesting sites, their success partly depends on their distance from suitable nesting sites. Habitat connectivity, which is increased by both flower strips or green roofs, is required to maintain bee populations due to the relatively low flight distances of wild bees, a topic that I addressed experimentally. There are at least four ways to study bee flight distances, including radio-transmitters (e.g. Carreck et al. 1999), genetic markers (Chapman et al. 2003, Knight et al. 2005), translocation experiments (Gathmann and Tscharntke 2002) or mark-recapture/mark-reobserve studies (Zurbuchen et al. 2010a,b), which each introduce a different bias, making the comparison of studies with different approaches problematic. With translocation experiments, where bees are removed from their nest and released at different distances from the nest, foraging distances are likely overestimated, as a returning bee covers the distance back to the nest only once, while for foraging, the distance would be covered twice. In mark-recapture-studies, on the other hand, the probability to find a bee at higher distances from the nest decreases because of the squared increase in the surface to be searched, leading to a likely underestimation of flight distances. The experimental approach I took is described in the next section. By tagging 2689 bee individuals (1808 females and 881 males) belonging to six small-bodied species and using a mark-release-observe approach in a habitat with a homogenous flower cover all year long, namely the Munich Botanical Garden, I was able to show that average flight distances in the studied Megachilidae species (a) follow the body size-flight distance correlation found in previous studies (Gathmann and Tscharntke 2002, Greenleaf et al. 2007) and (b) are below 150 m (chapter 5), making this distance a rule of thumb for planning greening measures.

METHODOLOGICAL INNOVATIONS

For this doctoral research, the Munich Botanical Garden was an ideal study site as it has a high floral coverage all season long and well-established bee populations. Moreover, with on average 1000 visitors per day between April and September it has a high potential for citizen science projects. Citizen science means involving lay people in the gathering of scientific data. In the case of my flight distance study (chapter 5), the visitors of the Botanical Garden were asked to record the location of a tagged bee (see color photos of Figure 1 in chapter 5), which added additional survey hours and resulted in over 150 additional sighting data points for the analysis. As the visitor paths through the garden are leading to all large flower beds, it is probable that the garden was well ‘covered’ by observations. Visitors of the Botanical Garden often focus on flowers (often photographing them), thus they were likely to notice the individually-marked wild bees with the colorful dots on their thoraxes. My study approach with the individually numbered bees required no special taxonomic knowledge, and by reporting sightings either via GPS (for instance when this information was stored along the photograph on a smartphone) or by marking the location on a garden plan handed out to visitors, most of the foraging distances reported by garden visitors could be included in the total pool of data.

From a methodological point of view, the Munich Botanical Garden presented another advantage for studying wild bees, having been established at its current location between 1912 and 1914 (it opened on 10 May 1914), it includes highly stable habitats with flower and bee populations that appear to have persisted for many years. Although the floral composition is artificial and contains a lot of non-native species, it guarantees a large number of foraging resources for bees all season long, without the application of pesticides in amounts typical for agricultural landscapes. Based on an assessment of the wild bee fauna 1997/98 (Bembé et al. 2001), I could compare the 2017/2018 species composition with the bee fauna 20 years ago. By excluding changes in floral resources, changes habitat structure (fragmentation), as well as the use of agrochemicals, I was able to correlate shifts in the species spectrum with changes in the climate. No other environmental parameter at the study site matches the directionally increase in warm-loving species (described above in chapter 3). Such an observation is only possible at a study site with constant conditions over a long period of time.

Advances in electronic data storage allow new approaches for documenting bee species. Instead of collecting physical voucher specimen by killing the animals and storing them in museums and zoological collections, close-up macro-photography pictures taken *in-situ* can be stored on servers and then can be accessed worldwide. This allows researchers to check the identification of vouchers without the need of visiting the physical specimen, saving money and time and enabling cooperation over large distances. Such a photo-documentation-approach, of course, only works in specimens and species with a sufficient number of features that can be seen from the outside. This is true for many Megachilidae, but not for species for which genital preparations or fine microstructural features are required for identification. Such are, for instance, needed in the wild bee genera *Sphecodes*, *Lasioglossum* and *Halictus*, but also in certain groups of *Andrena, Nomada* or *Bombus*. For the wild bees occurring in Bavaria, however, macro-photographical identification is feasible for most genera, although taxonomic experience is necessary to be able to recognize bee sex and genus in the field. Also, different features need to be photographed in males and females and in the different genera.

To achieve high-resolution pictures from all sides of the specimen, I needed to immobilize the bees, which I did via chill anesthesia by catching the individual and keeping it in a small vial on ice for a few minutes. Depending on the species, its flight season, and its size, the cooling and also the warm-up phase will take more or less time. Generally, small individuals (< 7 mm) loose the rigor of cold after about a minute, leaving little time to get all details documented. This is problematic, because one cannot get back to the specimen once it has warmed up and has flown away, so one needs to know all the features needed for identification and also needs to be fast enough to document these. Additionally, the production of a photo voucher *in-situ* takes longer than the collection of a specimen in the field, limiting the area that can be assessed in a certain time using this method. Another limitation to the photo-based identification of bee females is that individuals with pollen load usually cannot be identified, as the pollen generally obscures the color of the scopae, which often is an important identification feature. On the other hand, an advantage of photo documentation over a physical specimen is that the colors do not fade over time and that additional information, for example, pictures of the food plants or the habitat, can be linked with the voucher photos more easily than with needled specimen.

Although photo-documentation cannot replace voucher collection, it is a great way of non-invasive biodiversity documentation, which is becoming increasingly important in times of drastic decreases in many insect taxa worldwide (Sánchez-Bayo and Wyckhuys 2019). The increased public interest in wild bees requires approaches that do not involve unnecessary killing of insects, that increase the acceptance of biodiversity research in public, and that motivate people to get involved in scientific data collection. Expert-labeled images in database are also the *sine qua non* for machine learning and computer-based future identification methods via computer vision. Lastly, studying bees in the wild via photo-documentation allows the documentation of behavioral patterns and linking those to photo vouchers. For instance, I was able to observe the copulation of *Nomada flavoguttata* (chapter 9), which had never been reported before, and could document this behavior via macro-photography. The males grab the females' antennae with their antennae, probably for chemical signal transfer, as glands are seen in histological thin sections of the male antennae. Similar behaviors are also seen in other wild bee species: In *Osmia cornuta*, males in copula position rhythmically move their antennae, but do not touch the females' antennae (Felicioli et al. 1998), suggesting that volatile, not liquid, pheromones are applied onto the females. In *Megachile* and *Xylocopa*, by contrast, males bring their modified fore or middle leg basitarsus in contact with the female flagellae (Wittmann and Blochtein 1995, Wittmann et al. 2004), pointing to the transfer of pheromones from tarsal glands. In males of *Anthophora plumipes*, finally, sexual pheromones produced in abdominal glands are transferred with the hind legs to specialized setae of the elongate middle legs that then brush them onto the females' antennae (Wittmann et al. 2004).

FACTORS INFLUENCING THE BEE SPECIES COMPOSITION

The observation methods described above in combination with a statistical analysis of historic and current data on wild bees for both Munich and all of Germany revealed several factors influencing local faunas. Hierarchical Bayesian Models showed that extinction risk in German wild bees is best explained by a species´ habitat preferences and its flight time. Species with narrow habitat preferences (defined as occurrence in one or two of the six habitats forests and heaths; meadows; hedgerows; wasteland and nutrient-poor sites; raw-soil sites with little vegetation, such as sand dunes, heathland, steppes, and sand or gravel pits; or urban areas, including gardens and parks) are more threatened than habitat generalists (defined as species occuring in three to six of these habitats), and species adapted to urban habitats, and species flying in spring are less threatened than late-flying summer species (chapter 2). While specialist bees (both habitat and foraging specialists) have for long been considered more threatened than generalists due to their dependence on a particular resource (e.g. Scheper et al. 2014), the increased threat of late-flying bees to my knowledge had not been demonstrated before and is not so easily explained. It is most likely linked to the sparse flower availability in the summer months, as mass-flowering crops are not in bloom anymore and meadows are cut, while in the spring fruit trees are flowering and meadows are not mown jet. This is a factor particularly important for rural areas, where large parts of the habitat are determined by the agricultural planting and harvesting regime. In cities, on the other hand, biomass production may not fluctuate as much with the seasons. Urban habitats are often flower-rich throughout the year as gardens and balconies are maintained blooming for aesthetic reasons.

If food scarcity in rural areas is a problem contributing to the high exinction risk of summer-flying bee species, as suggested by my German-wide statistical analysis (chapter 2), one would expect that spring- and summer-flying bee species in urban areas would not differ from each other in their extinction probabilities. To test this, I used three urban managed greenspaces for which bee diversity assessment have been made 20 years ago and compared those data with today´s species spectrum. At the Allacher Lohe forest and heath, species numbers have decreased from 135 species in the 1990s to 80 in 2018, while the numbers for the Virginia Depot have increased from 32 to 44, and those from the Munich Botanical Garden from 78 to 106 over essentially the same 20-year period (which points to climate change as a driver; below). At the Allacher Lohe, there were severe construction works by building and operating the marshalling yard since 1988, impacting habitat layout and connectivity. At the Virginia Depot, in contrast, which was long off-limits to public due to its military use and is nowadays maintained by experts from the Landesbund für Vogelschutz (LBV), a high floral diversity with little distraction has increased the value of this inner-city biotope.

As shown in the study that forms chapter 3 of this thesis, the Munich Botanical Garden can be considered as having been constant in its floral and nesting resources for bees since 1914, as layout and species composition have remained virtually unchanged. This allowed me to disentangle floristic changes from climate change, specifically shorter winters and increasing temperatures in spring and summer, as the possible explanations for the increase in warm-loving bee species over the past 20 years. Although the factors floral resources, nesting sites, and warmer temperatures are normally not easily separated, the comparison of the different study sites examined in this study (as summarized in Table 2 in chapter 1) points towards the positive effect of warmer temperatures *per se* for wild bee species diversity in Munich. Warming was similar for the Allacher Lohe, the Virginia Depot and the Munich Botanical Garden over the last 20 years, whereas the development of floral and nesting resources at the three sites has been different. While the Virginia Depot has increased in plant richness and variable nesting locations for wild bees due to the habitat enhancement measures by the Landesbund für Vogelschutz, the Botanical Garden has stayed constant in these aspects, and the Allacher Lohe has lost floral and nesting resources due to the construction of the marshalling yard (see Table 2 in chapter 1). Comparing this with the detected species diversity changes (increased species numbers at both the Botanical Garden and the Virginia Depot and a decreased number at the Allacher Lohe) shows that wild bee species can indeed be supported by increasing the diversity and blooming time of plant species and making available different nesting sites (and nest building materials). However, when flower diversity remains unchanged (as in a botanical garden), warmer temperatures support more wild bees, as I found by comparing the Munich Botanical Garden's bee diversity in 1997 with that in 2017 (chapter 3).

The finding that flight season does not explain bee species extinction (absence) or persistence at the three study sites over the last 20 years indicates sufficient food supply throughout the season for the studied sites (cf. Grimm et al. 2008). However, flower richness and nesting resources, not any climate warming, are the only plausible parameters explaining the high numbers of wild bee species at the one-to-two-year-old flower strips: The 68 species recorded during the flower strips' first season represent 21% of the 324 species ever recorded for Munich and 29% of the 232 species recorded between 1997 and 2017.

Taken together, the results of this doctoral work highlight the importance of protected urban sites for bee conservation. Such areas apparently can sustain a high diversity of bees over a long time (at least 20 years, see chapter 4). By contrast, bees occurring in German agricultural areas and even in protected sites within agricultural areas are decreasing (Hallmann et al. 2017, Seibold et al. 2019, Hofmann et al. 2019, chapter 2). Additionally, sites with initially low attractiveness for wild bees can be enhanced by greening measures like the establishment of flower strips.

FUTURE RESEARCH QUESTIONS AND PROSPECTS

During times of habitat fragmentation and biodiversity loss, urban habitats are becoming an important wildlife refuge. This has been recognized with a resolution of the 9th UN Conference of the Parties to the Convention on Biological Diversity, which states that urban space will play a role in reaching the goals of the convention and therefore, their involvement in biodiversity conservation needs to be promoted. Although the number of publications about biodiversity in cities reached over 600 already by 2008 (Werner and Zahner 2009), many questions remain unsolved. Thus, little is known about how the different factors influencing city environments interact. To apply successful protection measures for animals and plants, researchers and political decision makers need to work together and adapt conservation measures that have worked in rural habitats to the city context. Challenges for plant and animal life in the urban environment are large areas of sealed surfaces, high density of building complexes, unusual (and heterogeneous) wind, sun, and artificial light conditions, and changed rain (water) retention and air moisture. Especially inner cities often have little greenspace, making habitat connectivity a main issue in urban planning. Large-scale mark-release-re-observe experiments are needed to investigate how well such small habitat patches are connected and which measures best support migration and exchange of individuals (gene flow), especially in the case of understudied, but highly threatened insects. For such personnel-intensive research, an important aspect is the inclusion of interested and motivated lay volunteers. This yields an increase in working hours and areal coverage not possible for a single researcher (even when assisted by a group of students), while at the same time increasing the environmental education of the contributing lay scientists and their families or friends, who will learn about the studied organisms while collecting data. This again is likely to increase their motivation to contribute to nature conservation via profound and knowledge-based action as well as donations, being in line with one of the slogans of the International Day for Biological Diversity:

> “One only protects what one knows”.

References

Amiet, F., and Krebs, A. (2014). Bienen Mitteleuropas. Gattungen, Lebensweise, Beobachtung. *Haupt Verlag,* Bern, Switzerland. 424 pages.

Baldock, K. C., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., ... and Staniczenko, P. P. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology and Evolution* 3: 363-373.

Banaszak-Cibicka, W., and Żmihorski, M. (2012). Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation* 16: 331-343.

Batáry, P., Kurucz, K., Suarez-Rubio, M., and Chamberlain, D. E. (2018). Non-linearities in bird responses across urbanization gradients: A meta-analysis. *Global change biology* 24: 1046-1054.

Bates, A. J., Sadler, J. P., Fairbrass, A. J., Falk, S. J., Hale, J. D., and Matthews, T. J. (2011). Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PloS ONE* 6: e23459.

Bembé, B., Gerlach, G., Schuberth, J., and Schönitzer, K. (2001). Die Wildbienen im Botanischen Garten München. *Nachrichtenblatt der bayererischen Entomologen* 50: 30-41.

Berndtsson, J. C. (2010). Green roof performance towards management of runoff water quantity and quality: A review. *Ecolological Engineering* 36: 351–360.

Blank, L., Vasl, A., Levy, S.,Grant,G., Kadas, G., Dafni, A., Blaustein, L. (2013). Directions in green roof research: A bibliometric study. *Building and Environment* 66: 23–28.

Bowler, D. E., Buyung-Ali, L., Knight, T. M., Pullin, A. S. (2010). Urban greening to cool towns and cities: A systematic review of the empirical evidence. *Landscape and Urban Planning* 97: 147–155.

Braaker, S., Ghazoul, J., Obrist, M. K., and Moretti, M. (2014). Habitat connectivity shapes urban arthropod communities: the key role of green roofs. *Ecology* 95: 1010-1021.

Braaker, S., Obrist, M. K., Ghazoul, J., and Moretti, M. (2017). Habitat connectivity and local conditions shape taxonomic and functional diversity of arthropods on green roofs. *Journal of Animal Ecology* 86: 521-531.

Brenneisen, S. (2006). Space for urban wildlife: designing green roofs as habitats in Switzerland. *Urban habitats* 4*:* 27-36.

Burger, F., Ruhnke, H., and Dorn, M. (2004). Rote Liste der Wildbienen (Hymenoptera: Apidae) des Landes Sachsen-Anhalt. *Berichte des Landesamtes für Umweltschutz Sachsen-Anhalt* 39*:* 356-365.

Burger, F. (2005). Materialien zu Naturschutz und Landschaftspflege: Rote Liste Wildbienen unter Mitarbeit von Kaluza, S., Baldovski, G., Franke, R., Langner, D., Liebig, W.-H., Sammorey, T., and Scholz, A. *Sächsisches Landesamt für Umwelt und Geologie Dresden*. 37 pages.

Burger, F. unter Mitarbeit von Körner, F., Poller, U., Reum, D, and Winter, R.. (2010). Rote Liste der Bienen (Insecta: Hymenoptera: Apidae) Thüringens. *Thüringer Landesanstalt für Umwelt und Geologie*: 267-280.

Burger, F., and Frommer, U. (2010). On the spread of *Halictus scabiosae* (Rossi, 1790) in Thuringia and Saxony (Hymenoptera, Apidae). *Entomologische Nachrichten und Berichte* 54: 127-129.

Cane, J. H., and Sipes, S. (2006). Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. *Plant-pollinator interactions: from specialization to generalization*: 99-122.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ... and Kinzig, A. P. (2012). Biodiversity loss and its impact on humanity. *Nature* 486: 59.

Carreck, N. L., Osborne, J. L., Capaldi, E. A., and Riley, J. R. (1999). Tracking bees with radar. *Bee World* 80: 124-131.

Chapman, R. E., Wang, J., and Bourke, A. F. G. (2003). Genetic analysis of spatialforaging patterns and resource sharing in bumble bee pollinators. *Molecular Ecology* 12: 2801-2808.

Dathe, H. H., and Saure, C. (2000). Rote Liste und Artenliste der Bienen des Landes Brandenburg (Hymenoptera: Apidae). Beilage zum Heft 1. *Naturschutz und Landschaftspflege in Brandenburg* 36 pages.

Davis, B. N. K. (1978). Urbanisation and the diversity of insects. Pages 126-138 in Mound, L. A., Walo, N. (eds.). Diversity of Insect Faunas. Symposia of the Royal Entomological Society of London. *Blackwell Scientific Publications*, Oxford, UK.

Dicks, L.V., Ashpole, J.E., Dänhardt, J., James, K., Jönsson, A., Randall, N., Showler, D.A., Smith, R.K., Turpie, S., Williams D.R. and Sutherland, W. J. (2017). Farmland Conservation. Pages 245-284 in: Sutherland, W. J., Dicks, L.V., Ockendon, N., and Smith, R. K. (eds) What Works in Conservation 2017. *Open Book Publishers*, Cambridge, UK.

Dubitzky, A. and Schönitzer, K. (2001). The propodeal corbicula of *Andrena proxima* and allied species (Hymenoptera, Andrenidae). *Apidologie* 32: 429-434.

Ehrlich, P., and Ehrlich, A. (1981). Extinction: the causes and consequences of the disappearance of species. *Random House*, Munich, Germany. 305 pages.

Esser, J., Fuhrmann, M., and Venne, C. (2010). Rote Liste und Gesamtartenliste der Wildbienen und Wespen (Hymenoptera: Apidae, Crabronidae, Sphecidae, Ampulicidae, Pompilidae, Vespidae, Tiphiidae, Sapygidae, Mutillidae, Chrysididae) Nordrhein-Westfalens. *Ampulex* 2: 5-60.

Exley, E. M. (1974). A contribution to our knowledge of Australia´s smallest bees with descriptions of new species (Hymenoptera: Colletidae: Euryglossinae). *Australian Journal of Entomology* 13: 1-9.

Felicioli A., Isidoro N., Romani R., Bin F., Pinzauti M. (1998). Ethological and morphological analysis of mating behaviour in *Osmia cornuta* Latr. (Hymenoptera, Megachilidae). *Insect Social Life* 2: 137–144.

Fernandez-Canero, R., and Gonzalez-Redondo, P. (2010). Green roofs as a habitat for birds: A review. *Journal of Animal and Veterinary Advances* 9: 2041–2052.

Fetridge, E. D., Ascher, J. S., and Langellotto, G. A. (2008). The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea). *Annals of the entomological Society of America* 10*:* 1067-1077.

Fortel, L., Henry, M., Guilbaud, L., Guirao, A. L., Kuhlmann, M., Mouret, H., Rollin, O., and Vaissière, B. E. (2014). Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. *PloS ONE* 9*:* e104679.

Freyer, B., Surböck, A., Heinzinger, M., Friedel, J. K., and Schauppenlehner, T. (2011). ÖPUL-Evaluierung LE07-13: Bewertung des viehlosen biologischen Ackerbaus und seiner agrarökologischen Leistungen im österreichischen Trockengebiet (Endbericht). Umwelt-und Wasserwirtschaft (BMLFUW) Wien, Austria.160 pages.

Frommer, U., and Flügel, H. J. (2005). Zur Ausbreitung der Furchenbiene *Halictus scabiosae* (Rossi, 1790) in Mitteleuropa unter besonderer Berücksichtigung der Situation in Hessen. *Mitteilungen des internationalen entomologischen Vereins* 30: 51-79.

Gathmann, A., and Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology* 71: 757-764.

Getter, K. L., and Rowe, D. B. (2008). Media depth influences *Sedum* green roof establishment. *Urban Ecosystems* 11: 361–372.

Gonsalves, S. M. (2016). Green roofs and urban biodiversity: their role as invertebrate habitat and the effect of design on beetle community. Portland State University, Dissertations and Theses. Available from http://pdxscholar.library.pdx.edu/open_access_etds/2997/ (accessed 14 Feb. 2017).

Goulson, D. (2013). An overview of the environmental risks posed by neonicotinoid insecticides. *Journal of Applied Ecology* 50: 977-987.

Goulson, D., Nicholls, E., Botías, C., and Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347: 1255957.

Greenleaf, S. S., Williams, N. M., Winfree, R., and Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia* 153: 589-596.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., and Briggs, J. M. (2008). Global change and the ecology of cities. *Science* 319: 756-760.

Gusenleitner, F., and Schwarz, M. (2002). Weltweite Checkliste der Bienengattung *Andrena*: mit Bemerkungen und Ergänzungen zu paläarktischen Arten (Hymenoptera, Apidae, Andreninae, Andrena). *Entomofauna,* Supplement 12: 1280 pages.

Haaland, C., Naisbit, R. E., and Bersier, L.-F. (2011). Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity* 4: 60-80.

Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T. u. Thies, C. (2009). Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *Journal of Applied Ecology* 46: 1106-1114.

Hall, D. M., Camilo, G. R., Tonietto, R. K., Ollerton, J., Ahrné, K., Arduser, M., ... and Goulson, D. (2017). The city as a refuge for insect pollinators. *Conservation Biology* 31: 24-29.

Hallmann, C. A., Foppen, R. P., van Turnhout, C. A., de Kroon, H., and Jongejans, E. (2014). Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* 511: 341.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., ... and Goulson, D. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PloS ONE* 12: e0185809.

Hassall, C. (2014). The ecology and biodiversity of urban ponds. *Wiley Interdisciplinary Reviews: Water* 1: 187-206.

Hernandez, J. L., Frankie, G. W., and Thorp, R. W. (2009). Ecology of urban bees: a review of current knowledge and directions for future study. *Cities and the Environment (CATE)* 2: 1-15.

Hofmann, M. M., Fleischmann, A., and Renner, S. S. (2018). Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. Oecologia 187: 701-706.

Hofmann, M. M., and Renner, S. S. (2018). Bee species recorded between 1992 and 2017 from green roofs in Asia, Europe, and North America, with key characteristics and open research questions. Apidologie 49: 307-313.

Hofmann, M. M., Zohner, C. M., and Renner, S. S. (2019). Narrow habitat breadth and late-summer emergence increase extinction vulnerability in Central European bees. Proceedings of the Royal Society B 286: 20190316.

Hopfenmüller, S. (2014). Folgt die Efeu-Seidenbiene *Colletes hederae* Schmidt and Westrich, 1993 dem Ausbreitungsweg der Furchenbiene *Halictus scabiosae* (Rossi, 1790) in Bayern? (Hymenoptera: Apoidea). *Nachrichtenblatt der bayerischen Entomologen* 63: 2-7.

Jin, N., Klein, S., Leimig, F., Bischoff, G., and Menzel, R. (2015). The neonicotinoid clothianidin interferes with navigation of the solitary bee *Osmia cornuta* in a laboratory test. *Journal of Experimental Biology* 218: 2821-2825.

Kirmer, A., and Tischew, S. (2014). Etablierung von artenreichen Feldrainen und mehrjährigen Blühstreifen: ein Beitrag zur Erhöhung der Biodiversität in produktiven Agrarlandschaften. Tagungsband zum 22. Landschaftstag "Zwischen Zuckerrübe und Elbe - Magdeburg im Landschaftsraum Börde", 10 pages.

Knight, M. E., Martin, A. P., Bishop, S., Osborne, J. L., Hale, R. J., Sanderson, R. A., and Goulson, D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology* 14: 1811-1820.

Kratschmer, S.A. (2015). Summen auf den Dächern Wiens. Masterarbeit. Universität für Bodenkultur, Vienna, Austria. 112 pages.

Kruschke, J.K. (2010). Doing Bayesian Data Analysis; A Tutorial with R and BUGS. Academic Press, Burlington, MA. 542 pages.

Ksiazek, K., Tonietto, R., and Ascher, J. S. (2014). Ten bee species new to green roofs in the Chicago area. *The Great Lakes Entomologist* 47: 87-92.

Lister, B. C., and Garcia, A. (2018). Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences* 115: 10397-10406.

Magle, S. B., Fidino, M., Lehrer, E. W., Gallo, T., Mulligan, M. P., Ríos, M. J., ... & Gramza, A. (2019). Advancing urban wildlife research through a multi-city collaboration. *Frontiers in Ecology and the Environment* 17: 232-239.

Mandery, K., Kraus, M., Voith, J., Wickl, K.-H., Scheuchl, E., Schuberth, J., and Warncke, K. (2003a): Faunenliste der Bienen undWespen Bayerns (Hymenoptera: Aculeata) mit Angaben zur Verbreitung und Bestandssituation. – *Beiträge zur bayerischen Entomofaunistik* 5: 47–98.

Mandery, K., Voith, J., Kraus, M., Weber, K., and Wickl, K. H. (2003b). Rote Liste gefährdeter Bienen (Hymenoptera: Apidae) Bayerns. *Bayerisches Landesamt für Umweltschutz 166*: 198-207.

Mandery, K., Kosuch, J., and Schuberth, J. (2008).Untersuchungsergebnisse zum Artstatus von *Andrena decipiens* SCHENCK, 1861, *Andrena flavilabris* SCHENCK, 1874, und ihrem gemeinsamen Brutparasiten *Nomada stigma* FABRICIUS, 1804. *Nachrichtenblatt der bayerischen Entomologen* 57*:* 30-41.

Mann, G. (1994). Ökologisch-faunistische Aspekte begrünter Dächer in Abhängigkeit vom Schichtaufbau. Diplomarbeit. Universität Tübingen, Germany.

Magura, T., Nagy, D., and Tóthmérész, B. (2013). Rove beetles respond heterogeneously to urbanization. *Journal of Insect Conservation* 17: 715-724.

Matteson, K. C., Ascher, J. S., and Langellotto, G. A. (2008). Bee richness and abundance in New York City urban gardens. *Annals of the Entomological Society of America* 101: 140-150.

McCleery, R. A., Moorman C. E., and Peterson M. N. (2014). Urban wildlife conservation: theory and practice. *Springer*, New York. 406 pages.

McKinney, M. L. and Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450– 453.

McKinney, M. L. (2005). Urbanization as a major cause of biotic homogenization. *Biological conservation* 127: 247-260.

McKinney, M. L. (2008). Effects of urbanization on species richness: a review of plants and animals. *Urban ecosystems* 11: 161-176.

Messer, A. C. (1984). *Chalicodoma pluto*: the world's largest bee rediscovered living communally in termite nests (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*: 165-168.

Michener, C. D. (2007). The Bees of the World. Johns Hopkins *University Press*. Baltimore, Md, USA. 992 pages.

Mitchell, E. A., Mulhauser, B., Mulot, M., Mutabazi, A., Glauser, G., and Aebi, A. (2017). A worldwide survey of neonicotinoids in honey. *Science* 358: 109-111.

Myrup, L. O. (1969). A numerical model of the urban heat island. *Journal of Applied Meteorology* 8: 908-918.

Nagy, D. D., Magura, T., Horváth, R., Debnár, Z., and Tóthmérész, B. (2018). Arthropod assemblages and functional responses along an urbanization gradient: a trait-based multi-taxa approach. *Urban forestry and urban greening* 30: 157-168.

Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R. R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K. K. Y., Rowe, B. (2007). Green roofs as urban ecosystems: ecological structures, functions, and services. *BioScience* 57: 823–833.

Pickett, S. T. A., Cadenasso, M. L., Grove, J. M., Nilon, C. H., Pouyat, R. V., Zipperer, W. C., and Costanza, R. (2001). Urban Ecological Systems: Linking Terrestrial Ecological, Physical, and Socioeconomic Components of Metropolitan Areas. *Annual Review of Ecology and Systematics* 32: 127-157.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., and Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution* 25: 345-353.

Rühl, D. (1977). Rote Liste ausgewählter Gruppen der Hautflügler (Hymenoptera). Blatt-, Halm-und Holzwespen (Symphyta), Stechimmen und Goldwespen (Aculeata). 1. Fassung, Stand 15.3. 1977. Rote Liste der gefährdeten Tiere und Pflanzen in der Bundesrepublik Deutschland. Greven (Kilda). *Naturschutz aktuell* 1: 22-30.

Sánchez-Bayo, F., and Wyckhuys, K. A. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* 232: 8-27.

Saure, C. (1996). Urban habitats for bees: the example of city of Berlin. *Linnean Society Symposium Series* 18:47-54.

Saure, C. (2005). Rote Liste und Gesamtartenliste der Bienen und Wespen (Hymenoptera part.) von Berlin mit Angaben zu den Ameisen. Der Landesbeauftragte für Naturschutz und Landschaftspflege/Senatsverwaltung für Stadtentwicklung (Hrsg.): Rote Listen der gefährdeten Pflanzen und Tiere von Berlin. 61 pages.

Scheper, J., Reemer, M., van Kats, R., Ozinga, W. A., van der Linden, G. T., Schaminée, J. H., ... and Kleijn, D. (2014). Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of Sciences* 111: 17552-17557.

Scheper, J., Bommarco, R., Holzschuh, A., Potts, S. G., Riedinger, V., Roberts, S. P., ... and Wickens, V. J. (2015). Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology* 52: 1165-1175.

Scheuchl, E., and Willner, W. (2016). Taschenlexikon der Wildbienen Mitteleuropas: Alle Arten im Porträt. *Quelle und Meyer Verlag,* Wiebelsheim, Germany. 920 pages.

Schindler, M. (2005). Biologie kleptoparasitischer Bienen und ihrer Wirte (Hymenoptera, Apiformes). Doctoral dissertation. University of Bonn, Germany. *Eigenverlag,* Bonn, Germany. 120 pages.

Schmid-Egger, C. (2005). *Proxiandrena* subgen. nov. und Revision der west-und zentralpaläarktischen Arten der *Andrena proxima*-Gruppe (Hymenoptera, Apidae). *Revue suisse de Zoologie* 112: 1029-1044.

Schmid-Egger, C., and Witt, R. (2014). Ackerblühstreifen für Wildbienen–Was bringen sie wirklich. *Ampulex* 6: 13–22.

Schmidt, S., Schmid-Egger, C., Morinière, J., Haszprunar, G., and Hebert, P. D. (2015). DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central

European bees (Hymenoptera, Apoidea partim). *Molecular Ecology Resources* 15: 985-1000.

Schmidt, K., and Westrich, P. (1993). *Colletes hederae* n.sp., eine bisher unerkannte, auf Efeu(*Hedera*) spezialisierte Bienenart. *Entomologische Zeitschrift* 103: 89-112.

Schuberth, J. (2000). Artenhilfsprogramm *Andrena rufizona*. Im Auftrag des Bayerischen Landesamtes für Umweltschutz. 16 pages.

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarli, D., ... and Linsenmair, K. E. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574: 671-674.

Shochat, E., Lerman, S., and Fernández-Juricic, E. (2010). Birds in urban ecosystems: population dynamics, community structure, biodiversity, and conservation. Agronom Monograph 55. *Urban Ecosystem Ecology*: 75-86.

Smissen, J. (2001). Die Wildbienen und Wespen Schleswig-Holsteins–Rote Liste. Landesamt für Natur und Umwelt des Landes Schleswig-Holstein. 138 pages.

Steffan-Dewenter, I., Potts, S. G., and Packer, L. (2005). Pollinator diversity and crop pollination services are at risk. *Trends in Ecology and Evolution* 20: 651-652.

Stutz, B. (2010). Green roofs are starting to sprout in American cities. *Yale Environment 360.* Available from https://e360.yale.edu/features/green_roofs_are_starting_to_sprout_in_american_cities. (accessed 16 Feb. 2017).

Sukopp, H., Blume, H. P., Kunick, W. (1979). The soil, flora and vegetation of Berlin's wastelands. Pages 115-132 in Laurie, I. C. (ed.). Nature in Cities. *John Wiley*. Chichester, UK.

Tabares-Velasco, P.C., Zhao, M., Peterson, N., Srebric, J., Berghage, R. (2012). Validation of predictive heat and mass transfer green roof model with extensive green roof field data. *Ecological Engineering* 47: 165–173.

Takebayashi, H., Moriyama, M. (2007). Surface heat budget on green roof and high reflection roof for mitigation of urban heat island. *Building and Environment* 42: 2971–2979.

Theunert, R. (2002). Rote Liste der in Niedersachsen und Bremen gefährdeten Wildbienen mit Gesamtartenverzeichnis. *Informationsdienst Naturschutz Niedersachsen*: S.138-160.

Tischendorf, S., Frommer, U., Flügel, H. J., Schmalz, K. H., and Dorow, W. H. (2009). Kommentierte Rote Liste der Bienen Hessens: Artenliste, Verbreitung, Gefährdung. *Hessisches Ministerium für Umwelt, Energie, Landwirtschaft und Verbraucherschutz*. 152 pages.

Tonietto, R., Fant, J., Ascher, J., Ellis, K., and Larkin, D. (2011). A comparison of bee communities of Chicago green roofs, parks and prairies. *Landscape and Urban Planning* 103: 102-108.

Tschumi, M., Albrecht, M., Bärtschi, C., Collatz, J., Entling, M. H., and Jacot, K. (2016). Perennial, species-rich wildflower strips enhance pest control and crop yield. *Agriculture, Ecosystems and Environment* 220: 97-103.

United Nations, Department of Economic and Social Affairs, Population Division (2018). The World’s Cities in 2018—Data Booklet (ST/ESA/ SER.A/417)

Warncke, K., and Westrich, P. (1984). Rote Liste der Bienen (Apoidea). In: Blab, J., Nowak, E., Trautmann, W., and Sukopp, J. (Hrsg.): Rote Liste der gefährdeten Tiere und Pflanzen in der Bundesrepublik Deutschland. Greven (Kilda): 21-50.

Werner, P., and Zahner, R. (2009). Biologische Vielfalt und Städte – Eine Übersicht und Bibliographie. *BfN-Skripten* 245: 1-51.

Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. *Linnean Society Symposium Series* 18: 1-16.

Westrich, P. (2018). Die Wildbienen Deutschlands. *Eugen Ulmer,* Stuttgart, Germany. 824 pages.

Westrich, P., Schwenninger, H. R., Dathe, H. H., Riemann, H., Saure, C., Voith, J. and Weber, K. (1998). Rote Liste der Bienen (Hymenoptera: Apidae) Deutschlands (Bearbeitungsstand: 1997). *Schriftenreihe für Landschaftspflege und Naturschutz* 55: 119-129.

Westrich, P., Schwenninger, H. R., Herrmann, M., Klatt, M., Klemm, M., Prosi, R., and Schanowski, A. (2000). Rote Liste der Bienen Baden-Württembergs. *Landesanstalt für Umweltschutz Baden-Württemberg.* 48 pages.

Westrich, P., Frommer, U., Mandery, K., Riemann, H., Ruhnke, H., Saure, C., and Voith, J. (2008). Rote Liste der Bienen Deutschlands (Hymenoptera, Apidae). *Eucera* 1: 33-87.

Westrich, P., Frommer, U., Mandery, K., Riemann, H., Ruhnke, H., Saure, C., and Voith, J. (2011). Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. *Naturschutz und Biologische Vielfalt* 70: 373-416.

White, R. L., Eberstein, K., and Scott, D. M. (2018). Birds in the playground: Evaluating the effectiveness of an urban environmental education project in enhancing school children’s awareness, knowledge and attitudes towards local wildlife. *PloS ONE* 13: e0193993.

Wiesbauer, H. (2017). Wilde Bienen: Biologie–Lebensraumdynamik am Beispiel Österreich–Artenporträts. *Ulmer,* Stuttgart, Germany. 376 pages.

Williams, N. S. G., Lundholm, J., Scott MacIvor, J. (2014). Do green roofs help urban biodiversity conservation? *Journal of Applied Ecology* 51: 1643–1649.

Wittmann, D., and Blochtein, B. (1995). Why males of leafcutter bees hold the females’ antennae with their front legs during mating. *Apidologie* 26: 181–196.

Wittmann, D., Schindler, M., Blochtein, B., and Bahrouz, D. (2004). Mating in bees. How males hug their mates. *Proceedings of the 8th IBRA International Conference of Tropical Bees*: 374–380.

Woodcock, B. A., Bullock, J. M., Shore, R. F., Heard, M. S., Pereira, M. G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., Peyton, J., Hulmes, S., Hulmes, L., Sárospataki, M., Saure, C., Edwards, M., Genersch, E., Knäbe, S., Pywell, R. F. 2017. Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science* 356: 1393-1395.

Yamamuro, M., Komuro, T., Kamiya, H., Kato, T., Hasegawa, H., and Kameda, Y. (2019). Neonicotinoids disrupt aquatic food webs and decrease fishery yields. *Science* 366: 620-623.

Zhou, Y., Varquez, A. C., and Kanda, M. (2019). High-resolution global urban growth projection based on multiple applications of the SLEUtH urban growth model. *Scientific data* 6: 34.

Zohner, C. M., and Renner, S. S. (2014). Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. *Ecology Letters* 17: 1016-1025.

Zurbuchen, A., and Müller, A. (2012). Wildbienenschutz-von der Wissenschaft zur Praxis. Bristol-Schriftreihe, Haupt Verlag AG, Bern, Switzerland. 162 pages.

Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S., and Dorn, S. (2010a). Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology* 79: 674-681.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., and Dorn, S. (2010b). Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation* 143: 669-676.

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Appendix – Invited articles

Hofmann, M. M. (2016). Dialog der Bienen – Wie Bienenvölker einen neuen Wohnort auswählen. Fatum 5: 80-83.

Hofmann, M. M. (2017). Hoch hinaus – Wildbienen auf Gründächern. Gebäude-Grün 2: 25-29.

Hofmann, M. M., and Fleischmann, A. (2019). Über das schwierige Leben der Wildbienen in Stadt und Land. Jahrbuch des Vereins zum Schutz der Bergwelt 84: 239-248.

Hofmann, M. M., and Renner, S. S. (2019). Bye, bye Biene - Welche ökologichen Eigenschaften machen Wildbienen zu bedrohten Arten? Gesellschaft für Biologisches Systematik Newsletter 36: 28-31.

Dialog der Bienen – Wie Bienenvölker einen neuen Wohnort auswählen

Hofmann, M. M.

Fatum 5: 80-83.
2016

Dialog der Bienen

Wie Bienenvölker einen neuen Wohnort auswählen

A*pis mellifera*, die Honigbiene, ist wohl das bekannteste und beliebteste Insekt der Welt. Etwa 200 Milliarden Bienen befinden sich im Besitz von Imkern und leisten einen bedeutenden Beitrag zur Nahrungsversorgung des Menschen: Sie sind die wichtigsten Bestäuber vieler Nutzpflanzen. Was viele nicht wissen - die Honigbiene ist nur eine von weltweit etwa 20.000 Bienenarten.[1] Anders als die meisten Wildbienen hat die Honigbiene eine soziale Lebensweise. Im Bienenschwarm gibt es eine Königin und viele Arbeiterinnen. Im Laufe ihres Lebens erledigen die Arbeiterinnen verschiedenste Aufgaben für ihr Volk. Nach dem Schlupf ist die Biene zunächst im „Innendienst“ tätig. Das bedeutet, dass sie Brutzellen säubert, die Larven und die Königin versorgt und Wachs für den Bau von Waben und den Abschluss der Brutzellen produziert. Nach gut zwei Wochen ist sie am Eingang des Bienenstocks für die Bewachung ihres Volkes zuständig. In dieser Zeit bilden sich die Wachsdrüsen zurück, die sie als Sammlerin nicht mehr braucht. Ab etwa dem zwanzigsten Tag nach dem Schlupf wechselt die Biene endgültig in den „Außendienst“. Sie sammelt Pollen und Nektar und versorgt so das Bienenvolk mit Nahrung.

Im späten Frühjahr und Frühsommer ist es für die Honigbienen an der Zeit zu schwärmen. Zu dieser Zeit sind die Bienenvölker am größten. Mit insgesamt 20 000 bis 30 000 Individuen wird ihnen der Stock zu klein und sie beginnen neue Kolonien zu bilden. Jedes Volk bringt tausende von Drohnen (=männliche Bienen) hervor, deren einzige Funktion ist, die jungen Königinnen zu befruchten. Außerdem legt die alte Königin in besonders große Waben Eier, aus denen neue Bienenköniginnen heranwachsen sollen. Die Larven werden dazu von den Arbeiterinnen ausschließlich mit Gelée royale, dem Weiselfuttersaft, ernährt, und entwickeln sich so zu fruchtbaren Jungköniginnen. Die alte Königin verlässt mit etwa 10 000 Bienen ihre Kolonie, um ein neues Volk zu gründen. Ist das zurückbleibende Volk groß genug, schwärmen außerdem so lange auch die neu schlüpfenden Königinnen, bis nur noch so wenige Arbeiterinnen übrig sind, dass sie keinen weiteren Schwarm abspalten können. Die verbleibenden Jungköniginnen kämpfen nun um die Vorherrschaft im ursprünglichen Schwarm. Die Siegerin wird die neue Königin und der Schwarm nimmt wieder an Größe zu.

Für die schwärmenden Bienen gilt es, einen geeigneten neuen Wohnort für ihr Volk zu finden. Gelingt es dem Imker nicht, den Schwarm einzufangen und in einen künstlichen Bienenstock zu übersiedeln, kann es sein, dass der Schwarm verwildert und sich einen natürlichen Nistplatz sucht. Hierbei bevorzugen Honigbienen hohle Baumstämme von etwa 40 Liter Volumen in einer Höhe von circa 5 Metern.[2] Gerne werden verlassene Stöcke verstorbener Völker genutzt, da schon vorhandene Waben den Materialaufwand für den Nestneubau verringern. Doch wie können sich tausende von Bienen auf einen Wohnraum einigen? Wie bewerten sie die Qualität der verschiedenen Möglichkeiten? Und wie gelingt es ihnen, den ganzen Schwarm dann auch zur richtigen Stelle zu leiten?

Beobachtet man einen Bienenschwarm, der sich beispielsweise an einem Ast niedergelassen hat, kann man erkennen, dass auf der Oberfläche des Schwarms einige Bienen den so genannten Schwänzeltanz aufführen. Der Schwänzeltanz wurde bereits von Aristoteles beschrieben und ab 1920 von Karl von Frisch genauer untersucht.[3] In der Regel dient der Schwänzeltanz dazu, den Futtersammlerinnen im Bienenstock die Lage und Entfernung von Nahrungsquellen mitzuteilen. Dazu „schwänzelt“ die Biene, die eine rentable Nektarquelle entdeckt hat, indem sie ihren Hinterleib rüttelt. Je länger diese Schwänzelstrecke ist, desto weiter ist die Nahrung entfernt. Die Richtung, in der das Futter zu finden ist, wird relativ zum Sonnenstand angegeben. So können weitere Sammlerinnen die Nahrungsquelle besuchen. Wird dieser Schwänzeltanz allerdings auf einem Schwarm ausgeführt, wechselt er seine Bedeutung. Nun gibt er nicht die Position einer Futterquelle, sondern den Standort einer Nistmöglichkeit an.

Schwärmt ein Bienenschwarm, sammeln sich die meisten Bienen zunächst um die Königin herum, um diese zu schützen und sich gegenseitig warm zu halten. Durch den Stoffwechsel der dicht gedrängten Bienen, bzw. falls nötig auch durch Muskelzittern, gelingt es dem Schwarm, eine Temperatur von 34 – 36 °C im Inneren des Schwarms bzw. immerhin noch 17 °C an der Außenseite zu halten. Einige der ältesten Bienen allerdings, die bisher als Nahrungssammlerinnen tätig waren, verlassen ihre Kolonie und begeben sich auf die Suche nach neuen Nistmöglichkeiten. Während sie normalerweise nach farbigen, duftenden Blumen suchen, werden sie nun von dunklen Löchern und Spalten angezogen. Hat eine Kundschafterin einen potentiellen Nistplatz gefunden, fliegt sie um den Eingang und

Von den Bienen und den Blümchen
Bild: Michaela Hofmann

Michaela Hofmann

studierte Biologie an der LMU. Ihren Schwerpunkt setzte sie auf Ornithologie und Entomologie. Schon in ihrer Masterarbeit beschäftigte sie sich mit den Wildbienen des Botanischen Gartens München. Einem Thema, dem sie sich nun auch in ihrer Promotion widmen will.

dann in den dunklen Hohlraum hinein. Durch ein Ablaufen der Wände sowie das Durchfliegen des Nistplatzes versucht sie, die Größe des Hohlraums abzuschätzen.[4] Falls sie ihre Entdeckung als geeignet empfindet, kehrt sie zum Schwarm zurück und berichtet mittels des gerade beschriebenen Schwänzeltanzes von ihrer Entdeckung. Je energischer dieser durchgeführt wird, desto hochwertiger ist der neue Wohnraum zu bewerten.

Zunächst kann man beobachten, dass auf der Oberfläche des Schwarmes für verschiedene Nistplätze geworben wird. Je energischer eine Kundschafterin für ihren Nistplatz wirbt, desto mehr andere Kundschafterinnen werden angeregt, den Nistplatz auch zu besuchen und zu bewerten. Befinden auch sie den Hohlraum als geeignet, werden auch sie energisch für diesen Standort Werbung machen und so immer mehr Befürworterinnen für diese Stelle anwerben. Im Laufe der Zeit verschwinden minderwertige Nistplatzvorschläge aus dem Vorschlagspool, weil jede einzelne Kundschafter-Biene nach einer gewissen Zeit aufhört, einen Standort zu bewerben. Hat sie bis zu diesem Zeitpunkt nicht genügend neue Befürworterinnen angeworben, wird diese Alternative nicht mehr berücksichtigt. Über diesen Mechanismus wird im Laufe der Zeit eine Mehrheitsmeinung gebildet, wodurch der neue Standort für den Schwarm als ausgewählt gilt. Diese beeindruckende Art der Konsensfindung ohne Worte kann durchaus als Dialog der Bienen betrachtet werden. Im Gegensatz zu Diskussionen in Menschen-Gemeinschaften haben die Bienen aber einen großen Vorteil: Sie alle verfolgen das gemeinsame Ziel, einen bestmöglichen Nistplatz für ihren Schwarm zu finden.

Sind sich dann alle Bienen eines Schwarmes einig (was je nach Witterung auch mal mehrere Tage lang dauern kann), kommt es zur nächsten Kommunikationsaufgabe: Wie koordiniert man eine Gemeinschaft mit mehreren Tausend Individuen, sodass alle gleichzeitig aufbrechen und in die richtige Richtung fliegen? Mit einfachem Losfliegen ist es nicht getan, da die meisten Bienen zunächst nicht die geeignete „Betriebstemperatur“ haben. Wie erwähnt ist der Schwarm außen meist nur etwa 17 °C warm, was nicht reicht, damit eine Biene fliegen kann. Um mit ihrer Flugmuskulatur die fast 250 Schläge pro Minute zu schaffen, die sie braucht, um abzuheben, muss der Bienenkörper erst einmal auf etwa 35 °C aufgeheizt werden. Würde man eine kältere Biene in die Luft werfen, würde diese einfach zu Boden fallen, statt wegzufliegen.

Auch in diesem Fall übernehmen die Kundschafterinnen eine wichtige Aufgabe. Sie treten in Dialog mit den kühlen Bienen an der Schwarmoberfläche und informieren sie über den anstehenden Abflug. Natürlich geschieht das nicht mit Worten, aber man kann den Dialog trotzdem hören. Etwa eine Stunde bevor ein Bienenschwarm abfliegt, ist ein hundertfaches, hohes Summen zu hören. Jeder einzelne Pfiff dauert nur etwa eine Sekunde und besteht aus einem ansteigenden Ton, ähnlich wie der eines startenden Formel-1-Autos. Dieses Geräusch wird von den Kundschafterinnen erzeugt.[5] Nach der Einigung auf einen geeigneten Nistplatz laufen sie hektisch auf der Schwarmoberfläche umher und bleiben dann immer wieder stehen, um ihre Brust gegen eine der unbeweglichen, kühlen Bienen zu drücken. Dabei ziehen sie die Flügel eng über dem Hinterleib zusammen und vibrieren leicht mit ihnen, was ein hochfrequentes Geräusch erzeugt. Zwischen diesen Pfeifsignalen führen die Kundschafterinnen weiterhin den Schwänzeltanz aus, um über den Standort des neuen Heims für den Schwarm zu informieren. Dieses „Wachrütteln“ führt dazu, dass sich die ruhenden Bienen auf den Abflug vorbereiten, was man kurz vor dem Abflug auch mit einer Wärmebildkamera nachweisen kann: Der Brustbereich aller Bienen hat die nötige Flugtemperatur von etwa 35 °C erreicht.

Der Abflug selbst wird von sogenannten Schwirrläuferinnen koordiniert. Diese laufen kurz vor dem Abflug summend mit ausgebreiteten Flügeln über den Schwarm und drängen die anderen Bienen auseinander. Es überrascht nicht, dass es sich auch bei

Neue Wege der Tierethik

Die Fortsetzungsfolge *Neue Wege der Tierethik* verfolgt einen inklusiven Ansatz. Sie lässt Personen unterschiedlicher (Fach-)Hintergründe mit verschiedenen Perspektiven auf Tiere zu Wort kommen und schlaglichtartig einzelne kontroverse Aspekte und Ansätze aus dem Bereich der Tierethik beleuchten. Themenvorschläge, Anregungen und Kritik sind jederzeit erwünscht.

Von den Bienen und den Blümchen 2

Bild: Michaela Hofmann

den Schwirrläuferinnen um die Kundschafterinnen handelt, die zunächst pfeifend und später abwechselnd pfeifend und schwirrend über den Schwarm laufen. Durch dieses Signal hebt der Schwarm schließlich ab, und schon entsteht die nächste Herausforderung – der koordinierte Flug zum neuen Nistplatz. Auch dieser wird von den Kundschafterinnen gelenkt. Sie durchfliegen den Schwarm immer wieder schnell in Richtung des neuen Nistplatzes, um sich an der Spitze angelangt wieder zurückfallen zu lassen.[6] Durch das schnelle nach vorne Schießen im Schwarm leiten sie ihre Kolonie zum Nistplatz. Für die letzten Meter wechseln sie allerdings ihre Strategie. Statt einer visuellen Leitung, die den Bienenschwarm grob in die Nähe des Nistplatzes bringt, geben sie olfaktorische Signale, um ihren Artgenossen den Weg zum Eingang des neuen Wohnortes zu weisen. Sie platzieren sich um die Öffnung des Nistplatzes und heben ihren Hinterleib, wodurch sie Duftstoffe abgeben, die den Weg ins neue Heim weisen. Erstaunlicherweise reichen weniger als 5 % ortskundige Bienen, um eine Mehrheit an unwissenden Bienen erfolgreich zu lenken und ans Ziel zu führen.

Endlich am Ziel angekommen bezieht der Bienenschwarm sein neues Domizil und beginnt sofort mit dem Aufbau von Waben und dem Anlegen von Futterreserven. Bis zum Winter muss es dem Volk gelingen, genug Honig eingelagert zu haben, um die kalte Jahreszeit zu überstehen. Im nächsten Jahr beginnt das Spiel dann von neuem. Die Kolonie wächst, und irgendwann formt ein Teil der Bienen einen neuen Schwarm, der sich wiederum ein neues Heim suchen muss.*

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* Wer noch genauer wissen will, wie sich ein Honigbienenschwarm koordiniert und mit welchen Experimenten man dies entschlüsselte, dem empfehle ich die Lektüre von Thomas D. Seeleys *Bienendemokratie - Wie Bienen kollektiv entscheiden und was wir davon lernen können*, erschienen im Fischerverlag (2015), ISBN:978-3-596-19407-0.

f-mag.de/05-80

---

1 Charles D. Michener, The bees of the world (Baltimore und London: JHU Press, 2000).

2 Thomas D. Seeley, und Roger A. Morse. „The nest of the honey bee (Apis mellifera L.).“ in Insectes Sociaux (Heidelberg: Springer Verlag, 1976), 495-512.

3 Karl von Frisch, und Rudolf Jander. „Über den Schwänzeltanz der Bienen“ in Zeitschrift für vergleichende Physiologie (Heidelberg: Springer, 1957), 239-263.

4 Thomas D. Seeley. „Measurement of nest cavity volume by the honey bee (Apis mellifera).“ in Behavioural Ecology and Sociobiology (Heidelberg: Springer, 1977), 201-227.

5 Thomas D. Seeley, und Jürgen Tautz. „Worker piping in honey bee swarms and ist role in preparing for liftoff“ in Journal of Comparative Physiology (Heidelberg: Springer, 2001), 667-676.

6 Madeleine Beekman et al., „How does an informed minority of scouts guide a honey bee swarm as it flies to its new home?” in Animal Behaviour (Amsterdam: Elsevier, 2006): 161-171.

Hoch hinaus –
Wildbienen auf Gründächern

Hofmann, M. M.

Gebäude-Grün 2: 25-29.
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Wildbienen auf Gründächern

Hoch hinaus!

Artenreiche extensive Dachbegrünung als Lebensraum zahlreicher Wildbienen

Gründächer erfreuen sich einer immer größeren Beliebtheit. Neben den vielfach belegten Vorteilen, wie beispielsweise dem Schutz der Dachabdichtung, der Wärmedämmung oder der erhöhten Wasserrückhaltung, haben Gründächer auch einen Einfluss auf die städtische Pflanzen- und Tierwelt. Da Grünraum in der Stadt rar ist, werden diese künstlichen Ersatzhabitate auf den Dächern von einer Vielzahl von Organismen besiedelt. Arthropoden, also Gliedertiere wie Insekten oder Spinnen, sind zahlenmäßig besonders stark auf begrünten Dächern vertreten.

Eine der bedeutendsten und auffälligsten Insektengruppen stellen dabei die Wildbienen dar. Alleine in Deutschland gibt es 571 Arten[1], doch viele davon sind inzwischen gefährdet. Der Einsatz von Neonikotinoiden und anderen Umweltgiften, die Intensivierung in der Landwirtschaft und die Zerstörung des Lebensraums tragen dazu bei, dass die Zahl der Insekten, vor allem der blütenbesuchenden Arten wie Bienen, in den letzten Jahren drastisch zurückging. Dabei spielen besonders die Wildbienen als Bestäuber eine wichtige Rolle in unserem Ökosystem.

Es mag überraschen, dass trotz der Bedeutung und auch der bekannten Gefährdung dieser Tiergruppe relativ wenig über den Einfluss von Gründächern auf Wildbienen bekannt ist. Weltweit gibt es nur knapp 40 wissenschaftliche Studien, die sich mit diesem Thema beschäftigen. Von diesen haben viele den Fokus aber ganz generell auf Arthropoden gelegt und behandeln Bienen nur als Teilaspekt ihrer Untersuchung. Nur neun Studien beschäftigen sich ausschließlich mit Wildbienen auf Gründächern[2–10]. In Nordamerika wurden schwerpunktmäßig Gründächer in Chicago, Halifax und Toronto untersucht, während die neuere europäische Gründachforschung überwiegend in der Schweiz stattfindet.

Von den weltweit etwa 20.000 Wildbienenarten[11] konnten 236 auf Gründächern nachgewiesen werden. Da Gründächer meist sehr trocken und warm sind, waren viele der nachgewiesenen Wildbienen wärmeliebende Arten und werden normalerweise an Trockenrasenstandorten gefunden. Generell waren sowohl Arten- als auch Individuenzahlen höher, wenn die Pflanzenvielfalt auf den untersuchten Dächern größer war. Intensivdächer wiesen in allen Untersuchungen ein größeres Art- ▸

OPTIGRÜN

Extensivbegrünung mit Gehölzen durch partielle Substratanhügelungen gelten als ökologisch sehr wertvolle Dachbegrünungsformen.

spektrum auf als extensive Dachbegrünungen[2,8,12,13]. Dabei können Gründächer für Wildbienen prinzipiell zwei Funktionen haben: Nahrungsquelle durch die dort blühenden (einheimischen) Pflanzenarten, aber auch Nistmöglichkeit für bodennistende Arten (bei Gründächern mit genügend dicker, eher trockener Auflage).

Nicht nur die Begrünungsart, sondern auch die Gebäudehöhe kann einen Einfluss auf die Artzusammensetzung auf Gründächern und deren Nutzung durch Wildbienen haben. In einer Studie, die die Besiedelung künstlicher Nisthilfen für Hohlraumbrüter untersuchte, wurde festgestellt, dass zwar elf Bienenarten und 16 Wespenarten derartige Nisthilfen annehmen, mit zunehmender Gebäudehöhe die Anzahl der fertiggestellten Brutzellen aber abnimmt[14]. Weniger groß scheint der Einfluss der Gebäudehöhe auf die Nutzung des Dachs als Nahrungsquelle zu sein. Auch auf Dächern von bis zu 130 Metern Höhe wird die Blütezeit der Dachvegetation erkannt und gezielt beispielsweise von Honigbienen und Hummeln angeflogen15. Studien aus Nordamerika konnten zeigen, dass die trockenheitsresistenten und deswegen bei Dachbegrünung häufig verwendeten Sedum-Arten zu ihrer Blütezeit intensiv als Nahrungsquelle genutzt werden[9]. Es scheint auch keine Pollenlimitation auf Gründächern zu geben, das heißt die dort wachsenden Pflanzen werden durch die anwesenden Bestäuber hinreichend gut bestäubt, sodass das künstliche Aufbringen von Pollen den Samenansatz nicht mehr weiter erhöht[5].

Betrachtet man die Nahrungspräferenzen der festgestellten Arten, lässt sich allerdings Folgendes feststellen: Oligolektische Bienen, also Bienen, die sich auf wenige Pflanzenarten als Nahrungsquelle spezialisiert haben, sind auf Gründächern im Vergleich zu sich in der Nähe befindlichen Bodenstandorten unterrepräsentiert[4,8,13,16,17]. Das liegt daran, dass viele Pflanzenarten, auf die zahlreiche Wildbienen spezialisiert sind, nicht als Gründachbepflanzung geeignet sind, während die typischen Gründacharten, wie beispielsweise Sedum spp., keine auf sie spezialisierten Bienenarten vorweisen.

Auch bei den Nistgewohnheiten zeigt sich ein Trend. Die Zahl der im Boden nistenden Wildbienen ist im Vergleich zu Bodenhabitaten reduziert[4,6,8]. Auf Gründächern findet man dafür überdurchschnittlich viele oberirdisch nistende Wildbienen. Auch diese Beobachtung überrascht nicht, wenn man bedenkt, dass die meisten Wildbienen, die im Boden ihre Nester anlegen, trockene, sandig-lehmige Substrate von mindestens 20 Zentimetern Tiefe bevorzugen und somit zumindest das flache Substrat extensiver Dachbegrünungen kaum nutzen können. Es hat sich aber gezeigt, dass man durch das Aufschütten kleiner Substrathügel beziehungsweise das Schaffen von Sandlinsen oder das Aufstellen kleiner Sandkästen durchaus künstliche Nisthilfen schaffen kann[2,7]. Bisher ist aber unklar, wie hoch die Sterblichkeit in solchen Nisthilfen ist, da die Wildbienenbrut auf Dächern vermutlich extremeren Temperaturschwankungen ausgesetzt ist, als das bei natürlichen Bodennestern der Fall wäre.

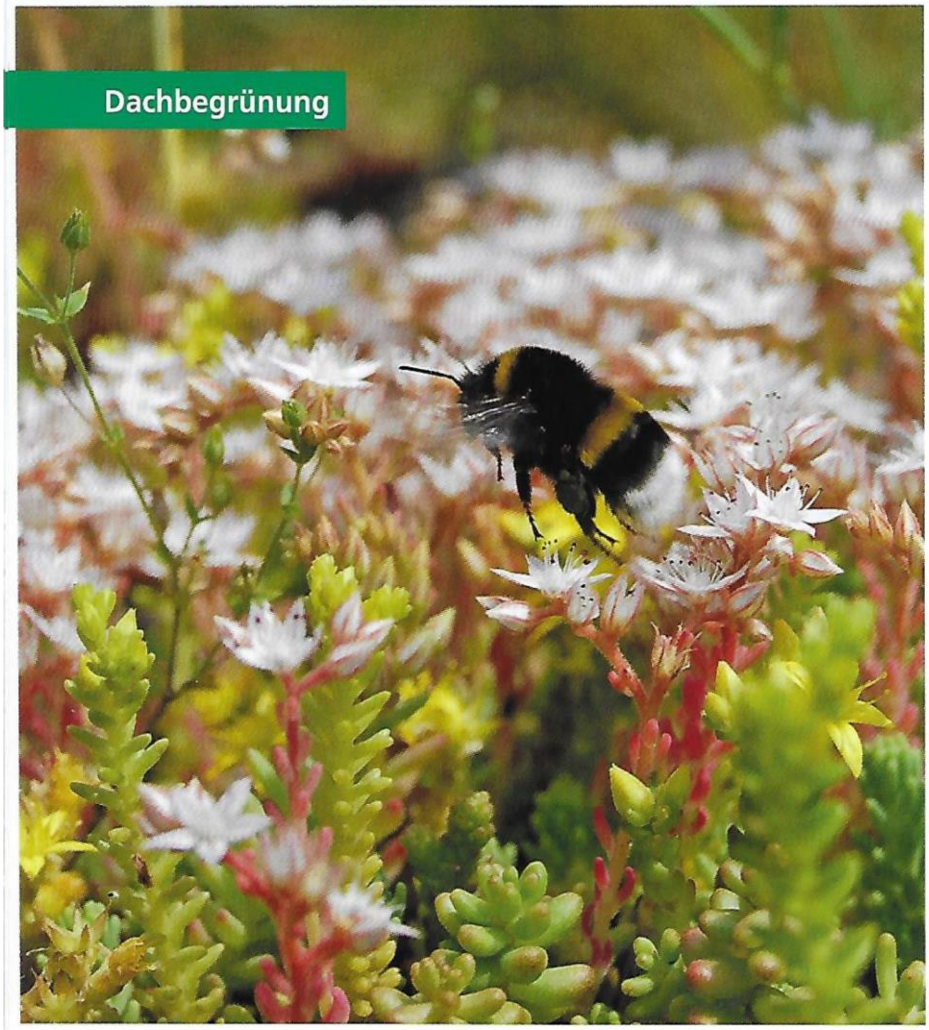
Generell spiegeln die beiden beschriebenen Trends, nämlich die Zunahme der oberirdisch in Hohlräumen nistenden Arten sowie die Abnahme von Nahrungsspezialisten auf Gründächern, Muster wider, die typisch für urbane Gebiete sind[18]. Diese Muster werden auf Gründächern sogar noch verstärkt festgestellt.

Unklar ist, ob bevorzugt größere oder kleinere Wildbienenarten Gründächer nutzen. Da größere Arten generell mobiler sind und bei der Nahrungssuche somit auch größere Distanzen zurücklegen[19], kann man vermuten, dass dies auch die Neubesiedlung von Gründächern erleichtert. In der Tat konnte eine Studie aus Toronto diese Erwartung bestätigen[9]. Allerdings zeigten andere Studien das umgekehrte Bild, nämlich die Besiedlung der Gründächer durch überwiegend kleinere Bienenarten[5,8]. Teilweise lassen sich diese Ergebnisse auf unterschiedliche Sammlungsmethoden (Kescherfänge vs. Bodenfallen) zurückführen, doch auch beim Vergleich von Studien mit vergleichbarer Methodik lassen sich Unterschiede feststellen. Möglicherweise gibt es regionale Unterschiede, oder es verändert sich die Grö-

▶


OPTIGRÜN

Extensivbegrünung mit Totholz als Nistmöglichkeit für Wildbienen



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Wildbiene bei der Nahrungsaufnahme auf dem Gründach

ßenzusammensetzung der Arten auch im Verlauf der Zeit. Denkbar wäre, dass die Dächer zunächst von größeren Arten angeflogen werden, die dort Nahrung suchen, während kleinere Arten Dächer auch als Niststandort verwenden und erst im Lauf der Zeit eine Population aufbauen können. Eine Untersuchung zu diesem Thema fehlt bisher allerdings.

Häufig wird angenommen, dass Gründächer als Trittsteine genutzt werden, die die fragmentierten städtischen Grünrauminseln verbinden. In der Tat konnte dieser Effekt für mobile Arten, wozu die Wildbienen zählen, bestätigt werden[20,21]. Wie rege der Austausch zwischen einzelnen Gründächern und angrenzenden Boden-

FBB

Auf jeder Dachbegrünung zu finden: die Honigbiene. Hier sogar mit Bienenstock zur Honiggewinnung.

habitaten aber genau ist, bedarf noch weiterer Untersuchungen. In fast allen Studien wurde festgestellt, dass trotz relativ großer Artenzahlen auf Gründächern vergleichbare Flächen am Boden in der Regel höhere Arten- und Individuenzahlen aufweisen[4–6,20,22], was darauf hindeutet, dass die verknüpfende Wirkung der Gründächer nicht für alle Wildbienenarten zu gelten scheint.

Nichtsdestotrotz zeigen die existierenden Studien, dass Gründächer von vielen Wildbienenarten genutzt werden können. Eine bienenfreundliche Dachgestaltung mit einheimischen Pflanzenarten sowie mit vielfältigem, unterschiedlich hohem Substrat sowie vieler Mikrostrukturen verspricht daher einen Beitrag zum Erhalt dieser bedeutenden Insektengruppe zu leisten. ■

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Die Literatur

1 Schmidt, S., Schmid-Egger, C., Morinière, J., Haszprunar, G. & Hebert, P. D. N. DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees (Hymenoptera, Apoidea partim). Mol. Ecol. Resour. 15, 985–1000 (2015).

2 Brenneisen, S. The natural roof (NADA). Res. Proj. Rep. Use Extensive Green Roofs Wild Bees Univ. Wädenswil Wädenswil Switz. (2005).

3 Colla, S. R., Willis, E. & Packer, L. Can green roofs provide habitat for urban bees (Hymenoptera: Apidae)? Cities Environ. 2, 4 (2009).

4 Tonietto, R., Fant, J., Ascher, J., Ellis, K. & Larkin, D. A comparison of bee communities of Chicago green roofs, parks and prairies. Landsc. Urban Plan. 103, 102–108 (2011).

5 Ksiazek, K., Fant, J. & Skogen, K. An assessment of pollen limitation on Chicago green roofs. Landsc. Urban Plan. 107, 401–408 (2012).

6 Ksiazek, K., Tonietto, R. & Ascher, J. S. Ten bee species new to green roofs in the Chicago area. Mich. Entomol. Soc. 47, 87 (2014).

7 Brenneisen, S., Käppeli, S. & Schneider, R. Förderung gefährdeter Wildbienen auf Flachdächern - Forschungsprojekt im Mandat für Pro Natura. (2014).

8 Kratschmer, S. A. Summen auf den Dächern Wiens. (Universität für Bodenkultur, 2015).

9 MacIvor, J. S., Ruttan, A. & Salehi, B. Exotics on exotics: Pollen analysis of urban bees visiting Sedum on a green roof. Urban Ecosyst. 18, 419–430 (2015).

10 Walker, E. A. Green roofs as urban habitat for native plant seedlings and wild bees. (2016).

11 Michener, C. D. The bees of the world. (Johns Hopkins University Press, 2007).

12 Madre, F., Vergnes, A., Machon, N. & Clergeau, P. A comparison of 3 types of green roof as habitats for arthropods. Ecol. Eng. 57, 109–117 (2013).

13 Witt. Populationen von Wildbienen und Wespen auf Gründächern. Stadt+Grün 37–42 (2016).

14 MacIvor, J. S. Building height matters: nesting activity of bees and wasps on vegetated roofs. Isr. J. Ecol. Evol. 62, 88–96 (2016).

15 Mann, G. Vorkommen von Tieren auf begrünten Hochhäusern. Dach Grün 3, 24–28 (2005).

16 Mann, G. Ökologisch-faunistische Aspekte begrünter Dächer in Abhängigkeit vom Schichtaufbau. (Universität Tübingen, 1994).

17 Westrich, P. Wildbienen: die anderen Bienen. (Pfeil, 2015).

18 Hernandez, J. L., Frankie, G. W. & Thorp, R. W. Ecology of urban bees: a review of current knowledge and directions for future study. Cities Environ. CATE 2, 3 (2009).

19 Greenleaf, S. S., Williams, N. M., Winfree, R. & Kremen, C. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596 (2007).

20 Braaker, S., Ghazoul, J., Obrist, M. K. & Moretti, M. Habitat connectivity shapes urban arthropod communities: the key role of green roofs. Ecology 95, 1010–1021 (2014).

21 Braaker, S., Obrist, M. K., Ghazoul, J. & Moretti, M. Habitat connectivity and local conditions shape taxonomic and functional diversity of arthropods on green roofs. J. Anim. Ecol. (2017). doi:10.1111/1365-2656.12648

22 MacIvor, J. S. & Lundholm, J. Insect species composition and diversity on intensive green roofs and adjacent level-ground habitats. Urban Ecosyst. 14, 225–241 (2011).

Bye, bye Biene – Welche ökologischen Eigenschaften machen Wildbienen zu bedrohten Arten?

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Bye, bye Biene

Welche ökologischen Eigenschaften machen Wildbienen zu bedrohten Arten?

Weltweiter Insektenrückgang

Derzeit ist das Insektensterben in aller Munde. Diverse Studien haben gezeigt, dass die Zahl der Insekten in allen untersuchten Gruppen, von Käfern über Hautflügler bis hin zu den Schmetterlingen, weltweit rückläufig ist, sowohl in den Tropen als auch bei uns (Sanchez-Bayo und Wyckhuys, 2019). So ging beispielsweise in Puerto Ricos Luquillo Regenwald die Biomasse von Insekten in den letzten 30 Jahren um das Zehnfache bis Sechzigfache zurück, was sich auch in den ebenfalls rückläufigen Bestandszahlen der von Insekten abhängigen Vögeln und Reptilien zeigt (Lister und Garcia, 2018). Besonderes Aufsehen hat auch die so genannte Krefeld-Studie von Hallmann und Kollegen aus dem Jahr 2017 erregt. Sie hat gezeigt, dass die Biomasse von Fluginsekten in den letzten 27 Jahren sogar in Schutzgebieten um 75% zurückgegangen ist, im Sommer sogar um über 80%. Besonders gut ist der beobachtete Rückgang bei den Bienen untersucht, da diese wichtige Bestäuber sind und somit von großem wirtschaftlichem Interesse. Es zeigt sich, dass die Zerstörung des Lebensraumes durch die Intensivierung der Landwirtschaft und die zunehmende Verstädterung, der Druck durch Parasiten und Pathogene, der Einsatz von Pestiziden, seit Mitte der 1990ger Jahre vor allem von Neonikotinoiden, und der Mangel an ausreichenden Nahrungspflanzen über das ganze Jahr verteilt, den Rückgang der Wildbienen vorantreiben.

Die Gefährdung der Bienen aufgrund ihrer Lebensweise

Neben diesen äußeren Faktoren können aber auch die biologischen Eigenschaften einzelner Arten einen Einfluss auf ihren Gefährdungsgrad haben. Es gibt Arten, die hohe Ansprüche an ihren Lebensraum haben, aber es gibt auch Generalisten, die fast überall zu finden sind. Manche Arten sind auf wenige Nahrungspflanzen spezialisiert, andere fliegen ein großes Spektrum an Pflanzen zum Nahrungserwerb an. Es gibt Arten, die nur im Frühling fliegen, und andere, die erst im Sommer auftauchen. Wieder andere Arten kann man das ganze Jahr über beobachten, manchen in mehreren Generationen. Die meisten der in Deutschland vorkommenden Bienen sind nur zwischen 4.5 und 13.5 Millimeter lang (so etwa 92% von 436 Arten). Andere Arten, wie beispielsweise die violette Holzbiene *Xylocopa violacea* erreichen eine Größe von bis zu drei Zentimetern. Auch gibt es Arten, die ihre Nester in selbstgegrabenen Gängen anlegen, während andere bereits existierende Hohlräume, wie Käferfraßgänge oder sogar die Löcher einer im Garten vergessenen Flöte, als Nest nutzen. Manche Arten fressen sich ihre Nesröhren in Totholz, andere nagen sich in das Mark von Pflanzenstängeln hinein, um dort ihre Brutzellen anzulegen. In Deutschland bilden außer der Honigbiene nur die Hummel und manche Schmall- und Furchenbienen größere Völker mit Arbeiterinnen und einer Königin.

Anthidium oblongatum *bereit zum Abflug* | *Foto: Michaela Hofmann, Virginia Depot München, Juli 2018*

Um den Einfluss all dieser Faktoren auf den Gefährdungsgrad von Wildbienen zu untersuchen, haben wir eine Matrix aller Rote-Liste-gelisteten Arten mit ihren Eigenschaften erstellt und mit Hierarchischen Bayesischen Modellen untersucht, wie stark der Gefährdungsstatus von diesen Faktoren beeinflusst wird. Dabei flossen auch die verwandtschaftlichen Beziehungen der Bienen mit ein. Es zeigte sich, dass besonders spät fliegende Sommerarten und Arten mit einer engen Habitatpräferenz bedroht sind, während früh fliegende Arten, sowie Arten, die man auch in Städten häufig antrifft, weniger gefährdet sind. Abbildung 1 fasst das zusammen.

Wildbienenschutz in Stadt und Land

Die Ergebnisse der Analyse geben Hinweise darauf, wie Wildbienen effektiv geschützt werden können. Zum einen bieten Städte wertvollen und schützenswerten Lebensraum. Der urbane Raum kann durch geeignete Maßnahmen, wie die Förderung von Nahrungs- und Nisthabitaten zu einem wichtigen Rückzugsraum für Bienen werden, die es in Bereichen intensiver Landwirtschaft zunehmend schwer haben. Besonders fördern sollte man hier die in Städten deutlich unterrepräsentierten bodennistenden Arten, die aufgrund der Flächenversiegelung, aber auch der wenigen in städtischen Gärten zugäng-

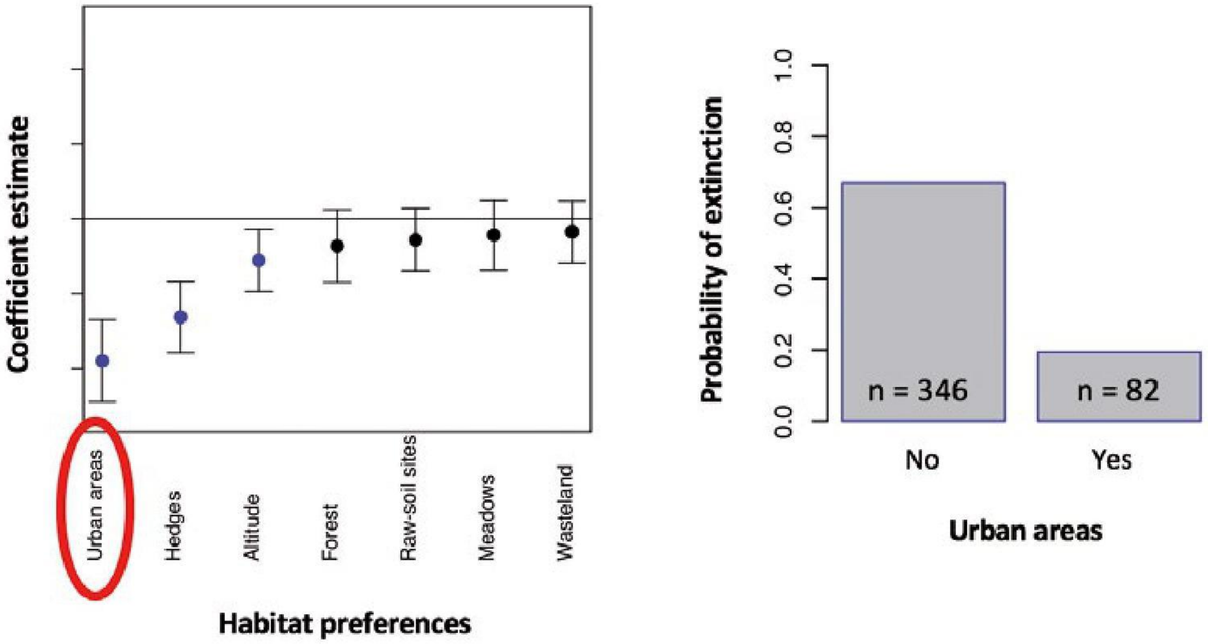

Abbildung 1. Relative Wichtigkeit verschiedener Habitate und des Vorkommens in Städten auf die Wahrscheinlichkeit von (lokaler) Extinktion. Modifiziert aus Hofmann et al. (2019).

lichen freien Bodenstellen, Schwierigkeiten haben, geeignete Nistplätze zu finden. Hier kann schon ein kleiner Bereich mit offen liegender Erde in Privatgärten oder an Straßenrändern helfen, diese Arten zu unterstützen. Zum anderen zeigt sich, dass man insbesondere im Sommer durch optimierte Mahd-Strategien und die Anlage von Blühstreifen das Nahrungsangebot für Bienen und andere Bestäuber verbessern muss, um dem aktuellen Trend rückläufiger Bestandszahlen entgegenzuwirken. Ein positiver Nebeneffekt ist außerdem die optische Aufwertung der Landschaft durch Blütenpflanzen.

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Hofmann, M. M., C. M. Zohner, and S. S. Renner. 2019. Narrow habitat breadth and late-summer emergence increase extinction vulnerability in Central European bees. Proceedings of the Royal Society B, https://doi.org/10.1098/rspb.2019.0316, 6 March 2019, Lister, B. C. und A. Garcia, 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proceedings oft he National Academy of Sciences 115(44): E10397-E10406. https://www.pnas.org/content/115/44/E10397
Sanchez-Bayo, F., und K. A. G. Wyckhuys, 2019. Worldwide decline of the entomofauna: A review of ist drivers. Biological Conservation 232: 8-27. https://www.sciencedirect.com/science/article/pii/S0006320718313636

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Wildbienen in Deutschland

In Deutschland gibt es über 565 Arten von Wildbienen, in Europa knapp 2000 Arten und weltweit sogar über 20.000 Arten. Die deutschen Wildbienen unterscheiden sich auf vielfältige Weise in ihrer Lebensweise und in ihren Ansprüchen an den Lebensraum. Während polylektische Arten eine Vielzahl von Nahrungspflanzen nutzen, sind oligolektische Arten auf eine oder wenige Pflanzenarten spezialisiert und daher von diesen abhängig, weshalb diese Arten häufiger bedroht sind wie die Nahrungsgeneralisten. Es gibt Bienen, die ihre Nester in selbstgegrabenen Gängen im Boden anlegen, während andere bereits existierende Hohlräume, z.B. Käferfraßgänge, nutzen. Trotz ihrer Vielfalt haben viele Wildbienen eines gemeinsam – sie sind bedroht. 52% der Arten sind gefährdet, vom Aussterben bedroht oder als extrem selten eingestuft; und 7% gelten bereits als verschollen.

Michaela Hofmann | Foto: Jana Jarczak

Susanne Renner | Foto: privat

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Über das schwierige Leben der Wildbienen in Stadt und Land

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Über das schwierige Leben der Wildbienen in Stadt und Land

von **Michaela M. Hofmann & Andreas Fleischmann**

Keywords: *Bionomie, Insektenrückgang, Blühstreifen*

In Deutschland gibt es 585 Wildbienenarten mit den unterschiedlichsten Lebensweisen. Es gibt solitär lebende oder staatenbildende Bienen, Kuckucksbienen, Nahrungsgeneralisten und Nahrungsspezialisten, sowie die verschiedensten Strategien zum Sammeln von Nektar und Pollen und der Anlage von Nestern. Gemeinsam ist fast allen, dass sie durch die zunehmende Versiegelung von Flächen und die Intensivierung der Landwirtschaft bedroht sind. Es fehlen Nistplätze und blütenreiche Flächen für das Sammeln ihrer Nahrung, und der Einsatz von Insektiziden setzt ihnen zusätzlich zu. Im landwirtschaftlich genutzten Raum ist eine deutliche Abnahme der Biodiversität zu beobachten, während Städte für Wildtiere aller Art als Rückzugsort zunehmend an Bedeutung gewinnen. Grünflächen und Parkanlagen, aber auch Gründächer, können Lebensraum für Wildbienen sein. Da diese aber häufig nur wenige hundert Meter fliegen, ist es wichtig, diese urbanen Habitate mit genügend blühenden Flächen zu vernetzen.

Wenn man von Bienen spricht, haben die allermeisten Menschen sofort das Bild der Honigbiene (*Apis mellifera*) im Kopf. Ihre Lebensweise ist uns vertraut, ihr Honig beliebt und ihre Leistung als Bestäuber geschätzt. Da ist die Überraschung oft groß, wenn man erfährt, dass die Honigbiene nur eine der 585 in Deutschland vorkommenden Bienenarten ist (SCHEUCHL & SCHWENNINGER, 2015) – weltweit sind es sogar mehr als 20.000 Bienenarten (ASCHER & PICKERING, 2017). In den Alpen kommen generell weniger Wildbienen-Arten vor als im wärmebegünstigteren Flachland, allerdings gibt es gerade bei den Hummeln einige Alpenspezialisten, die vor allem oberhalb der Baumgrenze vorkommen. Auch bei den Maskenbienen und den Sandbienen gibt es spezialisierte alpine Arten, und die Scheinlappenbienen (Gattung *Panurginus*) kommt sogar ausschließlich im Alpenbogen vor, bei uns in Deutschland mit zwei Arten.

Im Gegensatz zur Honigbiene leben die meisten Wildbienen solitär, das bedeutet, dass jedes Bienenweibchen als „Einsiedlerin“ - sozusagen als einzige Arbeiterin und Königin zugleich – ein Nest anlegt und für den eigenen Nachwuchs mit Nektar und Pollen verproviantiert; es werden keine Bienenschwärme gebildet und es gibt keine Arbeitsteilung. Nur wenige Wildbienenarten, z.B. die meisten Hummeln oder manche Schmal- und Furchenbienen, haben eine soziale Lebensweise mit der Aufteilung des Volks in Königin(nen) und Arbeiterinnen. Die Nistweise ist bei Wildbienen sehr vielfältig. Etwa zwei Drittel der heimischen Wildbienen nisten unterirdisch in selbst gegrabenen Gängen (ZURBUCHEN & MÜLLER, 2012). Andere Arten legen ihre Nester in markhaltigen Stängeln oder in Totholz an, und wieder andere Bienen nutzen leerstehende Schneckenhäuser, um dort ihre Brutzellen hineinzubauen. Am besten lässt sich das Nistverhalten der Wildbienen bei Arten beobachten, die oberirdische Hohlräume besiedeln, da diese Arten häufig auch künstliche Nisthilfen annehmen (sogenannte „Insektenhotels“, vgl.

Abb. 1a), wobei der Begriff „Hotel" hier völlig unangebracht ist, denn es sind Nistgänge für den Wildbienennachwuchs, nur wenige Wildbienenarten – zumeist Männchen- schlafen tatsächlich auch als ausgewachsene Tiere nachts in diesen Nisthilfen). Hier legen sie ihre Nester in Bambusröhrchen oder angebohrten Holzblöcken an (Abb. 1b), die Käferfraßgänge im Totholz oder Löcher in Hangabbruchkanten simulieren.

Abb. 1 a und b: Wildbienennisthilfen (Fotos: Andreas Fleischmann).

Ein Wildbienenweibchen legt in seinem Leben je nach Art etwa 10 bis 20 Brutzellen an. Jede Brutzelle wird mit Nektar und Pollen verproviantiert und mit einem Ei versehen. Aus befruchteten Eiern entwickeln sich Wildbienenweibchen, aus unbefruchteten Eiern schlüpfen Männchen. Manche Arten verkleiden die Wand der Brutzellen mit Blattstücken, Pflanzenhaaren oder gar Blütenblättern, um den Nachwuchs zu schützen. Hat man Blattschneiderbienen der Gattung *Megachile* bei sich im Garten, kann man das an den ausgeschnittenen Blättern beispielsweise von Rosen erkennen (Abb. 2). Auch Gartenwollbienen (*Anthidium manicatum*, Abb. 4) lassen sich beim Sammeln von Nistmaterial beobachten. Weibchen dieser Art schaben mit ihren Beinen Pflanzenhaare vom Wollziest (*Stachys sp.*) oder ähnlichen „haarigen" Pflanzen und tragen diese dann zu Kugeln geformt zu ihrem Nest. Die Gartenwollbienenmännchen zeigen sehr territoriales Verhalten und vertreiben männliche Artgenossen, aber auch Honigbienen und andere Insekten, die sich in ihr Revier wagen.

Abb. 2: Ein Weibchen der Buntfarbigen Blattschneiderbiene (*Megachile versicolor*) schneidet ein Blattstück für ihre Brutzelle. (Foto: Andreas Fleischmann).

Abb. 3: Männchen der Fuchsroten Mauerbiene (*Osmia bicornis*) an einer Nisthilfe. (Foto: Andreas Fleischmann).

Abb. 4: Eine weibliche Gartenwollbiene (*Anthidium manicatum*) auf Deutschem Ziest (*Stachys germanica*). (Foto: Andreas Fleischmann).

Die Art und Weise, wie Wildbienen den Pollenvorrat für ihre Brut sammeln, ist ebenfalls unterschiedlich, man kann drei grundsätzliche Sammelweisen unterscheiden: Manche Arten, wie z.B. die Maskenbienen (*Hylaeus*), schlucken den gesammelten Pollen und tragen ihn in ihrem Kropf zum Nest („Kropfsammlerinnen"). Viele Bienen sammeln wie die Honigbienen den Pollen an ihren Hinterbeinen („Beinsammlerinnen"), entweder in sogenannten Pollenkörbchen (Corbiculae), das sind grubenförmige Vertiefungen der Hinterschienen, oder in speziellen Haarbürsten. Und wieder andere Arten haben eine Haarbürste an der Unterseite des Abdomens, mit der der Pollen aufgenommen und zum Nest transportiert wird („Bauchsammlerinnen"). Bei der Gemeinen Löcherbiene (*Heriades truncorum*) kann man beispielsweise beobachten, wie sie durch Vibrationen des Hinterleibs auf Korbblütlern Pollen sammelt (Abb. 5). Während polylektische Bienen (Nahrungsgeneralisten), zu denen auch die Honigbiene zählt, nicht sehr wählerisch sind und ein großes Spektrum an Futterpflanzen nutzen, gibt es auch Bienenarten, die auf eine oder wenige Pflanzenarten spezialisiert sind und nur an diesen Pollen sammeln. Solche Bienen nennt man oligolektisch (Nahrungsspezialisten – genauer: Pollenspezialisten) – ihre Larven können nur den Pollen von wenigen, manchmal nur von einer einzigen Pflanzenart verwerten, ganz wie es auch bei Schmetterlingen Spezialisten gibt, deren Raupen nur an einer Futterpflanze fressen. Leider sind viele dieser Nahrungsspezialisten unter den Wildbienen bedroht, denn wenn an einem Standort ihre Pollenquelle verschwindet, verschwindet auch die zugehörige Biene.

Nicht jede Wildbiene ist eine sprichwörtlich fleißige Biene, wenn es darum geht, den eigenen Nachwuchs zu versorgen. Wie im Vogelreich gibt es auch bei Wildbienen Kuckucke, genauer Kuckuckshummeln und Kuckucksbienen (Abb. 6). Diese Arten dringen in die Nester ihrer Wirte ein und lassen im Fall der Kuckuckshummeln ihren Nachwuchs durch das Wirtsvolk aufziehen (sogenannte sozialparasitische Arten). Im Fall der Kuckucksbienen legen sie ihre Eier in die Brutzellen der Wirtsbienen und ernähren sich vom Nahrungsvorrat, den sie dort finden (sogenannte Diebesparasiten). Um im Wirtsnest nicht aufzufallen, betreiben viele Arten Geruchsmimikry, was bedeutet, dass die parasitierende Bienenart den Geruch der Wirtsbiene nachahmt (TENGÖ & BERGSTRÖM, 1977). Manche dieser Duftstoffe werden möglicherweise sogar im Verlauf der Kopulation vom Männchen auf das Weibchen übertragen (SCHINDLER et al., 2018).

Abb. 5: Eine Gemeine Löcherbiene (*Heriades truncorum*) sammelt Pollen auf Rainfarn (*Tanacetum vulgare*). (Foto: Andreas Fleischmann).

Abb. 6: Eine Rothaarige Wespenbiene (*Nomada lathburiana*) am Nest der Weiden-Sandbiene (*Andrena vaga*). (Foto: Andreas Fleischmann).

In Deutschland sind alle Wildbienen nach dem Bundesnaturschutzgesetz besonders geschützt, das bedeutet, es ist verboten, Wildbienen nachzustellen, sie zu fangen, zu verletzen, zu töten oder ihre Entwicklungsformen, Nist-, Brut, Wohn-, oder Zufluchtsstätten der Natur zu entnehmen, zu beschädigen oder zu zerstören. Dennoch sind 31 Arten vom Aussterben bedroht, 197 Arten gefährdet und weitere 42 Arten stehen auf der Vorwarnliste (vgl. Rote Liste der Bienen Deutschlands, verfügbar unter https://www.wildbienen.info/downloads/rote_liste_bienen_fassung_5.pdf oder per QR-Code).

Wie viele andere Insektengruppen sind auch Wildbienen vom massiven Insektensterben betroffen. Denn ihr Lebensraum wird nicht nur, wie der vieler Tiere, durch den enormen Flächenverbrauch und durch Versiegelung immer weiter reduziert (damit verlieren sie Nistplätze und Nahrungspflanzen). Blütenbesuchende Insekten leiden zudem an den Folgen der intensiven, industrialisierten Landwirtschaft, unter Monokulturen (die oft keinerlei Nahrung in Form von Pollen und Nektar bieten), der Entfernung von Hecken und blütenreichen Ackerrandstreifen, dem Grünlandumbruch, der Umstellung von Heu- auf Silagemahd, die kaum mehr blühende Blumenwiesen aufkommen lässt und dem Einsatz von Herbiziden, die blühende Nahrungspflanzen in Äckern und Feldern vernichten. Diejenigen Bienen, die in einer solch blütenarmen, ausgeräumten Landschaft nicht verhungern, fallen oft dem Einsatz von Insektiziden (z.B. aus der Wirkstoffgruppe der Neonikotinoide) zum Opfer (GOUSLON, 2013; GOULSON et al., 2015). Neueste Studien zeigen, dass sogar die oftmals extra für Bienen angelegten Blühstreifen an Ackerrändern zur tödlichen Insektenfalle werden, wenn nebenan im Feld Insektengifte ausgebracht werden, da die Blütenpflanzen dort diese Gifte ebenfalls aufnehmen und in Nektar und Pollen abgeben (GOULSON, 2013). Doch nicht nur auf intensiv landwirtschaftlich genutzten Flächen greift das Insektensterben um sich. In den letzten Jahren reduzierte sich die Biomasse der Fluginsekten sogar in Naturschutzgebieten um bis zu 75 % (HALLMANN et al., 2017). Besonders genau sind die Rückgänge bei den Wildbienen für die Gruppe der Hummeln untersucht (z.B. CAMERON et al., 2011). Sie sind, wie die anderen Bienen und Insekten auch, allgemein durch den Verlust bzw. die Fragmentierung ihres Lebensraumes bedroht, aber auch durch Pestizide. Bei den Honigbienen kommen hier noch Parasiten und Krankheitserreger hinzu, die sich besonders durch Wanderimkerei und weltweiten Bienenhandel so schnell verbreiten, wie noch nie zuvor (POTTS et al., 2010). Eine weit verbreitete Fehleinschätzung ist es hingegen, dass am derzeit festgestellten drastischen Insektenrückgang auch die Klimaerwärmung mit schuld sein könnte. Es ist schon lange bekannt und nachgewiesen, dass ein Temperaturanstieg eher zu einer Vermehrung der Insektenanzahl führen würde, denn wärmeliebende Insekten sind in mediterraneren Klimaten, und natürlich den Tropen, schon immer zahlreicher als in mehr nördlichen Breiten. Insofern würde der Klimawandel alleine eher zu einer höheren Zahl an Insekten bei uns führen (wie in den letzten 20 Jahren am Botanischen Garten München gezeigt wurde, siehe HOFMANN et al., 2018) – nur, dass wir davon nichts bemerken, weil die vielen negativen, oben geschilderten, menschgemachten Einflüsse diesen Effekt bei weitem aufheben. Um unseren Bestäubern zu helfen, müssten diese negativen Effekte reduziert werden, z.B. durch die Erhöhung des Blütenangebotes, durch den Verzicht oder zumindest die deutliche Reduzierung des Einsatzes von Glyphosat und Neonikotinoiden und durch die Wiederherstellung kleinräumig strukturierter Lebensräume, die zugleich Nahrung und Nisträume für Wildbienen bieten (GOULSON et al., 2015). Nur so können Wildbienen die drohenden Ausfälle der Bestäubung durch Honigbienen, die ebenfalls stark bedroht sind (vgl. HAEFEKER, 2019, in diesem Jahrbuch), möglicherweise ausgleichen (WINFREE et al., 2007).

Während Flächen, auf denen intensive, industrialisierte Landwirtschaft betrieben wird, zunehmend verarmen, bieten Städte oft einen Rückzugsraum für viele Tierarten und weisen inzwischen zum Beispiel bei Vögeln häufig eine größere Vielfalt als das Umland auf (REICHHOLF, 2007). Auch Bienen können das Blütenangebot von Kleingartenanlagen, städtische Grünflächen und Parks oder auch Gründächern nutzen. Insbesondere über den Einfluss von Gründächern auf Wildbienen ist allerdings insgesamt noch sehr wenig bekannt, was überrascht, wenn man bedenkt, dass beispielsweise in München etwa 20% aller Dachflächen begrünt sind, was einer Vegetationsfläche von über 3 Millionen Quadratmetern entspricht (ANSEL et al., 2015). Weltweit gibt es nur knapp 40 Studien, die sich mit diesem Thema beschäftigen (z.B. BRENNEISEN, 2005; KRATSCHMER, 2015; WITT, 2016). Von den weltweit etwa 20.000 Wildbienenarten konnten 236 auf Gründächern nachgewiesen werden (HOFMANN & RENNER, 2017). Da Gründächer meist sehr trocken und warm sind, sind viele der dort nachgewiesenen Arten eher wärmeliebend und werden normalerweise auf Trockenrasenstandorten gefunden. Generell sind sowohl Arten- als auch Individuenzahlen höher, wenn die Pflanzenvielfalt auf den untersuchten Dächern höher ist. Intensivdächer wiesen in allen Untersuchungen ein größeres Artspektrum auf als extensive Dachbegrünungen (MADRE et al., 2013; KRATSCHMER, 2015) . Eine bienenfreundliche Dachgestaltung mit vielfältigem, unterschiedlich hohem Substrat sowie vieler Mikrostrukturen verspricht daher, einen kleinen Beitrag zum Erhalt dieser bedeutenden Insektengruppe zu leisten.

Auch die Anlage von Blumenwiesen und Blühstreifen in Städten kann Bienen helfen. Während Blühstreifen in der Agrarlandschaft subventioniert werden (z.B. KULAP Kulturlandschaftsprogramm in Bayern, Österreichisches Agrarumweltprogramm ÖPUL) und inzwischen auch schon mehrfach untersucht wurden (PACHINGER, 2012; RAMSEIER, 2016), ist über den Effekt von Blühstreifen in der Stadt noch wenig bekannt. Dieses Thema wird derzeit in einem Projekt des Botanischen Instituts der Ludwig-Maximilians-Universität München unter Leitung von Frau Professor Renner erforscht. Es wird untersucht, welche Pflanzenarten besonders gut von den heimischen Bestäubern genutzt werden. Neben der Zusammensetzung der verwendeten Saatmischungen ist aber auch wichtig, in welchen Abständen die Blühstreifen angelegt werden, da viele Wildbienenarten relativ geringe Sammelflugdistanzen von nur wenigen hundert Metern haben (ZURBUCHEN & MÜLLER, 2012). Ein großer Abstand zwischen Futterpflanzen und geeigneten Niststandorten ist in vielerlei Hinsicht nachteilig für Wildbienen (ZURBUCHEN et al., 2010). Bei längeren Sammelflugdistanzen und somit längeren Flugzeiten können weniger Brutzellen verproviantiert werden. Gleichzeitig wird der Nahrungsvorrat pro Zelle weniger, was zu kleineren Nachkommen führt. Ist das Wildbienenweibchen lange von seinem Nest weg, steigt auch die Wahrscheinlichkeit, dass Brutparasiten (Kuckucksbienen, Schlupfwespen, etc.) erfolgreich ins Nest eindringen können. Durch den erhöhten Flugaufwand altern die Bienenweibchen zudem schneller.

Wie weit Wildbienen verschiedener Körpergrößen in einem idealen Habitat normalerweise fliegen, wird derzeit in einem Mitmachprojekt im Botanischen Garten München erforscht. Studenten der LMU markieren das ganze Jahr über Wildbienen mit farbigen Punkten oder Num-

Abb. 7: Männchen der Gehörnten Mauerbiene (*Osmia cornuta*) mit der Rückennummer 92. (Foto: Andreas Fleischmann).

mernplättchen (Abb. 7), und versuchen durch Wiederfundbeobachtungen Rückschlüsse auf ihre Lebensdauer, Futterpräferenzen und natürlich ihre Flugdistanzen zu ziehen. Um möglichst viele Beobachtungen zu sammeln, sind die Besucher des Botanischen Gartens München sowie alle Münchner aufgerufen, Sichtungen solcher markierter Bienen zu melden. Im vorletzten Jahr konnte so eine Biene verfolgt werden, die 724 m vom Ort des Markierens entfernt wiederbeobachtet wurde.

Quellenverzeichnis:

ANSEL, W., ZEIDLER, J. & ESCH, T. (2015): Fernerkundliche Identifizierung von Vegetationsflächen auf Dächern zur Entwicklung des für die Bereiche des Stadtklimas, der Stadtentwässerung und des Artenschutzes aktivierbaren Flächenpotentials in den Städten. Abschlussbericht des Entwicklungsprojektes gefördert unter dem Az 30299 von der Deutschen Bundesstiftung Umwelt.

ASCHER, J.S., PICKERING, J. (2017): Bee species guide (Hymenoptera: Apoidea: Anthophila). Discover Life. http://www.discoverlife.org/mp/20q?guide=Apoidea_species&flags=HAS.

BEMBE, B., GERLACH, G., SCHUBERTH, J., & SCHÖNITZER, K. (2001): Die Wildbienen im Botanischen Garten München. *Nachrichtenblatt der bayerischen Entomologen, 50(1/2)*, 30-41.

BRENNEISEN, S. (2005): The natural roof (NADA). Research Project Report on the Use Extensive Green Roofs *Hochschule Wädenswil, Switz.*

CAMERON, S. A., LOZIER, J. D., STRANGE, J. P., KOCH, J. B., CORDES, N., SOLTER, L. F., & GRISWOLD, T. L. (2011): Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*, *108*(2), 662-667.

GOULSON, D. (2013): An overview of the environmental risks posed by neonicotinoid insecticides. *Journal of Applied Ecology, 50*, 977-987.

GOULSON, D., NICHOLLS, E., BOTÍAS, C., & ROTHERAY, E. L. (2015): Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957.

HALLMANN, C. A., SORG, M., JONGEJANS, E., SIEPEL, H., HOFLAND, N., SCHWAN, H. & GOULSON, D. (2017): More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, *12*(10), e0185809.

HAEFEKER, W. (2019): Imkerei als Frühwarnsystem für die Artenvielfalt. Jb. Verein zum Schutz der Bergwelt, München: 227–238.

HOFMANN, M. M., FLEISCHMANN, A., & RENNER, S. S. (2018): Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. *Oecologia, 187 (3),* 701-706.

HOFMANN, M. M., & RENNER, S. S. (2017): Bee species recorded between 1992 and 2017 from green roofs in Asia, Europe, and North America, with key characteristics and open research questions. *Apidologie 49*(1): 00-00. DOI: 10.1007/s13592-017-0555-x.

KRATSCHMER, S. A. (2015): Summen auf den Dächern Wiens. Universität für Bodenkultur, Wien.

MADRE, F., VERGNES, A., MACHON, N. & CLERGEAU, P. (2013): A comparison of 3 types of green roof as habitats for arthropods. *Ecological Engineering. 57*, 109–117.

PACHINGER, B. (2012): Wildbienen (Hymenoptera: Apidae) auf Blühstreifen in Niederösterreich und im Burgenland (Österreich). *Beiträge zur Entomofaunistik, 13*, 39-54.

POTTS, S. G., BIESMEIJER, J. C., KREMEN, C., NEUMANN, P., SCHWEIGER, O., & KUNIN, W. E. (2010): Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution, 25*(6), 345-353.

RAMSEIER, H., FÜGLISTALLER, D., LÄDRACH, C., RAMSEIER, C., RAUCH, M., & WIDMER ETTER, F. (2016): Blühstreifen fördern Honig-und Wildbienen. *Agrarforschung Schweiz, 7*(6), 276-283.

REICHHOLF, J. H. (2007): *Stadtnatur: eine neue Heimat für Tiere und Pflanzen.* Oekom-Verlag.

SCHEUCHL, E., & SCHWENNINGER, H. R. (2015): Kritisches Verzeichnis und aktuelle Checkliste der Wildbienen Deutschlands (Hymenoptera, Anthophila) sowie Anmerkungen zur Gefährdung. *Mitteilungen des Entomologischen Vereins Stuttgart, 50*(1), 3-225. verfügbar unter: http://www.wildbienen-kataster.de/login/downloads/checkliste.pdf.

SCHINDLER, M., HOFMANN, M. M., WITTMANN, D., & RENNER, S. S. (2018): Courtship behavior in the genus *Nomada*antennal grabbing and possible transfer of male secretions. *Journal of Hymenoptera Research 65*, 47-59.

TENGÖ, J., & BERGSTRÖM, G. (1977): Cleptoparasitism and odor mimetism in bees: Do *Nomada* males imitate the odor of Andrena females? *Science*, *196*(4294), 1117-1119.

WINFREE, R., WILLIAMS, N. M., DUSHOFF, J., & KREMEN, C. (2007): Native bees provide insurance against ongoing honey bee losses. *Ecology letters*, *10*(11), 1105-1113.

WITT, R. (2016): Populationen von Wildbienen und Wespen auf Gründächern. *Stadt+Grün* 37–42.

ZURBUCHEN, A., CHEESMAN, S., KLAIBER, J., MÜLLER, A., HEIN, S., & DORN, S. (2010): Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology*, *79*(3), 674-681.

ZURBUCHEN, A., & MÜLLER, A. (2012): Wildbienenschutz-von der Wissenschaft zur Praxis. Haupt Verlag AG.

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